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# AMPHIBIANS AND LAND REPTILES OF PORTO RICO

# With a List of Those Reported from the Virgin Islands

# By KARL PATTERSON SCHMIDT

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# INTRODUCTION

The new account of the amphibians and reptiles of Porto Rico and its dependent islands here attempted, while based on the fundamental work of Stejneger (1904), has an independent source in the collections made in the course of the Scientific Survey of Porto Rico and the Virgin Islands undertaken by the New York Academy of Sciences, in cooperation with the Porto Rican government and The American Museum of Natural History. These collections consist of a total of 1435 specimens, representing 33 of the 42 forms in the area covered by this report.

In the course of investigations on other groups of animals, 103 specimens of amphibians and reptiles were collected by F. E. Lutz, J. T. Nichols, R. W. Miner, H. E. Anthony and T. H. Jones previous to 1919.

It was my good fortune to conduct the first specifically herpetological field-work for this Survey in the summer of 1919, and for this opportunity I am indebted primarily to Miss Mary C. Dickerson, then Curator of Herpetology at The American Museum of Natural History, and to Dr. Henry C. Crampton, Dr. N. L. Britton and Dr. Ralph W. Tower, of the Porto Rico Committee of the New York Academy of Sciences. In carrying out this field-work, Mrs. Schmidt and I spent the period from August 3 to October 8 in investigations on Porto Rico and in making visits to the adjacent islands—Mona, Vieques and Culebra. Our collections amounted to 1253 specimens.

These collections were considerably enriched in 1926, by Messrs. H. E. Anthony and G. G. Goodwin, who collected 74 specimens on Mona Island, and 5 on Caja de Muertos, southeast of Ponce. This material includes a fine series of *Eleutherodactylus monensis*, which was wanting in my Mona Island collection, and the first herpetological specimens from Muertos Island.

# ITINERARY AND COLLECTIONS MADE

Mrs. Schmidt and I arrived at San Juan on August 3rd, 1919. The first week of our stay was spent at Santurce, which provided a convenient base for the necessary official visits in San Juan. There we were able also to do some introductory collecting, with our interest stimulated by a tree frog new to Porto Rico that was abundant in the hotel grounds. Rio Piedras and Cataño were also visited from Santurce. The next two weeks (August 11-24) we sojourned at Aibonito, at an altitude of about 2000 feet, in the heart of the coffee-belt. Daily excursions were made in this vicinity. Four days were spent at Coamo Springs, a truly delightful collecting locality, affording numerous species new to our collections.

On August 29 we returned to Santurce for a fresh start. With Mona Island as objective I went alone to Mayagüez (September 3). There I learned that it would be impossible to sail for Mona until September 6. This delay enabled me to make a productive trip to Maricao. The week of September 7-13 was spent in the trip to Mona Island, on which I was accompanied by E. M. Bruner, Forester of Porto Rico.

Returning to Santurce, where specimens were meanwhile accumulating, thanks to the interest of B. A. Wall, of Bayamon, we packed and stored the collection. On September 18 we left by rail for Ensenada, where we enjoyed the hospitality of Superintendent Boyd, of the Guanica Central, at "Canary Cottage."

Again returning to Santurce (September 28) I set forth on a threedays trip to El Yunque, where I camped in the Forester's Cabin at 1200 feet altitude, climbing to the peak on September 30. This was followed by a brief trip to Vieques and Culebra islands by means of a sloop chartered at Fajardo. On October 8 we sailed from San Juan for New York.

# OTHER MATERIAL EXAMINED :..

Besides the material collected by the Survey of Porto Rico and the Virgin Islands, all of which is deposited in The American Museum of Natural History, I have had the privilege of examining, thanks to the courtesy of Dr. W. C. F. McClure, the Porto Rican collection preserved at Princeton University.

Dr. Stuart T. Danforth, of the University of Porto Rico, at Mayagüez, kindly sent me both his personal collections and those of the University for examination in connection with this report.

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# PLAN OF WORK

"The Herpetology of Porto Rico" by Dr. Leonhard Stejneger (1904) is a work of exceptional merit. It remains a model for the exact and complete description of an insular fauna, and sets a high standard for systematic zoology in general. It is a pleasure to record here the usefulness of this volume. A copy accompanied me to Porto Rico in 1919 and proved most serviceable as a field manual, making possible the identification of most of the species and thus facilitating all phases of field study.

It was my first plan to prepare merely a supplement to Dr. Stejneger's report, embodying only the additions to our knowledge of the Porto Rican herpetological fauna since 1904. After a review of the necessary additions, in conference with Dr. H. C. Crampton, it was decided, however, to enlarge the scope of the work and present a renewed "complete account" both for the sake of increased usefulness to future students and to bring it into better accord with the similarly complete reports of other contributors to the Survey. The existence of Stejneger's report has greatly simplified the preparation of the present one. In the case of the numerous species whose definition has required no change. I have followed Stejneger's descriptions closely or quoted them verbatim, and I have availed myself of a large number of his text figures. especially for the illustration of key characters. The figures drawn for the present paper are designed to present the habitus of a number of species, and thus supplement Stejneger's otherwise complete illustration of the fauna. These figures are the work of Mrs. E. L. Beutenmüller, whose drawings have embellished so many herpetological papers. The half-tone figure of *Eleutherodactylus unicolor* was supplied through the courtesy of Dr. Steineger.

