

STUDIES ON THE FAUNA OF CURAÇAO AND OTHER
CARIBBEAN ISLANDS: No. 89.

THE LESSER ANTILLEAN AMEIVA
(Sauria, Teiidae)

RE-EVALUATION, ZOOGEOGRAPHY AND
THE EFFECTS OF PREDATION

by

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The *Ameiva* of the Lesser Antilles present an interesting case of isolated populations of related animals on a chain of islands that differ in size and proximity among themselves but form a geographic group. The situation is made still more interesting by the fact that at times in the Pleistocene the sea was 100 fathoms or more lower, and certain of the islands were then connected by land.

The discovery of a new species of *Ameiva* on Maria Island off the south coast of St. Lucia and the attempt to identify and place taxonomically the three specimens first sent to us by GARTH UNDERWOOD provided the stimulus to a brief re-survey of this neglected but, from a zoogeographic and evolutionary point of view,

extremely interesting set of forms. Of this new species we have been able to examine two additional specimens collected by Père ROBERT PINCHON of the Séminaire Collège, Fort-de-France, Martinique, and a series obtained by J. D. LAZELL, JR. in the summer of 1962, as well as 23 specimens collected by A. SCHWARTZ and assistants.

Since BARBOUR & NOBLE 1915, no one has seriously (re)studied the Lesser Antillean populations. We have re-examined all their material plus additional specimens more recently acquired by the Museum of Comparative Zoology. We have also seen the series from the northern islands obtained by WALTER AUFFENBERG and WAYNE KING of the University of Florida in 1958 and specimens from many parts of the Lesser Antilles collected by P. WAGENAAR HUMMELINCK. The scale counts from the University of Florida series are recorded in our tables; we have used Dr. HUMMELINCK's material primarily to check color characters. A few additional specimens were borrowed from the United States National Museum. A very recent, very large collection by Dr. SCHWARTZ is being studied by DENNIS PAULSON of the University of Miami and promises to provide the basis for a more definitive study of all the *Ameiva* of the Lesser Antilles.

We have here attempted to utilize again the samples available to us from a more modern point of view than that provided by BARBOUR & NOBLE and thus to reassess the level of differentiation and the relationship of the known forms. Only with this new information are we able to place to our own satisfaction the new St. Lucia *Ameiva*.

ACKNOWLEDGMENTS

We are indebted to Mr. G. WILLIAMS who collected and Professor GARTH UNDERWOOD who donated the first specimens obtained of the ameiva here described, to Père ROBERT PINCHON and Dr. ALBERT SCHWARTZ who permitted examination of additional specimens collected by them, and to JAMES D. LAZELL, JR. who obtained a further series for the Museum of Comparative Zoology. Notes on ecology and color in life have been provided by LAZELL. The photographs are by FRANK R. WHITE. Dr. PAULO VANZOLINI assisted in the early stages of the investigation. Drs. DORIS COCHRAN, WILLIAM RIEMER, J. GUIBÉ, Dr. P. WAGENAAR HUMMELINCK, Dr. M. BORSEMAN and Mr. C. M. BOGERT have provided comparative material. National

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DENNIS PAULSON, ALBERT SCHWARTZ, THOMAS FRAZZETTA, BRYAN PATTERSON and others have read the manuscript at various stages and have made helpful suggestions.

***Ameiva vanzoi* new species**

(Plate I-II)

Type: MCZ 69112, southernmost of two Maria Islands off the southeastern end of St. Lucia, British West Indies. James D. Lazell, Jr. coll. August, 1962. — Named in honor of Dr. Paulo Vanzolini, called by his friends "Vanzo."

Paratypes (all from same locality): MCZ 69113-19, same data as type: MCZ 59192-5, G. Williams coll. Two specimens uncatalogued, Père Robert Pinchon coll. Albert Schwartz, ASFS 18420-42, R. F. Klinikowski and A. Schwartz coll.

Diagnosis. Closest to *Ameiva fuscata* Garman, but differing in having the frontonasal wider than long (rather than longer than wide), four to five supraoculars (rather than three), the last supraocular separated from the occipitals by one row of scales (rather than two to five), twelve longitudinal rows of ventrals (rather than fourteen), a higher average number of transverse rows of ventrals (mean 35.7, rather than 32), a lower number of femoral pores (mean 26.8, rather than 29), differing also in the strong sexual dichromatism.

Description. *Head*. Nostril between two nasals. Anterior nasals broadly in contact. Frontonasal *wider* than long, in contact with loreal. Prefrontals broadly in contact. Frontal in contact with first three supraoculars. Frontoparietals always broadly in contact with 3rd supraocular, in contact with or separated from fourth supraocular which may be broken into smaller scales. 5-6 occipitals in transverse row, the paramedian, or the lateralmost, longest. 5-7 supraciliaries, the first or first two elongate, the first or the first two in contact with first supraocular, the others separated from the supraoculars by one row of granules. 6-7 supralabials. 6 infralabials, 3rd largest. Wedge of granules on throat penetrating forward for half the length of first chin shields, two of these granules especially enlarged at junction of first and second chin shields on

each side. None enlarged centrally in throat. Between the two throat folds a weakly enlarged band of scales tapering laterally.

Venter. 12 longitudinal and 34–38 transverse rows of scales. Enlarged scales of preanal region with a triangular arrangement in ♂ ♂, three scales, one anterior, two posterior most prominent, or a rosette (♀ ♀) with the enlarged scales peripheral to the primary triangle more conspicuous.

Limbs. 3 rows of antebrachials, outermost very wide. Brachials weakly enlarged, in 2 rows; postbrachials weakly differentiated. Enlarged scales on thigh largest near middle of length. 22–32 femoral pores. 2–3 rows on tibia strongly enlarged, second and third scales of outer series much the largest and often fused. Enlarged scales of tarsus continuous with enlarged scales covering 3rd and 4th toes. 38–49 lamellae under 4th toe. Tail scales straight, keeled, in regular rings, ca. 30–37 in 15th ring.

Size (snout-vent length): Longest ♂: 113 mm; longest ♀: 98 mm.

Sex dichromatism: Strongly marked (see Plate I).

Color in life. Notes by J. D. LAZELL, Jr., 30 July 1962: "Males very dark grey brown with obsolete stripes, chins pale bluish; throats slatey black. Bellies brilliant sulfur yellow. Undersides of hind legs, vent area, and entire tail brilliant sea blue patched with turquoise. – Females paler and browner, becoming dark on sides. Stripes dull ochre but no blue or yellow anywhere. – All have blue-grey dots on sides."

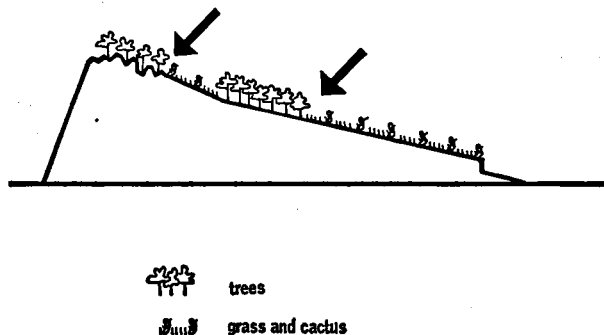


Fig. 42. Diagram of the habitat of *Ameiva vanzoi*, n. sp.: southernmost of two Maria Islands, ST. LUCIA. (J. D. Lazell, Jr. del.).

TABLE 12

LESSER ANTILLEAN *Ameiva*Number of transverse rows of ventrals
(counted longitudinally)

	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Grenada			2	3	5	4								
St. Vincent				3	7	13	4							
St. Lucia									1	13	17	4	1	
Martinique? ¹						1	1	1						
Dominica				1	6	8	6	1						
Guadeloupe									1	2				
Montserrat							2	3	4	4	3	2		
Redonda								1	3				1	
Nevis									1	1	2			
St. Kitts							2	8	14	4	2			
St. Eustatius							1	3	5	1				
St. Barts			2	3										
St. Martin						7	3	2	1	1				
Anguilla					3	8	8	5	2					
Antigua						2	3	7	1					
Barbuda						4	7	10	1					
Sombrero								1	2		1	1		

Distribution and Ecology

A. vanzoi is apparently confined to a single islet, the largest (300 ft. high) of the Maria Islands which lie off the east side of the small peninsula which forms the extreme southern tip of St. Lucia. The species is here very abundant.

A diagrammatic profile of the island on which *Ameiva* occurs is given in Fig. 42.² The beach leads up to a terrace with grass and cactus. On the middle slopes is a small, open and park-like woods with vines growing among the trees. Above this still another zone of grass and cactus, while the peak of the island is an area of large rocks with scattered trees.