I have adopted a conservative position on one phase of nomenclature. Excellent arguments might be advanced for treating several of the Porto Rican forms as subspecies rather than as full species. Such a nomenclature would reflect more information as to the actual relations of the forms concerned than binomial treatment. The species of *Typhlops* allied to *jamaicensis*, the fresh water turtle, and the Mona Island *Ameira* and *Cyclura* are cases in point. It is very difficult, however, to draw a line between insular subspecies and insular species, and our knowledge of many forms is manifestly imperfect. Any attempt at a trinomial arrangement of *Eleutherodactylus* is obviously impossible. I have accordingly left the matter for future consideration, preferably in connection with a new list of the West Indian fauna as a whole. So much work still remains to be done on the herpetological fauna of Porto Rico by some resident naturalist, especially with reference to the discrimination of the small tree frogs and their life histories, that the present account of the fauna is hardly more likely to be "final" than was that of Dr. Stejneger more than twenty years previously.

# Acknowledgments

It is a pleasure to acknowledge the cordial furtherance of the present work by the members of the Porto Rico Committee of the New York Academy of Sciences, by my various sometime colleagues of The American Museum of Natural History who took part in the Survey of Porto Rico and the Virgin Islands, and by nearly everyone with whom we came in contact in the course of the herpetological field-work.

We were especially indebted, when in Porto Rico, to Mr. and Mrs. B. A. Wall, of Bayamon; to Mr. E. M. Bruner, Forester of Porto Rico; to Mr. Marc Lejeune, of Mayagüez, to whom I owe the visit to Mona Island; and to Colonel George A. Shanton, Chief of the Insular Police.

In the course of the preparation of the report I have had the most cordial aid from various herpetologists. I have applied for information, for specimens or for advice to Dr. Leonhard Stejneger and Miss Doris Cochran, of the United States National Museum: to Dr. Thomas Barbour and Mr. Arthur Loveridge, of the Museum of Comparative Zoology; to Dr. G. K. Noble and Mr. Clifford H. Pope, of The American Museum of Natural History: to Dr. Emmett Reid Dunn, of Smith College; to Dr. Stuart T. Danforth, of the University of Porto Rico; and to Mr. H. W. Parker, of the British Museum (Natural History).

The friendly criticism and interest of Mr. Herbert F. Schwarz, now editor of the reports of the Survey of Porto Rico, have improved the present paper at innumerable points, both in minor details and in more important matters. My thanks (and still more those of the reader) are due to him for great patience with a difficult manuscript.

# PORTO RICAN HERPETOLOGY SINCE 1904

Stejneger presents an excellent historical review of the growth of our knowledge of the amphibians and reptiles of Porto Rico (1904, pp. 553-559). The small but interesting collection secured by W. W. Brown, Jr., on Mona Island in February, 1892, has since come to light and was reported on by myself (1926).

Subsequent to the collections made for the United States National Museum in 1899-1901, no mention of Porto Rican herpetology appeared until 1913, when Stejneger described the unusually interesting and extremely distinct *Ameiva wetmorei* from Rio Loco, near Guanica. The type was collected by Dr. Alexander Wetmore in the course of his investigations of the Porto Rican bird fauna.

The collections made by Mr. Charles F. Silvester, while on the staff of the expedition of the Carnegie Institution to Porto Rico in 1915, were reported upon by Fowler in 1918. Fowler figures *Ameiva wetmorei* and discusses variation in other species.

The discovery of bones referable to an extinct species of *Cyclura* in a cave near Ciales by Dr. Glover M. Allen and James Lee Peters, in 1917, filled an important gap in the distribution of this typically Greater Antillean genus. The species was described by Barbour (1919), the type being the extremities of a left humerus, with numerous additional limb-bones, jaws and vertebrae. Similar material was collected for the Scientific Survey of Porto Rico and the Virgin Islands by H. E. Anthony in 1916.

The herpetological collecting of the various workers who have taken part in the Scientific Survey of Porto Rico and the Virgin Islands has been described above.

Dr. E. Greywood Smyth, Entomologist for the Porto Rican Agricultural Experiment Station at Rio Piedras, has paid some attention to the amphibians and reptiles and in 1920 published a brief account of the food habits of the Anoles.

The food habits of Porto Rican lizards were subsequently analyzed in some detail by George N. Wolcott, in a paper published in 1924 in the Journal of the Department of Agriculture of Porto Rico.

A small collection made in the course of ornithological investigations in 1924-1925 was reported upon by Stuart T. Danforth (1925 and 1926). This material was subsequently purchased by the Field Museum of Natural History. Mr. Danforth has also collected on Desecheo Island, adding *Ameiva exsul* to the list from that island in 1926.