¹ Based on syntypes of *major* Duméril & Bibron which are provisionally regarded as Martinican in origin.

² The information summarized in the section is derived from the field notes of JAMES D. LAZELL, Jr.

TABLE 13

LESSER ANTILLEAN *Ameiva*Number of longitudinal rows of ventrals
(counted transversely)

	8	10	12	14	18	16	20
Grenada		1	13				
St. Vincent			10	17			
St. Lucia			37				
Martinique? ¹						3	
Dominica				22			
Guadeloupe							3
Montserrat				18			
Redonda				5			
Nevis				4			
St. Kitts				19	11		
St. Eustatius				10			
St. Barts			2	3			
St. Martin			9	5			
Anguilla			13	13			
Antigua				13			
Barbuda		2	19				
Sombrero			1	4			

Since all members of this genus are sun-loving animals, the *Ameiva* are concentrated in open areas, i.e. at the grassy lower margin of the woods and at the edge of the rocky zone at the peak, but they roam through the woods and grassy area between these two areas of concentration. In the woods the ameivas sometimes climb by the thick stems of the vines to the lower boughs of the trees and lie along them.

INTER-ISLAND RELATIONSHIPS

The numerical data on Lesser Antillean *Ameiva* that we have gathered in the effort to determine the relationships of *vanzoi* is given in Tables 12-15 and summarized in Table 16. Tables 17-18

¹ Based on syntypes of *major* Duméril & Bibron which are provisionally regarded as Martinican in origin.

compare the body patterns of adult males. We present these without much discussion or elaboration, in part because the pattern of resemblances revealed is a complex and confusing one, and in part because much additional material is being collected in all the islands by Dr. ALBERT SCHWARTZ, who will thus eventually provide a much better base for detailed conclusions.

We present in Table 19 our tentative assessment of the taxonomic value of the differences we have observed. We have united several currently used names under one species. We do so because two clear levels of difference are evident to us. Such a population as *erythroops* (St. Eustatius) is obviously closer to *erythrocephala* (St. Kitts) than to *griswoldi* (Antigua) or *pleii* (St. Martin) or these to each other. If *griswoldi* and *pleii* are species, then *erythroops* is more readily understood as a subspecies, if it is to be recognized taxonomically at all. There may even be geographic variation within islands (there are hints of this) ¹ but we have not dealt with this problem, first because we do not have adequate material, second because it is not germane to our problem of the placement of *vanzoii*.

Fortunately, *Ameiva vanzoi* is a quite distinct species by any criterion. Questions arise only in regard to its relationships.

We have diagnosed it by comparison with *A. fuscata* of Dominica but we must confess that a factor of geographic proximity has influenced our choice of "nearest relative." In reality, the problem of affinities and phylogeny in the Lesser Antillean ameivas is not a simple one.

The Lesser Antillean fauna is often described as an attenuated South American fauna. So it is for some forms.

But for the ameivas, as for *Anolis* and *Sphaerodactylus* ², there is no attenuation. These animals occupy, or did once occupy, almost every scrap or crumb of land available for colonization to the very tip of the island chain.

¹ Tables 14–15 show possible bimodality in some of the northern populations, especially St. Martin. Some persons may prefer to regard such intrainland differences as subspecific, the island populations as species.

² *Sphaerodactylus* is not known from Grenada or the Grenadines – the most southerly bank of the true Lesser Antilles – a very anomalous fact which again does correspond to the concept of attenuation.

More important, the ameivas run counter to an expectation which many think should apply to all members of a mainland fauna which extends with steadily diminishing diversity outward on an island chain: the expectation of a linear chain of relationships that mirrors clearly and without equivocation the immigrant pattern. This expectation does not correspond to the situation before us: there is in Lesser Antillean ameivas no obvious chain of relationships with each link closest in its affinities to its nearest neighbors. Instead the situation is more complex and we provide only a very tentative analysis.

The analysis will be clearest if we first describe the zoogeographic patterns that we see before us. These are three:

1. Cluster relationships

One sort of cluster relationship is very conspicuous in Lesser Antillean ameivas. We have mentioned it above as a reason for synonymizing several named forms. Thus the ameivas of St. Eustatius, St. Kitts, and Nevis are markedly more similar to each other than to the ameivas of any other of the islands. There are minor and rather subtle differences between the populations of each of the islands, but these are of another order of magnitude altogether from the differences which separate the populations of this group of islands from the ameivas of anywhere else.

The same precise phenomenon occurs with the ameivas of St. Martin, St. Barts, and Anguilla as compared with any other ameivas elsewhere. So also with the ameivas of Barbuda and Antigua.

This puzzle is very simply solved when it is realized that each of these sets of islands was once one large island only rather recently fragmented and stands on an undersea bank of considerable extent. Fig. 43 shows the existing islands and the banks as well as the species here recognized. In treating the zoogeography of the Lesser Antilles, we must deal with the banks and not solely with the present islands. Thus, as we see it, each bank has only one species on it and, with one exception, these species are endemic to their respective banks.

Cluster relationship involves also adjacent banks. Thus, the only case of a species occurring on more than one bank is *Ameiva ameiva*

TABLE 14
LESSER ANTILLEAN *Ameiva*

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Grenada			1			3	3	2	3	2											
St. Vincent					2	5	5	5	8	4	2	1									
St. Lucia									1	1	3	3	10	7	6	4	2	1			1
Martinique? 1									1	1											
Dominica									1	2	4	5	3	4	4						
Guadeloupe						1	1		1												
Montserrat									1	3	7	4	2		1						
Redonda				1				1	2		2										
Nevis												1	3								
St. Kitts												4	3	9	5	4	2	2			1
St. Eustatius											3	4	1								
St. Barts				1	1	1		1													
St. Martin				5	1	1	1	3	4												
Anguilla			2	6	5	5	8		1												
Antigua				1	3	2	2	2	1	1	3										
Barbuda			1	4	8	4	1		4												
Sombrero											2	3									

1 Based on syntypes of *major* Duméril & Bibron which are provisionally regarded as Martinican in origin.

TABLE 15
LESSER ANTILLEAN America

Femoral pores

	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	42
Grenada			1	1	4	6	2																						
St. Vincent			4	8	12	3																							
St. Lucia							1	1	4	11	12	6	2							1									
Martinique? ¹																			1	1									
Dominica									1	2	6	5	3	5															
Guadeloupe											2	1	7	4					1	1	1	1							
Montserrat													2	1	7	4			1	1	1								
Redonda											2	1	1	2															
Nevis																				1	2	1							
St. Kitts																			2	3	2	5	7	6	1	2	1		1
St. Eustatius																		3	3	2	1	1							
St. Barts									3	1	1																		
St. Martin					1	2	3	1	2	4	1																		
Anguilla						3	6	2	9	3	2	1																	
Antigua								1	3	2	2	1	3																
Barbuda					1	2	6	2	5	2	1	1																	
Sombrero																1				2	1								4

¹ Based on syntypes of *major* Duméril & Bibron which are provisionally regarded as Martinican in origin.

Sombro *g* CORVINA

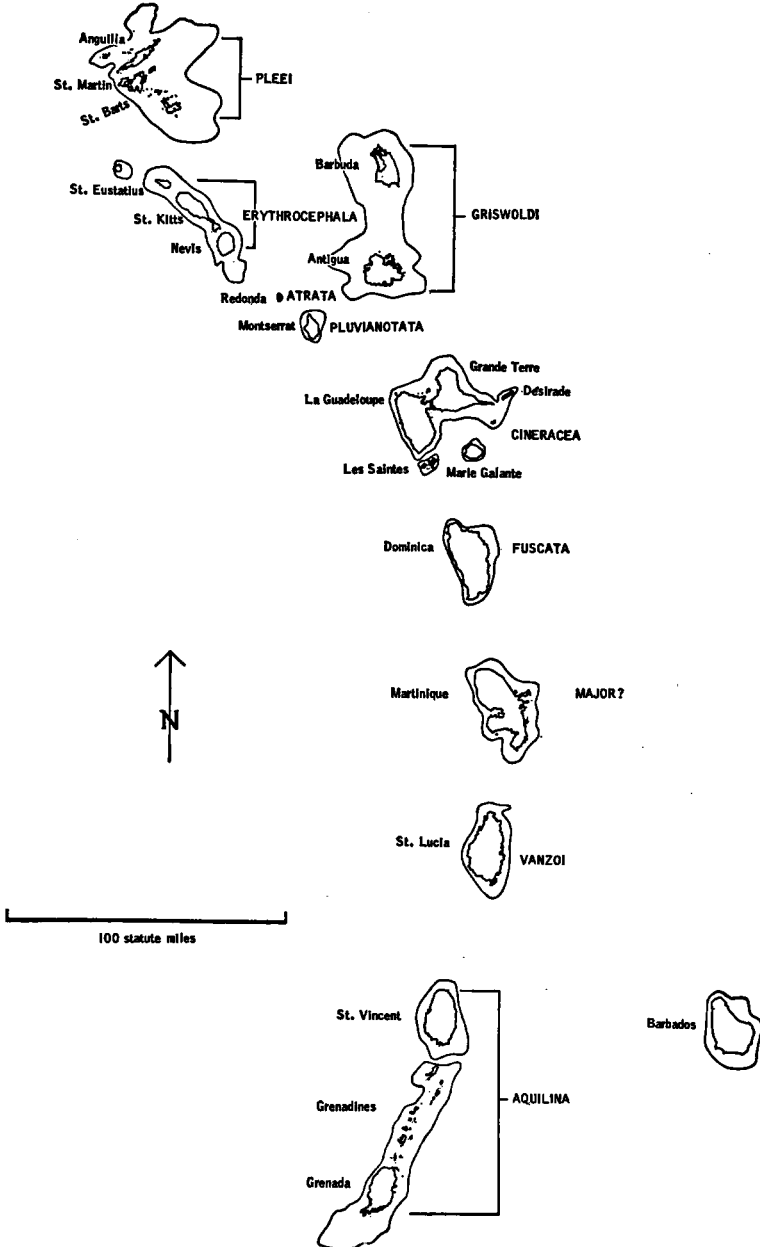


Fig. 43. Map of the distribution of *Ameiva* in the LESSER ANTILLES. - Species names in capitals.

TABLE 16

LESSER ANTILLEAN *Ameiva*

Summary of meristic characters
 (The assignment of *major* as the Martinican population is hypothetical)

N	TAXON	ISLAND	femoral pores	4th toe lamellae	transverse rows	longitudinal rows
14	<i>aquilina</i>	Grenada	16-20	35-39	29-32	10-12
27	<i>aquilina</i>	St. Vincent	17-20	35-41	30-33	12-14
37	<i>vanzoi</i>	St. Lucia	23-32	38-49	34-38	12
3	<i>major</i>	Martinique	31-33	38-39	32-34	18
22	<i>fuscata</i>	Dominica	26-31	38-44	30-34	14
3	<i>cineracea</i>	Guadeloupe	31-35	36-39	34-35	20
5	<i>atrata</i>	Redonda	27-30	35-40	34-38	14
18	<i>pluvianotata</i>	Montserrat	28-34	38-44	33-38	14
4	<i>erythrocephala</i>	Nevis	33-35	41-42	35-37	14
30	<i>erythrocephala</i>	St. Kitts	32-42	41-49	33-37	14-16
10	<i>erythrocephala</i>	St. Eustatius	30-34	38-41	33-36	14
13	<i>griswoldi</i>	Antigua	22-28	34-40	32-35	12
21	<i>griswoldi</i>	Barbuda	20-27	33-39	32-35	10-12
5	<i>plei</i>	St. Barts	22-25	32-37	30-31	12-14
13	<i>plei</i>	St. Martin	19-25	34-38	33-37	12-14
26	<i>plei</i>	Anguilla	20-26	32-40	32-36	12-14
5	<i>corvina</i>	Sombrero	29-37	40-42	34-38	12-14

aquilina on Grenada and St. Vincent. In this case the populations on the two banks are not even subspecifically distinguishable. The explanation would appear to be the extreme closeness of these banks (and even now the two larger islands are connected by a chain of smaller islands, the Grenadines).

Another pair of islands - Montserrat and Redonda - has banks almost as closely spaced. We have treated the *Ameiva* of these

TABLE 17

LESSER ANTILLEAN *Ameiva*

Color of male southern Lesser Antillean ameivas

Adult ♂ coloration (in alcohol)	(Sexual di- morphism)	Throat	Mesoptychium	Chest	Dorsum	Flanks
Grenada	+	Light, with scattered black spots covering one or few scales or (on chest) parts of scales.			Scattered light spots, most apparent on flanks, most obscure on dorsum.	
St. Vincent	+				Dark, with very light spots in several rows on dark ground.	
St. Lucia	+	Black	Black	Black, sharply distinct from light belly.	Dark, uniform	Light spots in several rows which become less regular ventrally.
Martinique? ¹	—	Light	Light	Light	Dark, uniform	Light spots in several rows which become less regular ventrally.
Dominica	—	Infuscated, but lighter than posterior areas.	Dark, the anterior border sharp.	Dark, merging into dark belly.	Dark, uniform.	Light spots in several rows which become less regular ventrally.
Guadeloupe	—	All light (whitish to whitish yellow)			Uniform grey-green above.	
Redonda	—	Black, patternless.			Black, patternless.	
Montserrat	—	Light	A few black pigment spots on mesoptychium and chest.		Mottled, mottling resulting from the coalescence of numerous round light spots.	

¹ Syntypes of *major* Duméril & Bibron 1839.

TABLE 18
LESSER ANTILLEAN *Ameiva*

Color of male northern Lesser Antillean ameivas

<i>Adult ♂ coloration (in alcohol)</i>	<i>(Sexual dimorphism)</i>	<i>Throat</i>	<i>Mesopterygium</i>	<i>Chest</i>	<i>Dorsum</i>	<i>Flanks</i>
Nevis St. Kitts St. Eustatius	—	<i>Light</i>	Intense <i>black</i> , with a blotch or indentation of <i>white</i> .	<i>Dark</i> , but not intensely black.	Transverse <i>dark</i> ripple-like markings, usually in two rows.	<i>Dark</i> , with obscure <i>light</i> spotting and vermiculation.
Antigua Barbuda	—	<i>Light</i>	<i>Black</i> invisible portion, sometimes white under fold.	<i>Black</i> , with irregular posterior border.	Irregular transverse <i>light</i> blotches, sometimes clearly composed of coalesced spots.	Obscure <i>light</i> transverse markings and spots.
St. Martin Anguilla St. Barts	—	<i>Light</i>	<i>Light</i>	<i>Light</i> , with variable encroachment of dark pigment from sides	Transverse rows of black bordered <i>light</i> spots nearly or quite contiguous.	Transverse rows of light spots continued onto flanks.
Sombroero	—	<i>Black</i> below			<i>Black</i> above	

two islands as species, but though they differ sharply in color, they are structurally very similar. Again distance and similarity – hence probably relationship – have a strong inverse correlation.

In still another case of cluster relationship of adjacent banks the ameivas of the St. Eustatius-St. Kitts-Nevis bank strongly resemble in throat pattern the ameivas of the Antigua-Barbuda bank. There are also very clear differences; there is no question of synonymy. But the resemblance between two adjacent populations in a rather special color pattern sets them apart from the remainder of the Lesser Antillean ameivas. The two banks have never been connected and are not very close; there is a probability that the similarity indicates that the population from one bank colonized the other, though the direction of colonization is not determinable; present winds and currents favor rafting from east to west.

At yet another level of cluster relationships all the ameivas of the islands north of Guadeloupe are more similar to each other, despite good differences, than any of them are to any southern Lesser Antillean species. We became acutely conscious of this when, in trying to prepare a key to Lesser Antillean *Ameiva*, we found that it foundered on every trial on the parallel squamational variability and parallel ontogenetic changes in pattern of the ameivas of the northern islands. Though the differences among them are striking, they are not quite absolute and they are connected by intermediate populations or even by individual variation in a way that suggests a genuine cluster relationship.

Still another cluster relationship is that between the *Ameiva* of Grenada and St. Vincent banks and that of Trinidad and Tobago on the continental shelf to the south. We have assessed the relationship here as subspecific and regard these southern populations as part of the *Ameiva ameiva* of the mainland of South America.