LISTS OF THE AMPHIBIANS AND LAND REPTILES OF PORTO RICO AND THE ADJACENT ISLANDS

I. PORTO RICO

- 1. Bufo lemur
- 2. Bufo marinus\*
- 3. Leptodactylus albilabris
- 4. Eleutherodactylus portoricensis
- 5. Eleutherodactylus gryllus
- 6. Eleutherodactylus locustus
- 7. Eleutherodactylus cramptoni
- 8. Eleutherodactylus antillensis

- 9. Eleutherodactylus brittoni
- 10. Eleutherodactylus wightmanae
- 11. Eleutherodactylus richmondi
- 12. Eleutherodactylus unicolor
- 13. Hemidactylus mabouia
- 14. Sphaerodactylus macrolepis
- 15. Anolis cuvieri
- 16. Anolis cristatellus
- 17. Anolis gundlachi
- 18. Anolis evermanni
- 19. Anolis stratulus
- 20. Anolis krugi
- 21. Anolis pulchellus
- 22. Anolis poncensis

- 23. *†Cyclura* portoricensis
- 24. Celestus pleii
- 25. Ameiva exsul
- 26. Ameiva wetmorei
- 27. Amphisbaena caeca
- 28. Amphisbaena bakeri
- 29. Mabuya sloanii
- 30. Typhlops platycephalus
- 31. Typhlops rostellatus
- 32. Epicrates inornatus
- 33. Dromicus stahli
- 34. Alsophis portoricensis
- 35. Alsophis antillensis
- 36. Pseudemys stejnegeri

# II. MONA ISLAND

The fauna of Mona Island, which adds six species to the above list, is as follows:

- 1. Eleutherodactylus monensis
- 2. Sphaerodactylus macrolepis
- 3. Anolis cristatellus
- 4. Cyclura stejnegeri
- 5. Ameira alboguttata

- 6. Mabuya sloanii
- 7. Typhlops monensis
- 8. Epicrates monensis
- 9. Alsophis variegatus

# III. DESECHEO ISLAND

Desecheo Island is rarely visited. Herpetological specimens were secured by Bowdish in 1901, by Lutz in 1914 and by Danforth in 1926. The species known are:

1. Anolis cristatellus

3. Alsophis portoricensis

2. Ameiva exsul

## IV. VIEQUES ISLAND

Ten species, all of them identical with Porto Rican forms, are known from the island of Vieques. These are:

- 1. Leptodactylus albilabris
- 2. Eleutherodactylus antillensis
- 3. Sphaerodactylus macrolepis
- 4. Anolis cristatellus
- 5. Anolis stratulus

- 6. Anolis pulchellus
- 7. Anolis cuvieri
- 8. Ameiva exsul
- 9. Mabuya sloanii
- 10. Alsophis antillensis

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# V. CULEBRA ISLAND

The Culebra fauna lacks *Sphaerodactylus*, which has doubtless merely been overlooked. It adds a Virgin Island form, *Dromicus exignus*, to the fauna under consideration. Its species are:

Leptodactylus albilabris	Ameiva exsul
Eleutherodactylus antillensis	Mabuya sloanii
Anolis cristatellus	Dromicus exiguus
Anolis stratulus	Alsophis antillensis
Anolis pulchellus	

## VI. CAJA DE MUERTOS ISLAND

Anthony and Goodwin secured four lizards and a snake from this island during their field-work in 1926. These represent three species:

Anolis cristatellus .11sophis portoriceusis Ameiva wetmorei

# HABITAT ASSOCIATIONS AND FAUNAL SUBDIVISIONS

Porto Rico includes a wide range of habitat conditions, from the extremely wet mountain rain forest of the Luquillo, where mountain palms and hardwoods are hung with lianas and draped with moss that never dries out, to the opposite extreme of aridity on the southwest corner of the island (near Guanica and Ensenada), where a cactus flora predominates. Some of the types of habitat, with distinct associations of reptiles and amphibians, appear to be the following:

- I. Northern Coastal Plain (Collections secured from Santurce, Rio Piedras, Bayamon and Mayagüez).
- II. Coffee Belt, 900-2000 ft. (Collections from Aibonito and Maricao).
- III. Deforested Hilltops, above 2000 ft. (Collections secured at Aibonito and Maricao).
- IV. High Rain Forest, 1200-3485 ft. (Collections secured from El Yunque, Luquillo Forest Reserve).
  - V. Pepino Limestones (Collection from Cataño).
- VI. Arid Limestones, southwestern Porto Rico (Collections from Coamo Springs, Ensenada and Salinas).

This list is quite inadequate from an ecological standpoint and in it only II, III and IV approach the definition of Biotopes, with recognizable Biocoenoses.

Turning first to the distribution of the fauna in Porto Rico itself, a

number of corrections are necessary in the account of the vertical distribution given by Stejneger. These will be presented in detail below, in the systematic discussion of the species. In general, recent observations show that altitude in itself has played a relatively small part in determining the distribution of the fauna. Thus Anolis pulchellus, which Steineger believed to be confined to the coastal plain, below 500 feet, is present at all altitudes, at least up to 2000 feet, in open fields; and Anolis krugi, for the most part confined to the coffee belt, is found as far down as Coamo Springs (500 ft. alt.) where the conditions of moisture and shade are suitable. The species which are abundant at the lower altitudes (i. e., on the coastal plain) and extend in varying degrees into the higher are the following:

- 1. Bufo lemur\*
- 2. Leptodactylus albilabris
- 3. Eleutherodactulus portoricensis 14. Amphisbaena caeca
- 4. Eleutherodactylus antillensis
- 5. Hemidactylus mabouia\*
- 6. Sphaerodactylus macrolepis
- 7. Anolis cuvieri
- 8. Anolis cristatellus
- 9. Anolis stratulus
- 10. Anolis pulchellus
- 11. Anolis poncensis\*

- 12. Ameira exsul\*
- 13. Ameiva wetmorei\*
- 15. Mabuya sloanii\*
- 16. Typhlops platycephalus\*
- 17. Typhlops rostellatus
- 18. Epicrates inornatus
- 19. Dromicus stahli
- 20. Alsophis portoricensis
- 21. Alsophis antillensis\*
- 22. Pseudemys stejnegeri\*

Of these only nine (marked with an asterisk) are, so far as known. confined to the coastal plain, or to altitudes below 500 feet. Bufo marinus may now be added to this list.

The species, on the other hand, which do not occur on the coastal plain or at least only as stragglers, are the following:

1. Eleutherodactylus gryllus 2. Eleutherodactylus locustus 3. Eleutherodactylus cramptoni 5. Eleutherodactylus brittoni 5. Eleutherodactylus richmondi 6. Eleutherodactylus wightmanae 12. Amphisbaena bakeri

Of these Eleutherodactylus cramptoni, E. unicolor and E. richmondi and E. locustus are confined, so far as known, to the peak of El Yunque: the others are probably most abundant in the coffee belt. Since nearly two-thirds of the coastal-plain species overlap the coffee belt in dis-

- 7. Eleutherodactylus unicolor 8. Anolis gundlachi
- 9. Anolis evermanni

- 10. Anolis krugi
- 11. Celestus pleii

tribution, it seems obvious that the distribution in altitude offers little basis for a faunal division. The changes due to cultivation, it may be assumed, have played an important part in the present distribution. The clearing of lowland forests, for example, has undoubtedly driven species to the coffee belt and to the residual forests, while the clearing of the hills has probably afforded access to the higher altitudes in the case of species originally confined to the more open spaces in the coastal plain.

The coastal-plain fauna, however, is not a homogeneous one. Anolis poncensis and Ameiva wetmorei and possibly Alsophis antillensis are confined to the arid or semiarid southwestern part of the island, and Eleutherodactylus antilleusis, Anolis cuvieri, Typhlops platycephalus and Typhlops rostellatus have not been recorded from that part of the island. Anolis poncensis and Ameira wetmorei are two of the most peculiar and striking species in the entire fauna, the latter being more closely related to species in Hispaniola and St. Croix than to other Porto Rican forms. I propose, then, to divide Porto Rico faunally into a humid district, comprising the greater part of the island, characterized by the presence of Eleutherodactylus antillensis, Anolis cuvieri and Typhlops rostellatus (besides the species of Eleutherodactylus confined to El Yunque); and an arid district, including the southwestern corner, characterized by the presence of Anolis poncensis and Ameira wetmorei. Various cacti form the most characteristic element in the flora of the arid district (Plate I), while the humid district was probably originally a forested area (Plates II and III), bordered by open spaces along the coast.

The contrast in habitat conditions between the arid area to the southwest and the dripping cloud forest of the Luquillo is extreme. The cloud forest affords ideal conditions for the tree frogs, and these are extraordinarily abundant in the moister belt above 1200 feet altitude.

The amphibian chorus in the rain forest on El Yunque is the most extraordinary I have heard. As one stands at the Forester's Cabin, at about 1300 ft. altitude, a roar of sound comes from the wooded ravine adjoining, and from the slopes above, making a veritable Babel of frog notes. One by one the individual voices can be dissociated from the general confusion. Those of *Leptodactylus albilabris* and *Eleutherodactylus portoricensis*, become separated first, since these are already familiar from the first night in Porto Rico. *E. portoricensis* here appears to have added several variations to its lowland notes, but in general its voice proves readily distinguishable. Next to these, the most insistent element in the chorus is a rapid click-clicking not unlike that of a telegraphic instrument, with a very insect-like quality. This proves to be

the note of the tiny Eleutherodactylus gryllus, and it was undoubtedly this note which Stejneger ascribed to the young of E. portoricensis. This clicking note comes also from the lower branches of the trees, probably up to a height of twenty feet. A fourth note, carefully run down, proves to be that of a large, green, long-horned grasshopper, and to the surprise of the collector another succession of sounds, even more characteristically grasshopper-like, beginning with a shrill prolonged note and ending with a series of clicks, proves to issue from the distended throat of still another Eleutherodactylus. Directing the attention, now, as much as possible away from the known elements of the chorus, one may distinguish a strikingly different element. A sad little series of whistles descending in the scale and becoming successively fainter proves to . belong to a very distinct species of small Eleutherodactylus (E. wightmanae), which sits on the ground or on the lower leaves of plants, and is certainly a most difficult species to discern, even when it is singing a foot away from the collector's ear. Another tiny species has a slow clicking note,-the sixth to be distinguished. There is still an undifferentiated chorus awaiting investigation, and three species of tree frogs (E. richmondi, E. unicolor and E. cramptoni) are known from El Yunque, whose notes I did not trace.

In the arid southwestern section there is no such wealth of amphibians and, while this is obviously due to the lack of moisture and hence is primarily an ecological difference, the differentiation of very distinct species confined to this area bears witness to so long a history of similar relations between topography and moisture that here habitat conditions have dominated the faunal history. The fact that this section of Porto Rico appears to be intimately related to the island of St. Croix, figures in my argument below on the relations of the faunae.

ORIGIN AND RELATIONS OF THE PORTO RICAN HERPETOLOGICAL FAUNA

# I. THE WEST INDIAN FAUNA

The origin of the West Indian fauna, specifically of the Greater Antillean fanna, has been a controversial topic among zoogeographers for a generation. Arguing from herpetological evidence, Stejneger (1904) and Barbour (1910, 1914, 1916) have maintained that the fauna is derived from the mainland by migration over land connections, and Anthony (1918) supports the same view from the standpoint of mammalogy. Matthew (1915, 1919) has been the chief exponent of the alternative theory that the Antilles have received their fauna through fortuitous dispersal without such connection. Anthony (1925), in summarizing the evidence from the mammalian fauna in an earlier volume of the present series, adopts a modified form of the "land-connection" hypothesis, and Matthew himself (1919), has agreed that the Greater Antillean islands may at some time have been united. The West Indian amphibians and reptiles appear to me to afford evidence supporting Anthony's conclusions, at least in a general way.

Comparison between the distribution of amphibians and reptiles and the distribution of mammals is made difficult by the much greater age of amphibian and reptile stocks. The arrival of the bulk of the West Indian reptile fauna may be contemporary with that of the earliest of the mammals, the insectivores, whose mammalian contemporaries are extinct. Reptilian distribution frequently affords clues to pre-mammalian faunal history. Thus Madagascar and New Zealand may be allowed to be oceanic islands so far as their mammalian faunae are concerned, while their Pre-Tertiary contacts with continental faunae are reflected in their amphibians and reptiles.

From a general review of the distribution of the reptiles I am convinced that they support the general theses of Matthew regarding the trend of dispersal from Holarctic centers and the want of evidence for Antarctic connections. I am equally convinced that reptilian distribution fails to support some of his secondary theses, especially with regard to the oceanic nature of the faunae of Madagascar and the West Indies. It is embarrassing to be so thoroughly an eclectic zoogeographer, and one finds oneself exposed to the fire of both schools.

My own general conclusions with regard to the West Indian fauna, based primarily on the herpetological evidence, are:

1. That the Greater Antilles received their fauna from Central America at a time so early that the continental fauna has subsequently undergone great changes, probably in Eocene or even in Pre-Tertiary time.

2. That the Greater Antillean fauna gives us a somewhat obscure representation of this earlier Central American fauna, most of which, in accordance with Matthew's general hypothesis, has moved on to South America.

3. That there has been a union of the larger islands during part of their existence, which has produced the uniformities in their faunae.

4. That the Lesser Antillean fauna is derived from South America, that it is a genuinely fortuitous one and that no land-bridge has existed through this chain in Tertiary time.

By way of general review of the Greater Antillean herpetological fauna, I have drawn up a list of the genera in tabular form.

List of Genera	Number of species native on the Greater Antillean Islands					
	Cuba	Jamaica	His- paniola	Porto Rico	Virgin Islands	
Amphibians						
1. Bufo * †	5	0	1	1	1	
2. Hyla *†	1	4	4	0	0	
<ol> <li>Leptodactylus* †</li> <li>Eleutherodactylus * †</li> </ol>	$\begin{array}{c} 0\\ 16\end{array}$	08	$\frac{1}{9}$	$\begin{vmatrix} 1 \\ 10 \end{vmatrix}$	$\frac{1}{2}$	
5. Sminthillus †	1		0	0	õ	
Reptiles						
1. Gonatodes *†	1	1	1	0	0	
2. Sphaerodactylus *†	5	6	5	1	1	
3. Hemidactylus †	1	1	2	1		
4. Aristelliger *	1	$\begin{vmatrix} 1\\0 \end{vmatrix}$	$1 \\ 0$	0		
5. Tarentola 6. Thecadactylus *†	0	0	0	0	1	
7. Anolis *†	$2\check{5}$	6	13	8	6	
8. Norops * †	1	0	0	0	0	
9. $Deiroptyx$		0	0	0		
10. Chamaeleolis			$\begin{array}{c} 0\\ 2\end{array}$			
11. Chamaelinorops           12. Xiphocercus	0	1	$\tilde{0}$	0 0	0	
13. Iguana	ŏ	ò	ŏ	Ŏ	1	
14. <i>Cyclura</i> *†	1	1	3	1	1	
15. Leiocephalus †	5	0	8	0		
16. Hispaniolus	01	$\begin{vmatrix} 0\\ 2 \end{vmatrix}$	$\frac{1}{3}$	0		
17. Celestus*           18. Sauresia	0		1	0 Î	0 0	
19. Wetmorena	Ŏ	Ŏ	ĩ	0	0	
20. Cricosaura	1	0	0	0		
21. $Ameiva^{\dagger}$	1 1	1	$\frac{8}{3}$	$\frac{3}{2}$	$\begin{vmatrix} 2\\ 1 \end{vmatrix}$	
22. Amphisbaena† 23. Cadea	$\frac{1}{2}$		0			
23. Caaea	õ	1	1	1	1	
$25. Typhlops \dagger \dots$	1	1	2	3	1	
26. Tropidophis*†	4	1	$\overline{2}$	0	0	
27. Epicrates†	$\frac{1}{2}$	$\begin{vmatrix} 1\\0 \end{vmatrix}$	$\frac{3}{0}$	$\begin{array}{c} 2\\ 0\end{array}$		
28. Tretanorhinus*	$\frac{2}{3}$		0	0	0	
30. Alsophist	3	ŏ	3	3	2	
31. Dromicus ?†	2	2	5	2	1	
32. Uromacer	0		5	0		
33. Hypsirynchus			1			
34. Ialtris 35. Pseudemys*	1		1		0	
36. Crocodylus*†	$\hat{2}$	1	1	0	0	
Total species	91	40	92	41	23	
Total genera Endemic genera	$\frac{29}{5}$	18	29 7	16 0	15 0	
Non - endemic genera not		-				
found in other islands	5	0	0	0	2	