2. In situ specialization

Here we deal with the phenomenon of unequal differentiation on islands. Once any population has got onto any island sufficiently distant so that colonization is a very rare event, it is essentially a closed genetic system. The founder population will in any event represent only a segment of the variability of the population from

TABLE 19

THE SPECIES OF LESSER ANTILLEAN *Ameiva* HERE RECOGNIZED

The type locality is cited after each name

TRINIDAD	<i>Ameiva ameiva tobagana</i> Cope 1879, p. 276 - Tobago (inc. <i>atrigularis</i> Garman 1887, p. 2 - Trinidad).
TOBAGO	
GRENADA	<i>Ameiva ameiva aquilina</i> Garman 1887, p. 3 - Grenada and
ST. VINCENT	St. Vincent.
ST. LUCIA	<i>Ameiva vanzoi</i> , new species - Maria Id., St. Lucia.
MARTINIQUE?	<i>Ameiva major</i> Duméril & Bibron 1839, p. 117 - "Cayenne ... La Trinité".
DOMINICA	<i>Ameiva fuscata</i> Garman 1887, p. 5 - Dominica (inc. <i>brachio-squamatum</i> Cope in Verrill 1892, p. 352 - Dominica).
GUADELOUPE	<i>Ameiva cineracea</i> Barbour & Noble 1915, p. 453 - Grand Isle off Petit Bourg on the coast of Guadeloupe.
MONTSERRAT	<i>Ameiva pluvianotata</i> Garman 1887, p. 6 - Montserrat.
REDONDA	<i>Ameiva atrata</i> Garman 1887, p. 8 - Redonda.
NEVIS	<i>Ameiva erythrocephala</i> Daudin 1802, p. 122 - St. Kitts (inc. <i>punctata</i> Gray 1838, p. 277 - "Demerara"; <i>erythroops</i> Cope 1871, p. 221 - St. Eustatius; <i>flaviceps</i> Bocourt ¹ 1874, p. 246-247 - "Cayenne").
ST. KITTS	
ST. EUSTATIUS	
SABA	None known
ANTIGUA	<i>Ameiva griswoldi</i> Barbour 1916, p. 216 - St. John's, Antigua.
BARBUDA	
ANGUILLA	<i>Ameiva pleii</i> Duméril & Bibron 1839, p. 114 - "Martinique ... Saint Domingue" (inc. <i>analifera</i> Cope 1869, p. 158 - St. Martin and St. Barts; <i>garmani</i> Barbour 1914, p. 312 - Anguilla; <i>nevisana</i> Schmidt 1920, p. 1 - "Nevis" ²).
ST. MARTIN	
ST. BARTS	
SOMBRERO	<i>Ameiva corvina</i> Cope 1861, p. 312 - Sombrero.

¹ This overlooked name, called to our attention by M. J. GUIBÉ, is published in the Mission Scientifique au Mexique, Reptiles et Batraciens, Reptiles, livraison 4, p. 246-247. The type has been examined and clearly belongs to the species of the St. Kitts, St. Eustatius, Nevis bank; BOCCOURT separated the unique type specimen - very reasonably - from the remainder of the series of three called *major* by Duméril & Bibron. This single specimen may have been the reason for BOULANGER's (1885) synonymy of *major* Duméril & Bibron with *punctata* Gray (= *erythrocephala* Daudin) - a judgment otherwise impossible to justify.

The catalogue locality "Cayenne" is, of course, as with many specimens dating from so early an epoch, evidently only the shipping point. (See above).

² The type, AMNH 1635, has been examined and proves to belong here in spite of BARBOUR's (1930, p. 79) suggestion that SCHMIDT's name was a synonym of *griswoldi*. The locality is undoubtedly incorrect; only *erythrocephala* is known on Nevis.

which the colony came (MAYR 1954, 1963). Once on its own, the direction and the speed of change in this population is under the influence of local forces and is not fully predictable.

The differences which separate Lesser Antillean ameivas are simple ones which can be imagined to have simple genetic bases. They are in no case complex modifications that seem to require sequential changes that must pass from one stage through another to arrive at the more specialized condition. It would not be too difficult to imagine that the stocks on all the islands were at one time much more alike and that most of the evolution that has occurred has occurred *in situ* on each island or bank.

The melanic ameivas of the Lesser Antilles – *atrata* of Redonda and *corvina* of Sombrero – are clear cases of strong local differentiation. Except in color the two are quite different from one another; there is no question of a special relationship between them. In squamation they are in each case close – in the case of *corvina* not very close – to one of the adjacent populations. Apart from pigmentation they have one other feature in common: they occur on very small (one mile square, or less), barren islands.¹

The etiology of melanism in lizards is still not very clear, but there does seem to be an association with very small, dry and barren islands. In any event, in these two melanic Lesser Antillean ameivas it is quite clear that local factors have been dominant and that color pattern is no clue to their ancestry.

The possibility of *in situ* specialization depends upon isolation. This requires some discussion of the effect on differentiation of the arrival of new colonists *before* the more distant population has attained full species level, i.e. while there is the possibility of introgression.

In this connection it may be worth while to contrast the extreme southern populations (Grenada-St. Vincent) with the northern ones (Montserrat north).

¹ There is a third melanic *Ameiva* thus far reported: *fuliginosus* of Swan Islands in the western Caribbean. This again is not closely related; again we deal with a small and barren island. Parallel cases are known in Mediterranean lacertids. Cf. the remarks by KRAMER in MAYR (1963) and papers by KRAMER cited in the bibliography of that book. MERTENS (1963) presents a short but excellent review of the general problem.

The southern populations we regard as conspecific with mainland *Ameiva ameiva*. The northern populations we tentatively regard as a complex of related full species, one on each bank.

The genetic effect of colonization attempts on any resident population will depend, of course, upon the frequency of their occurrence and may be expected to form a spectrum of conditions from so high a frequency that "swamping" will prevent any differentiation of the invaded local population to a frequency so low that it is utterly negligible for the course of evolution of the resident population.

The southern populations are very close to a very large source area for cross-water colonists – the mainland of South America – and to a major river (the Orinoco) which could produce rafts suitable for carrying colonists. We may assume that the frequency with which the Grenada-St. Vincent bank receives rafts is exponentially greater than the frequency for more northern banks. It may in fact be high enough at the present time to be preventing differentiation of the *Ameiva* on the Grenada and St. Vincent banks beyond the subspecific level.

The much higher probability of colonization of near islands, especially those which, like Grenada and St. Vincent, are near the outflow of a huge river, ensures that they are always the first to be colonized and that they are sure to be recolonized perhaps several times during any period in which distant islands are colonized.

It is on these islands therefore that competitive replacement might most plausibly occur. The special hazards of cross-water transport are mitigated by the shortness and speed of the voyage. The invader of near islands will therefore arrive better able to establish a colony. If colonization is frequent enough, there may yet arrive other colonizers of the same stock to replenish, freshen and sustain the original one and so to obviate any fluctuations in numbers that might have threatened to push it to the wall.

Without such advantages it is improbable that any cross-water invader has a real chance of displacing a thriving resident species. Even with these advantages replacement is not likely to be easy. The doctrine that mainland species are *usually* so superior that they will *readily* displace island species requires much testing. It may

well be that in the usual case success in colonization goes to an invader species only if its arrival coincides with a temporary or local decline of the resident, *or* if the invader seizes upon a niche or ecology unutilized by the resident species.

Upon distant islands the invader species swept out to sea on a long voyage must arrive with few advantages against any resident species. Both the length of the voyage and its rarity work against the invader. Arriving debilitated, it will have small chance of establishing itself even on an empty island; on an occupied one it will have almost no chance for even temporary establishment and the infrequency and improbability of the invasion must reduce the hope of rescue by recolonization to nullity.

Near and far islands are therefore in different categories as regards their colonization potential. The near islands are never fully outside the history of the adjacent mainland; the far islands have influence of the mainland attenuated to an extreme degree: here is the zone of maximum differentiation and, if space permits, radiation.

Introgession (and competitive replacement) from a neighboring mainland is thus the hazard which in theory should reduce and, in fact, appears to have reduced the distinctness of the southern populations of Lesser Antillean *Ameiva* – those of the Grenada and St. Vincent banks.

The northern Lesser Antillean *Ameiva* are in quite another state. They are far beyond the possible genetic influence of the *Ameiva* of the South American mainland. The possibility of introgession is here confined to interchange of colonists between the several northern banks and it is limited by the lesser frequencies of interchange where no large rivers sweep rafts to the sea. The factors here are: local currents, the size of island populations, the special transportation that might be provided by hurricanes etc.

It is very probable that the frequency of colonization among these island banks might be at levels such that it will still influence the resident populations without in any sense swamping them. The influence would probably be of two sorts: If the frequency of colonization were at certain critical frequencies, colonists might occasionally introgessively introduce genes or gene combinations

that were then favorably acted upon by local selection, *or*, if the level of differentiation were still further along, the invaders might provoke a selection in the invaded species of species recognition marks, e.g. distinctive colors and patterns.

It is certainly a striking fact that the Lesser Antillean *Ameiva* – the northern populations and in fact those south to St. Lucia – differ more strikingly in color than do some sympatric mainland *Ameiva*. It is an interesting possibility that this has selective significance, that the colors and patterns have meaning as species recognition marks developed because dispersal of *Ameiva* between most Lesser Antillean islands is just at a critical level.

In situ specialization, to sum up, depends on the factors influencing degree of isolation: distance to the colonizing area, size of the colonizing population, and special factors that enhance the probability (frequency) of colonizing voyages (presence or absence of large rivers, etc.). All of these increase or diminish the interval between colonizations. Strong differentiation, in the absence of contradictory evidence, implies long isolation.

3. Leap-frog or bypass relationship

With an unpatterned body and 20 longitudinal rows of belly scales, *Ameiva cineracea* on Guadeloupe is the most highly differentiated not only of Lesser Antillean ameivas but also is unlike *fuscata* of Dominica or *vanzoi* on St. Lucia or, in fact, any other surviving *Ameiva*. It is quite unlike any ameivas to the north. As it happens, the species north of Guadeloupe are more similar among themselves than they are to *fuscata* or *vanzoi*, but certainly *cineracea* is far from bridging the gap. It is in no way an intermediate or stepping stone in a linear series. If, as seems probable, the ameivas of the northern Leewards are remotely related to *fuscata* and *vanzoi*, the stock that produced them must ¹ have bypassed or leaped over the Guadeloupe bank. By an obvious analogy such a disjunct relationship may be called a leap-frog relationship. (Some evidence

¹ The word "must" here implies a hypothesis which, however, is supported by the known data: that on these small islands only one species of *Ameiva* may exist at any one time. Any hypothesis (e.g. of extinction) that avoids the hypothesis of one stock bypassing or overleaping another must have two species present on at least Guadeloupe during some period.

from other vertebrates suggests other instances of "leap-frog" pattern in the colonization of the Lesser Antilles.)

Ameiva cineracea is without any living close relative. There is one candidate – but this involves the question of the missing *Ameiva* of Martinique, one leap south from Guadeloupe – between the islands of Dominica and St. Lucia.

The all but ubiquity of ameivas – present or recently extinct – in the Lesser Antilles¹ plus the large size of Martinique and the absence of any reason to believe that it is ecologically unfavorable for *Ameiva* have always raised the issue of recent extinction as an explanation for the absence of the genus on this island.

Among described *Ameiva* there is one form – *Ameiva major* Duméril & Bibron 1839, said to come from "Cayenne" and "La Trinité" – that is a very possible candidate for the missing *Ameiva* of Martinique.

One of us (WILLIAMS) has examined the Paris types of *major* and can confirm that three of the four specimens very closely resemble *cineracea* in the absence of pattern in adults and in the very high number of ventral longitudinal rows. This *cineracea*-like form certainly does not occur on Trinidad and has never been collected again in Cayenne. The catalogue locality "Cayenne" is, as with many specimens reported on in the early 19th century, evidently only the shipping point.

PARKER (1935a and b) has already hesitantly suggested that *A. major* was the *Ameiva* of Martinique. His hesitations regarding his own suggestion were based on "the undoubted existence of an *Anolis* of Antillean affinities in Guiana." The record in question — of *A. sagrei* by BEEBE (1944) and BURT & BURT (1931) — is based on material at the American Museum of Natural History, AMNH 21272, 30675, 6790–92. One of us (WILLIAMS) has examined these specimens. All are misidentified and three of four are surely with wrong locality. One is *A. aeneus*, long known from the Georgetown area of British Guiana, the others are *A. oculatus* from the island of Dominica. Erroneous catalogue entries are clearly involved. Miss MARGARET BULLITT, formerly of the American Museum of Natural History Department of Herpetology has told us that AMNH 6790–92, listed as from Kaietur, British Guiana, have LUTZ as collector. "Other specimens listed on the same page, collected by Lutz, are from Dominica." One can thus discount PARKER's hesitations.

In addition to the resemblance to *cineracea* upon which PARKER placed emphasis, there is further indirect evidence for *major*'s Lesser Antillean affinities:

(1) One of the four syntypes of *major* does not resemble *cineracea* and was separated by BOCOURT 1874 as the type of a distinct species, *flaviceps*. This specimen belongs to the species of the St. Kitts- St.Eustatius-Nevis bank and the name falls therefore as a synonym of *erythrocephala* Daudin 1802. This single specimen may

¹ Barbados and Saba as well as Martinique are conspicuous exceptions, but they at least lie, in each case, to one side of the main sequence of islands and hence seem less anomalous.

have been the reason for BOULENGER'S (1885) synonymy of *major* Duméril & Bibron with *punctata* Gray 1839 (another synonym of *erythrocephala* Daudin 1802) — a judgment impossible to justify on the basis of the other three syntypes of *major*.

Clearly the reported locality "Cayenne" for the type of *flaviceps* is erroneous, and it is correspondingly suggestive as regards the remaining syntypes of *major* that the correct locality is Lesser Antillean, *not* mainland or the island of Trinidad.

(2) The label "La Trinité" was interpreted by DUMÉRIL & BIBRON as the island of Trinidad and they have been followed by all succeeding authors. However, on the west coast of Martinique is a village called Trinité, and L'HERMINIER, who collected Paris No. 1491, the syntype of *major* from Trinité, collected also the syntypes of *Leiocephalus herminieri* Duméril & Bibron which was said by these authors to have come from "les îles de la Trinité et de la Martinique". In this statement there seems to have been an error of inference. The specimen thought by DUMÉRIL & BIBRON to have come from the island of Trinidad has in this case also just the label "Trinité." The other three Paris specimens of *L. herminieri* are labelled "La Martinique" and a British Museum skeleton is also labelled "Martinique." There is thus good reason to believe that *L. herminieri* did occur on Martinique. (See the discussion of the provenance of *L. herminieri* by R. ETHERIDGE 1964, p. 56 footnote.) If this be true, the "Trinité" given as a locality by L'HERMINIER is more likely to be a place name on Martinique than the island of Trinidad some hundreds of miles to the south.

We cannot now firmly demonstrate the true provenance of *A. major*. However, if *major* is the lost *Ameiva* of Martinique, closest to *cineracea* of Guadeloupe¹, and if *vanzoi* of St. Lucia is closest to *fuscata* of Dominica, a kind of double leap-frog relationship is in the most literal sense obvious.

What is the rationale of such a leap-frog relationship? This question goes directly to the issue of the reality of the expectation of linear step-by-step colonization and evolution. It involves the mode of colonization itself, which for *Ameiva*, *Anolis* and *Sphaerodactylus* has probably been by raft.

One theory of island colonization takes as an objective measure of the likelihood of colonization of one island from another the

¹ There are very few characters separating the two "species." Persistence of very distinct pattern of light lines in *major* at a size very little smaller than a quite unlined (or dark lined) *cineracea*, some apparent difference in adult pattern, a tendency to a lower number of ventral rows in *major* than *cineracea*, and some difference in brachial squamation persuade us to provisionally hold the two nominal species distinct. However, the sample of each (3) is very small and we might easily be wrong. But, this in no way diminishes the distinctness of *cineracea* or *major* from other Lesser Antillean (or other) *Ameiva*. The leap-frog relationship still very conspicuously holds, since at the least the northern Lesser Antillean *Ameiva* must have overleaped *cineracea* or *major* or both to reach their present situation.

straight line distance between the two. On such a theory the step by step colonization of the Lesser Antilles is the only plausible hypothesis.

Even *a priori*, however, the mode of transport must be considered equally with distance. Most reptiles must be transported to oceanic islands by rafting. Rafting inevitably involves currents and the straight line distances between islands are quite irrelevant if currents ignore these straight line distances.

Thus there is for animals carried out to sea on rafts on the flood tide of the Orinoco no conceivable significance in the straight line distance between St. Vincent and St. Lucia or between Dominica and Guadeloupe. A raft from South America might randomly arrive on St. Vincent or on Dominica or on Guadeloupe or St. Lucia and only the currents (or the storms) of the moment and the survival powers of the animal so carried would make the nearer more likely than the remoter island.

It is very probably that rafts also occasionally set out from one island of the Lesser Antilles and land on another¹. Adjacent islands might then be populated by related stocks, but this possibility will be limited by the requirement that the available port of entry be not already pre-empted by a colony that has arrived from a more distant source.