\* Central American.

The number of species in this table is somewhat unsatisfactory for comparison on account of the inclusion of vicarious forms from outlying islands—the Cayman Islands with Cuba; Tortuga, Gonaives, Navassa and Beata with Hispaniola, and Mona with Porto Rico.

The Amphibians and Reptiles of the Greater Antilles represent 41 genera. Two of these, *Iguana* and *Thecadactylus* enter the region only in the Virgin Islands, and are present in the Lesser Antilles. They are consequently an alien element in the fauna, the more so as they are not specifically differentiated; it is extremely likely that *Iguana* was introduced by the Indians in the course of their wanderings, while the gecko is probably fortuitous through non-human agencies. A third genus, *Tarentola*, is represented only in Cuba and is otherwise African, specifically Mediterranean, in distribution. This still more alien form is well differentiated from its congeners and represents one of the most curious of genuinely discontinuous distributions. I suppose it to be an ancient "flotsam-jetsam" arrival.

Of the remaining 37 genera, 14 are endemic; 11 are generally distributed on the four larger islands, and 20 are represented on three or more of the islands. It is a curious fact that the endemic genera, with the exception of Cyclura, are confined to single islands, and thus do not contribute to the hypothesis of a former union. The 20 more widely distributed genera, however, all have vicariating forms from island to island, and a number of sections of genera, such as the giant Anoles. come near to being widely distributed endemic genera, like Cyclura. The endemic forms are chiefly minor end-stages or divergent branches which have arisen by local evolution, such as Chamaeleolis, Deiroptyx. Chamaelinorops, Xiphocercus, Hispaniolus, Sauresia, Wetmorena and Arrhyton. A few, however, are plainly relict forms, notably the Xantusid Cricosaura, the Iguanid Cyclura, the Hispaniolan snakes Uromacer and Ialtris, the Brachycephalid frog Sminthillus. Five genera, Leptodactylus, Sminthillus, Norops, Leiocephalus and Tretanorhinus, are neither endemic nor widely distributed, and this is a very heterogenous list, with no appreciable parallelism in distribution.

Eighteen genera occur both in the Greater Antilles and Central America, but 14 of these are likewise represented in South America, and these, with the 7 genera common to South America and the larger West Indian islands but absent in Central America, make the faunal relation with South America appreciably more intimate than with Central America. This very fact seems to me to accord best with the theory of the Central American origin of the fauna, on the supposition that the South American fauna is mainly of northern origin, as pointed out by Matthew in his general scheme of dispersal.

The degree of differentiation between the continental and West Indian representatives varies greatly, and at first glance appears to indicate varying ages of origin. Some of this variation, however, may be due to other factors than time of separation. Such an archaic-looking relict as *Cricosaura*, widely distinct from its continental allies, may perhaps represent about the same amount of evolution as has occurred in *Anolis* and its derived genera, the difference being the contrast between a declining group and an expanding one. The crocodiles, on the other hand, seem to belong to quite different invasions, *C. rhombifer* and *moreletii* being assignable to an earlier arrival, their ranges now entirely circumscribed by that of the modern wide-ranging, semi-marine *Crocodylus acutus*, whose wide distribution evidently has little bearing on the problem of land connections.

In a more detailed discussion of the genera I shall try to show that the faunal picture presented accords with a derivation from Central America at an early date, on the hypothesis of a southward trend in the migrations of the world as a whole, and that it is direct faunal relations with Central America, such as that of the Xantusiidae, which require explanation rather than the discontinuity in range of *Amphisbaena* or *Leiocephalus*.

Of the genera of Amphibians, Bufo, Hyla, Eleutherodactylus and Leptodactylus have a wide Neotropical distribution. The anomalous nature of the distribution of Leptodactylus will be discussed below. Sminthillus has a single Cuban species, and two others, Peruvian and Brazilian, have since been described. The discovery of additional species in this genus (originally described as monotypic) contributes to the likelihood that it is a natural group.