Thus Grenada and St. Vincent *ameivas* are the same, and local rafting may have achieved this result. But adjacent St. Vincent and St. Lucia populations are quite unlike and the adjacent Dominica and Guadeloupe populations are also quite unlike.

It is breaks in linear continuity such as these that need our special attention. The St. Vincent-St. Lucia case is perhaps easily accounted for by the hypothesis that from St. Vincent south *Ameiva* are very recent invaders from South America, while *Ameiva* from St. Vincent north represent one or several older invasions of the Lesser Antilles.

The case of *Ameiva cineracea* on Guadeloupe is crucial: Grant strong *in situ* specialization; the possibility of differentiation as extreme as in Guadeloupean *cineracea* depends upon strong isolation.

¹ But with no large rivers the probability (= frequency) of rafts is much diminished even though the distance a raft must travel is small.

Ameiva more than most lizards appear to be good water crossers; their present (or past) distribution on almost every scrap of Caribbean land indicates this. Presumably they cross shorter distances more easily than long ones. The development of strong differences between island *Ameiva* should thus be hampered by gene flow; in most cases perhaps this would amount only to "introgression", not "swamping." But very strong differences should indicate absence of gene flow for a long period, hence special isolation, special inaccessibility.

Short cross-water journeys have, we repeat, higher probability than long journeys, but a succession of short journeys may have as low probability as one long journey. In any event, once any long journey has in fact occurred, discussion of its theoretical prospective probability is no longer germane.

We submit that the most probable explanation of the extraordinary differentiation of Guadeloupean *cineracea* is long isolation, that long isolation was most probably achieved by a long, i.e. "leap-frog," cross-water journey – such that no populations of *Ameiva* then existed to slow the differentiation of the Guadeloupe population by genetic contamination. By such a long cross-water journey the requirement that we insisted upon above for strong *in situ* specialization – that the island be sufficiently distant that colonization is an extremely rare event – will be met as it would not be by short journeys.

There is a point here which may be important if the invasion of *cineracea*-stock is sufficiently old: in the Lesser Antilles the chain of islands from Sombrero to Eastern Guadeloupe (often spoken of as the Limestone Caribbees) are generally considered as being much older than the island-arc from Saba to western Guadeloupe and further south to Grenada. The first chain consists of islands of ancient volcanic origin which are mainly covered by sediments of considerable age; the second one comprises much younger volcanic islands, in which older formations (if present) have become obscured by younger volcanics. So it might be possible that *cineracea* on Guadeloupe once inhabited the southernmost of the northern islands, the one most likely to be reached by a long voyage from South America. It must be kept in mind that it is incorrect to suppose that the islands have all been available synchronously to

receive a waif fauna. For the older stocks of colonizers the northern, not the southern, islands may have been the first landfall.

Ameiva major, if it is from Martinique, would presumably be an element of the same invasion that resulted in *cineracea*. Its presence could be explained in several ways: (1) that Martinique was the port of entry and Guadeloupe the next successful colonization; (2) that Guadeloupe was the port of entry and Martinique a secondary colony; (3) whichever was the port of entry, the *cineracea-major* stock once included intervening Dominica in its range but has since been displaced on that island by a subsequent invasion by a stock already distinct at the species level.

It should be clear at this point that of the three patterns which we have here described, (1) *cluster relationship* and (3) *leap-frog relationship* are alternatives but that (2) *in situ specialization* is a component of each of the others. Beyond this the picture is more or less clear. Local factors plus degree of isolation determine the extent of *in situ specialization*. *Cluster relationships* depend upon the high probability that adjacent banks will receive colonists in one or both directions (or in the case of populations on one bank, upon the historical certainty that they were once a unit population when the bank itself was an emergent unit). *Leap-frog or bypass distributions* are, on the other hand, a discordant random element which interrupt the linear continuity of distributions on a chain of oceanic islands; they are the product of very improbable long sea-journeys¹ which nevertheless have a finite probability and therefore do sometimes occur. Once they have occurred and once the distant populations have differentiated in isolation, they may by the principle of ecological exclusion prohibit the successful colonization of the land mass they occupy by any stock less endowed adaptively or only equally endowed. Leap-frog colonists, once they have arrived at

¹ The length of the journey is, of course, the significant point and not that any islands are leaped over or bypassed. That long, very improbable sea journeys do sometimes occur cannot be doubted. The Galápagos Islands, 600 miles west of Ecuador, provide a clear case of multiple instances of such very long voyages. The distances in the Lesser Antilles, even to the northern tip of the chain, are very much less than the distance to the Galápagos.

species level, therefore, by their very existence may compel other stocks to leap-frog past them.

To summarize then, three groups of Lesser Antillean ameivas are evident: (1) *Ameiva ameiva aquilina* in Grenada, the Grenadines and St. Vincent is a mere subspecies of the common *Ameiva* of the South American mainland. We may speak of the *Ameiva ameiva* group. (2) *Ameiva cineracea* and *A. major* are, on the contrary, quite isolated, very specialized species, clearly forming a group by themselves. (This remains true whether or not *A. major* is the lost ameiva of Martinique.) We may speak of this as the *A. cineracea* group. (3) The remaining Lesser Antillean ameivas, though they are well-marked forms, can plausibly be considered together. On this hypothesis they comprise two subgroups (a) the southern species *A. vanzoi* of St. Lucia and *A. fuscata* of Dominica; (b) the species from Montserrat north. We may speak of the two subgroups together as the *fuscata* group.

It seems very probable that these three groups represent three times of invasion of the Lesser Antilles: (1) an ancient one by the *A. cineracea* group which arrived far out on the Lesser Antillean chain, probably by a long sea journey; (2) an invasion of more recent period by the *A. fuscata* group which has done some long leap-frogging as well as some shorter journeys; this has gone the farthest distance north; (3) a continuing invasion by the *Ameiva ameiva* group. This last has involved only short sea voyages, has gone the shortest total distance, and may still be subject to introgressive contamination by occasional colonists from the mainland.

This is a picture a bit more complex than the linear relationship often proposed for Lesser Antillean colonizations but it is not surprising or improbable.

COLONIZATION FROM THE NORTH OR THE SOUTH?

The whole of the foregoing discussion has been in terms of colonization from the south, ultimately from South America. We have omitted to mention any possibility that the Lesser Antilles have been populated by *Ameiva* invading from the north, from the Greater Antilles. This possible direction of entry into the Lesser

Antilles has always been too much neglected, though there has always been evidence pointing to its probability. The *Anolis bimaculatus* group (from Dominica north) have clear Greater Antillean affinities. There are other cases in which animals of Greater Antillean affinity occur only in the extreme northern Lesser Antilles (e.g. *Sphaerodactyles macrolepis* on the Anguilla bank, WAYNE KING 1962). There are also indications that there may have been other penetrations of this sort in the more distant past. ETHERIDGE (1964) has recorded the Greater Antillean lizard genus *Leiocephalus* fossil on Barbuda; his discovery makes the putative Martinique locality for *Leiocephalus herminieri* very much more plausible. There is, of course, a caveat to be entered here. Because northern South America does not now have suitable ancestral stocks does not prove that it did not have them in the fairly recent past, *i.e.* the Pleistocene. The example described by UNDERWOOD (1964) of a distinct species of a family (Anguidae) unknown in the Lesser Antilles discovered on Montserrat is presumptive evidence of this situation; the Lesser Antillean species is closely related to a species now confined to Central America; its presence on Montserrat is most easily accounted by the assumption that the related species once extended into northern South America and in fact to the South American source area for Lesser Antillean waifs.

In the specific case of *Ameiva* there is little to support a Greater Antillean source for the species north of St. Vincent. (The issue does not arise for the subspecies of South American *Ameiva ameiva*.) Relationship of Lesser Antillean *Ameiva* would surely be only with the *Ameiva chrysolaeama-A. exsul* group, not with the smaller Greater Antillean species (e.g. *wetmorei*, *polops*). All the endemic Lesser Antillean species are, however, quite as distinct from the Greater Antillean as from South American species; on morphological grounds there is no proper ground for choice. A judgment in favor of ultimate South American origin for the endemics can be rendered on the ground of the general sweep of the currents in the area from east to west and favoring rafting from the Orinoco rather than from the Greater Antilles. Very solid evidence of Antillean affinities would be needed to counter these higher probabilities of transport from the

south. The existence of breaks in linear continuity of relationship also favors southern origin, since the wide sweep of major currents would promote this, while any group coming down from the north would probably have to depend on the local currents between adjacent islands and would hence have a continuous distribution (as the *Anolis bimaculatus* group in fact does).

AMEIVA AND MONGOOSE

General Remarks

The restriction of the St. Lucian ameiva to a small islet off the coast of the large island raises again the spectre of the much advertised role of the introduced mongoose in the extinction of the West Indian fauna.

The only recent and major summary of the information on this point is by J. H. WESTERMANN (1953).¹ Unfortunately his paper is, as its subtitle states, "a review of the literature on the destruction and preservation of flora and fauna in the Caribbean area" and his remarks on amphibians and reptiles are borrowed, as he freely admits, from BARBOUR (1930a, 1937) and a few other sources.

It is an unfortunate but necessary statement that BARBOUR's comments under the species headings in his several lists (1930b, 1935, 1937) are very frequently misleading when not erroneous, and they are in no instances more commonly random or baseless than when he casually reports some form extinct.²

WESTERMANN's statements on amphibians and reptiles, since they somewhat elaborate BARBOUR's, cannot be accepted. His statements on the occurrences of mongoose seem to be better founded. However, his account of the "havoc" wrought by the mongoose, not surprisingly, is vitiated by the exaggerations of its sources.

We confine our discussions here to the relation of ameivas and mongoose. Table 20 is a listing of Lesser Antillean islands on

¹ See, however, also MYERS & URICH 1931.

² It was some of BARBOUR's unfounded remarks on the rarity of certain Haitian snakes that provoked ANTHONY CURTISS (1947), who really knew the fauna of the Port-au-Prince region in Haiti, to write a short and plaintive note on "the prevalence of snakes in Haiti."

TABLE 20
AMEIVA AND MONGOOSE

	Mongoose	<i>Ameiva</i>
Sombrero	—	+
Anguilla	—	+
St. Barts	—	+
St. Martin	+	+
Saba	—	—
St. Eustatius	—	+
St. Kitts	+	+
Nevis	+	+
Antigua	+	+
Barbuda	—	+
Montserrat	—	+
Redonda	—	+
Guadeloupe	+	confined to small islets off the coast or extinct
Marie-Galante	+	—
Désirade	—	—
Les Saintes	—	—
Dominica	—	+
Martinique	+	—
St. Lucia	+	confined to an islet off the coast
St. Vincent	+	+ ¹
Grenada	+	+
Barbados	+	—

which mongoose occurs or does not occur and the status of ameiva on these same islands.

There is no simple relationship here. Discounting Saba, which, as UNDERWOOD (1962) suggests, *Ameiva* may never have reached, the genus is absent without explanation on La Désirade and Les Saintes and on Diamond Rock off Martinique on which *Dromicus* still survives (observations by JAMES D. LAZELL, JR. who has recently collected on these islands). On the other hand, it survives handily along with the mongoose on St. Martin, St. Kitts and Grenada.

In some cases it is reported that *Ameiva* has survived by frequenting towns and the vicinity of human occupation. There are

¹) UNDERWOOD 1962, p. 160.

reports also of a period of near extinction and recovery (in Grenada, as also in Jamaica). It is very difficult to estimate the value of these stories. The genus *Ameiva* in general is a creature of the lowlands and of dry hot areas; it is often abundant on beaches; it is scarce or absent in mountains. On few of these islands, therefore, is it ever likely to have been island-wide. The casual and careless observer or one who did not himself observe or collect ¹ is very easily led to to totally wrong conclusions on the distribution and abundance of animals in such a situation.

The only valid generalization that would seem derivable from inspection of the distributions of mongoose and *Ameiva* in the Lesser Antilles is that the interaction of prey and a new predator is unpredictable. Even within one genus different species react differently, and whether this is a consequence of intrinsic differences between the species, or of the different ecologies of the islands, or of the total biological balance (*e.g.* native predators preying upon the new predator) is a problem still to be solved and to be solved differently for each individual case.

St. Croix: A case paralleling that of St. Lucia

The case which seems most clearly parallel to that of St. Lucia is the one presented by St. Croix. In this case we are fortunate to have in the recollections of GEORGE A. SEAMAN (pers. comm.) a history of the disappearance of *Ameiva* on a major island and its survival on a few islets off the coast. We tell the story almost in his own words.

Oddly there was no mention of *Ameiva* in the first report on the herpetology of St. Croix (GÜNTHER 1859). Mr. SEAMAN tells me that the NEWTONS, who collected the material reported on by GÜNTHER, lived in the center of the island – a clay region – which very likely did not have *Ameiva*. We start therefore – as usually with *Ameiva* – with a species which was never island-wide but was restricted always by ecological requirements – among these certainly the sandy soil in which they prefer to burrow.

As Mr. SEAMAN indicates, there is no way of knowing the size of the *Ameiva* population on St. Croix prior to 1884 ² – the year mongoose is reported to have been introduced from Jamaica – or even much later. In 1910, however, *Ameiva* were readily found in the town of Frederiksted. They were gradually pushed

¹ ANTHONY CURTISS (1947) has briefly described BARBOUR's collecting procedures unkindly but not inaccurately: "He used to send out blacks he met along the shore, retire to his boat, and buy what they brought in late that day." BARBOUR's own account, including a justification of this procedure, is found in BARBOUR & SHREVE 1935, p. 348-349.

² H. BEATTY (1944, p. 182) says the mongoose was introduced in 1867.

westward through the town until they inhabited only a narrow strip of land along the seashore. As their numbers dwindled, the size of apparently mature adults dwindled also from a form 6-7 inches to only 4-5 inches.

In 1949 when Mr. SEAMAN returned to the island after many years absence, he found only two small colonies of "emaciated" *Ameiva* still occupying the Frederiksted seashore. They were now isolated by a growing town. One colony was by the old "Fort" and the other alongside a lumber yard, about 500 yards to the south. Together the two colonies may have amounted to 100 individuals.

A new waterfront development has now taken up the area used by these last colonies of *Ameiva*. A check by Mr. SEAMAN in late 1964 discovered no *Ameiva* whatever.

In the town of Christiansted a very similar situation has apparently existed, though Mr. SEAMAN is less familiar with the area. The last *Ameiva* were personally seen about 1920 by Mr. SEAMAN in an old yard south of the Christiansted Fort - an open, rather sandy area bordering the sea. His information is that no *Ameiva* have been seen in this area for years.

It is of importance that the density of mongoose on St. Croix is higher than in the northern Virgin Islands; it is estimated at one to the acre. Even in the northern Virgins *Ameiva* (and the snake *Alsophis*) can be encountered only in the towns.

Mr. SEAMAN reports the survival of the St. Croix *Ameiva*, *A. polops*, on two islets only:

"*Protestant Cay*: A small colony still to be found here. Maybe 50 individuals. The population was much larger in the 1920's."

"*Green Cay*: The largest population of lizards left are on this small island. Also the largest specimens are to be met with here. I hesitate to hazard a population count, but there should be over a hundred. Mongoose were never released on this island."

The situation reported by Mr. SEAMAN in 1964 is almost precisely that recorded by CHAPMAN GRANT and HARRY BEATTY in 1936 (GRANT 1937). GRANT and BEATTY at that time estimated the population on Protestant Cay to be 35 individuals. On Green Cay BEATTY did not see any on one visit but on a second visit "observed many scurrying about the beach, a large number of these being young. I dissected a few and found that they were feeding on the species of semi-aquatic amphipods very abundant among the beached seaweed."

On Bush Island, a larger islet, no *Ameiva* have been found by Mr. SEAMAN nor were any found by GRANT and BEATTY. Mongoose were introduced on this island around 1912. Despite the cautionary remarks of the previous section, it certainly seems very plausible in this case that mongoose has contributed to the destruction of *Ameiva polops* on the mainland of St. Croix. The probable parallel with St. Lucia is very obvious. Still it is appropriate to call attention again to the very likely presence of many factors in each case of extinction: A species limited by its ecology to one type of soil is already subject to a large risk. Man himself also enters the picture. He may hunt the species or let it alone. He may build upon its breeding grounds or without any intention protect it from certain predators, or equally without intention expose it to others.

Man and his deliberate and unintended commensals and parasites have an incalculable effect. The mongoose is only one of the more obvious and extreme of man's modifications of the natural economy. The disturbance of the former equilibrium is, it must be repeated, unpredictable: each individual case will go to its individual conclusion.