Among the reptiles, geckos are notable for erratic distributions, though when critically examined their ranges are often found to be closely parallel to those of other groups. The Antillean geckos, however, are really heterogeneous in distribution. *Tarentola* and *Thecadactylus* have already been mentioned. *Gonatodes* is widely distributed in Central and South America, apparently ranging into the Antilles from the west. *Sphaerodactylus* has a wide neotropical distribution, but its wealth of Antillean species distinguishes it as an autochthonous genus, and its development is very like the other characteristically West Indian forms, such as *Ameira*, *Dromicus* or *Eleutherodactylus*. *Hemidactylus*, with *H*. *mabouia* on all the islands, appcars to be a house-gecko, and human agency may well have played a part in its distribution. It is somewhat remarkable that the genus *Hemidactylus* is unknown in Central America. I am not at all convinced that the African geckos commonly referred to *mabouia* are con-specific with the Antillean form. The East African and Madagascan species does not seem to me to be identical even with the West African one! *Hemidactylus brookii*, on the other hand, in Hispaniola, would appear to be an African form introduced by the slave-trade. *Aristelliger* is confined to Central America, Jamaica and Hispaniola. It is included in my list as Cuban because it reaches the Cayman Islands, whose faunal affinity is primarily Cuban. On the eoast of Yucatan this species is characteristic of the fringe of cays, and its · occurrence in the West Indies offers no anomaly.

The Ignanid genera include the monotypic and endemic Deiroptyx, Chamaeleolis, Chamaelinorops and Xiphocercus, Iquana, already mentioned, and Anolis, Norops, Cyclura, Leiocephalus and Hispaniolus. Norops seems to be a more primitive form than Anolis, with three continental species, and is a declining group in contrast with the expanding Anolis. The Cuban species is thus plainly a relict. Leiocephalus, with a number of species in Cuba and Hispaniola, is otherwise best developed in western South America, and is absent in Central America. I regard this also as a relict distribution, but of a group that is holding its own. Cyclura is even more interesting. The curious "combs" on its toes, though rather a trivial character, quite definitely ally its species more elosely to the Galapagan Conolophus and Amblyrhynchus (and the other Pacific genus as well, the Fijian Brachylophus) than to the Central American Ctenosaura. Ctenosaura extends southward as a wedge separating these allied forms, and I have endeavored elsewhere\* to show that the Ctenosaura have spread southward from the great Southwestern shield in North America. Leiocephalus lends itself to this interpretation if it be visualized as retreating before more advanced Iguanid genera, such as Sceloporus. Anolis, in the full flower of expansion, obscures distributional argument by its wealth of forms and closely-knit ranges. The only species of *Anolis* that is supposed to be common to Central America and Cuba is A sagrei, an inhabitant, like Aristelliger, of the off-shore eavs in the Bay of Honduras. The endemic genera require no comment except that *Xiphocercus* is represented in Colombia by a related or parallel form.

The Anguidae are represented in all four islands by *Celestus*. Two additional genera. *Sauresia* and *Wetmorena*, monotypic "end-stage"

<sup>\* 1922.</sup> Bull. Amer. Mus. Nat. Hist., XLVI, p. 611.

forms, are confined to Hispaniola. *Celestus* also occurs in Central America and its close ally, *Diploglossus*, is found in both Central and South America. *Celestus* and *Diploglossus* are plainly primitive genera, and the modern representatives of the family, the plated lizards (*Gerrhonotus*), have the same spatial relations with them as exist between *Ctenosaura* and *Cyclura*, or *Sceloporus* and *Leiocephalus*.

The Xantusiidae are a declining group composed of the North American genus Xantusia, the Central American Lepidophyma and the Cuban This distribution is not in accord with the above-cited Cricosaura. southward migrations, but this is a recurrent anomaly which requires a modification of the Matthewsian hypothesis of the dispersal of primitive forms. It must be recognized that evolution in the direction of habitat restriction may strictly parallel an evolution in which the primitive forms become peripheral by retreat in space. This is an obvious phenomenon among the Xantusids, which inhabit areas adjacent to what I have regarded as the probable center of dispersal of American lizards, but are plainly relicts among more modern and progressive forms. The species of Xantusia are curiously restricted as to habitat-X. vigilis by its association with the Yucca, X. henshawi by its rock-dwelling habitwhile both are doubtless nocturnal, as is Lepidophyma. The mainland Nantusids have retreated owing to habitat restriction, while the Cuban genus represents the other alternative, that of actual retreat, and appears as a true relict, though also rigidly confined to a single habitat. The case is directly comparable to that of the Central African lemurs. which escape their modern competitors by their nocturnal habits, while the Madagascan lemurs have survived through actual migration and the timely separation of their retreat.

The Teiidae are represented only by *Ameira*, though the West Indian species are divisible into two rather distinct sections. Ameivas are widely distributed on the South and Central American mainland, but the continental species are fewer than the West Indian. I suspect that the genus *Cnemidophorus* bears the same relation to *Ameira* as *Sceloporus* does to *Leiocephalus*, namely, that it is a more modern group of species, with *Ameira* more or less in retreat.