ADDENDUM

Because of the interest attaching to *Ameiva major* Duméril & Bibron, we feel that a modern description of the species should be available. We have therefore prepared the following, based primarily on Paris 1491 from "Trinité," which we hereby designate as lectotype:

Ameiva major

Head. Nostril between two nasals. Anterior nasals broadly in contact. Frontonasal much longer than wide, in contact with leroal. Prefrontals broadly in contact. Frontal short, in contact with first two supraoculars. Frontoparietals in contact with 3rd supraocular, well separated from 4th supraocular which is small. 4 occipitals, the two median smallest. 8 supraciliaries, the first two in contact with first supraocular. The others separated from the supraoculars by granules. 6-7 supralabials. 6 infralabials, 3rd largest. Wedge of granules on throat penetrating forward for more than half the length of first chin shields. A triangular zone of enlarged scales on middle of throat. A band of enlarged granules across the posterior throat, just in front of anterior throat fold. Between the two throat folds a band of still larger scales becoming smaller laterally.

Venter. 18 longitudinal and 35+ transverse rows of scales. Preanal enlarged scales numerous, relatively ill-defined against surrounding scales.

Limbs. *Ca* 3 rows of antibrachials, outermost very wide, inner not well defined. Brachials very poorly defined. No postbrachials. Enlarged scales of thigh widest near knee. Only one row very wide or distinct. Only two rows on tibia distinctly enlarged, the inner rather poorly defined. Enlarged scales of tarsus continuous with enlarged scales covering 3rd and 4th rows.

The juvenile 1855 shows there are pale eye-and pale flank-lines and rows of spots on lower flanks. The belly is light, the throat light bluish and the enlarged scales of mesoptychum with bluish spots. The sides of mesoptychum and skin under anterior fold are yellowish.

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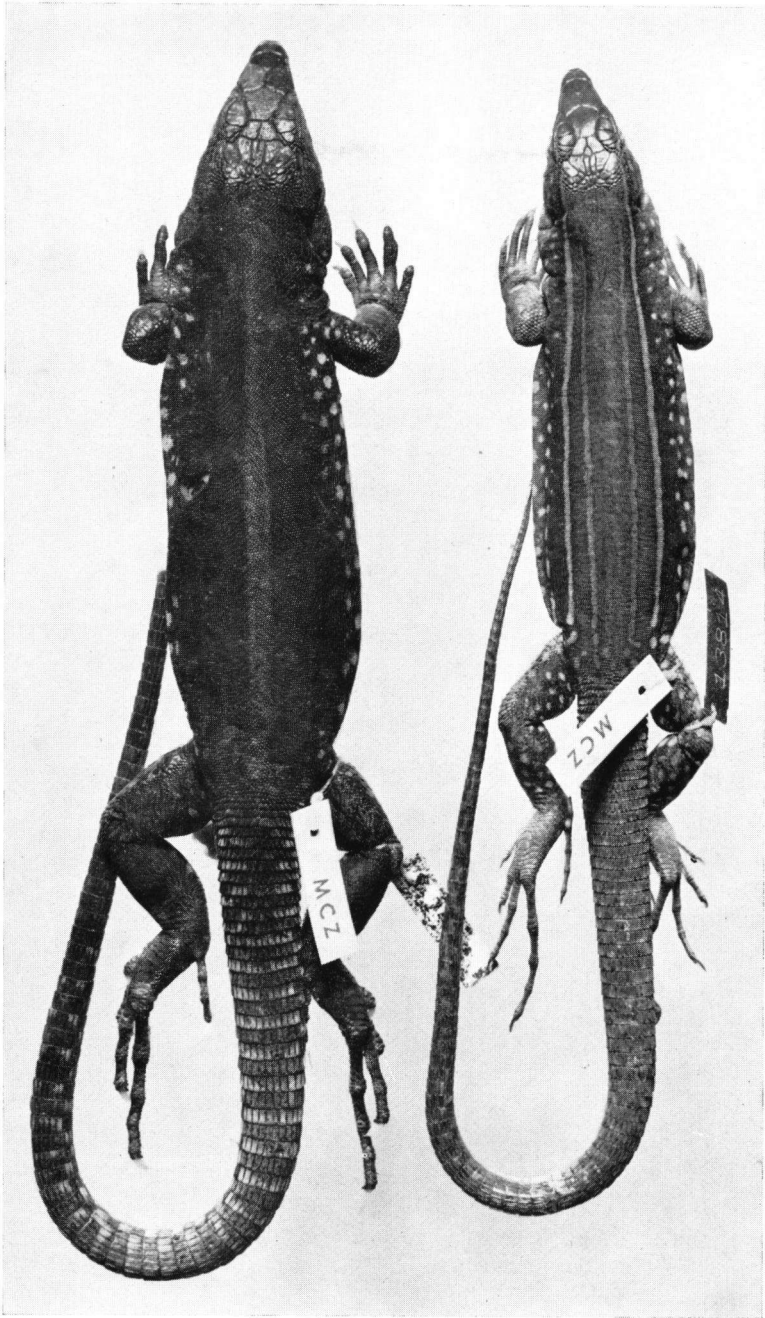


Plate I. *Ameiva vanzoi*, new species, from the Maria Islands, St. Lucia. — Dorsal views of male (left) and female (right).

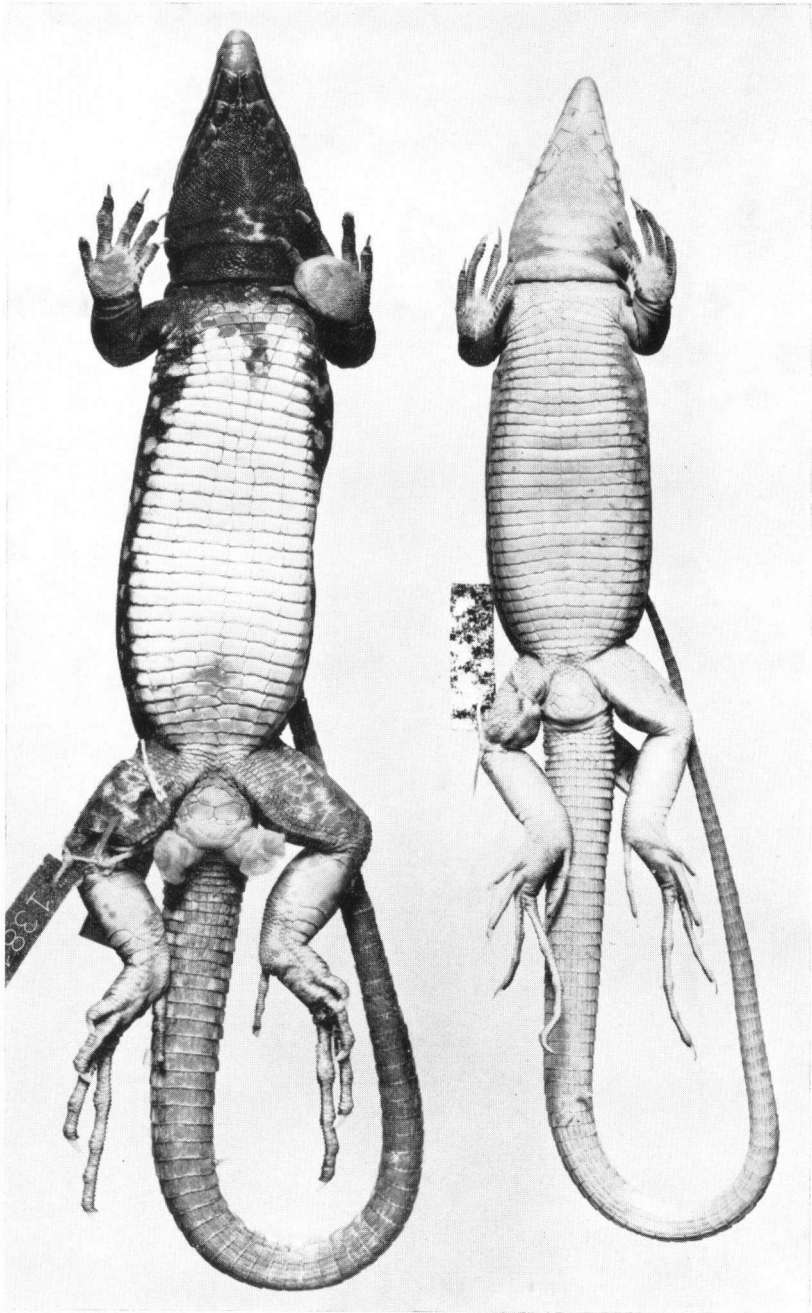


Plate II. *Ameiva vanzoi*, new species, from the Maria Islands, ST. LUCIA. – Ventral view of male (left) and female (right).