The Amphisbaenidae are well represented in the Antilles, with both *Cadea* and *Amphisbaena* in Cuba and *Amphisbaena* extending out to the Virgin Islands. Except for *Bipes*, which is present in west Mexico, the family is wanting in Central America, and the Antillean forms are thus relicts of a former type of dispersal. The evidence for the southward migration of the Amphisbaenians seems to me ample, even

without the direct evidence of the Oligocene fossil forms. *Rhineura*, confined to Florida, is quite obviously one of the many curious forms accumulated in the southeastern United States as a result of divergent migration from holarctic dispersal centers. The nearest relative of *Cadea* seems to be Venezuelan, while *Amphisbaena* itself is well represented almost throughout South America.

The only Scincoid genus is *Mabnya*, generally distributed in the tropics of the world, but nowhere speciating in the Americas as its does in the Old World. Its range in both hemispheres is nearly exclusive of that of the more northern and obviously more recent *Eumeces*.

Among snakes the Typhlopidae afford no especial evidence of faunal relation. The Antillean *Typhlops lumbricalis* was long supposed to be a widespread species occurring also in South America. Cochran (1924) and I (1920) have brought the distribution of the West Indian forms into harmony with that of other groups. The most notably primitive genus, *Anomalepis*, is Central and South American (or at least Panamanian and Peruvian), and *not* Antillean.

The Boidae are represented by two genera. *Epicrates* has a species on each of the larger islands and has split into three species in Hispaniola, with a separate species on Mona Island and another distinct form in the Bahamas (confined to Turk's Islands). *Tropidophis* fails to reach Porto Rico, and its principal radiation occurs in Cuba. *Epicrates* is wanting in northern Central America, but it reappears in South America. *Tropidophis* is said to have both South and Central American allies, but they are little known.

The relationship of the Colubrine genera are vague, but their nearest allies seem to be South American, with the exception of *Tretnorhinus*, which is found in Cuba and Central America.

*Pseudemys*, the single genus of fresh-water turtles, is quite as easily derivable from the Central American representatives as from the Floridian, and the existence of insular differentiation, which I am able to show for the Porto Rican specimens, makes it unnecessary to regard *Pseudemys* as a strictly recent arrival. The absence of other fresh-water turtles is highly remarkable, in view of the ancient character and great diversity of the American turtle fauna. It is no less anomalous to find in Cuba a fossil *Testudo* related to the Galapagan species, though its presence adds to the faunal relations between the Antilles and the Galapagos.

Crocodylus, finally, adds a distinctively Central American form to the West Indian fauna. The broad-snouted Cuban Crocodylus rhombifer is directly allied to C. moreletii of the adjacent parts of Mexico and the Yucatan peninsula. The wide-ranging, undifferentiated C. acutus floods over the ranges of these earlier forms. Crocodiles do not range beyond the Orinoco basin in South America, and evidently are more recent arrivals than the caimans or the alligators.

In support of my proposition (2) above, I have contrasted the distribution of such a group as *Sceloporus*, an essentially modern genus, with that of a more ancient Iguanid genus, *Leiocephalus*. *Sceloporus* is essentially Sonoran, with a wealth of North American species, and a broad overflow into Central America. *Leiocephalus* is West Indian and South American. Allowing for discrepancies and irregularities such as those I have discussed for the Xantusiidæ, the list of such pairs of genera is impressive:

Ancient, West Indian	Modern, Sonoran
Leiocephalus	Sceloporus
Cyclura	Ctenosaura
Celestus	Gerrhonotus
Ameira	Cnemidophorus
Mabuya	Eumeces

*Cnemidophorus*, among the genera listed as Sonoran, ranges widely into Sonth America. Otherwise its development is so closely similar to that of the other Sonoran genera that I am disposed to search for an explanation of this anomaly rather than remove it from the Modern, Sonoran list.

I am fully convinced that the fauna of the Greater Antilles reached these islands from Central America, and that the majority of the endemic forms represent a nearly contemporary faunal invasion. That an actual landbridge existed over which the migration took place, is my somewhat more hesitant belief. The existence of mammals and amphibians, even as a depanperate fauna, is evidence in favor of continental connection. The amphibian and reptile fauna exhibits a relatively greater diversity than does the mammalian. The sixteen families represented are:

# Amphibians

Bufonidae Hylidae		Brachycephalidae
	Reptiles	
Gekkonidae	Amphisbaenidae	Boigidae
lguanidae	Scineidae	Emydidae
Anguidae	Typhlopidae	Crocodilidae
Nantusiidae	Boidae	
Teiidae	Colubridae	

The Central American fauna has thirty-two families, but several of these are isolated groups which could scarcely be expected in the West Indies,—the Helodermatidæ and Xenosauridæ, for example. Others are obviously more recent arrivals and for this reason their presence is not to be expected; instances in point are the Ranidae, Plethodontidae and Crotalidae. The disproportion between the continental and Antillean faunæ in number of families is accordingly much reduced, perhaps about 26:16. It is a striking and important fact that the South American fauna is actually poorer in families of amphibians and reptiles than the Central American by four or five. If the Chelydridæ, Crocodilidæ and Plethodontidæ, which are essentially Central American and only enter South America at the northwest, are also excluded, the genuinely South American families number only twenty-five.

If the date of the supposed continental connection of the West-Indies be placed at the close of the Mesozoic, the relative wealth of amphibians and reptiles and the poverty in mammals are completely explained. Unfortunately, a connection so early in geological history does not account for the more recent members of the mammalian fauna, for which a Miocene date of arrival is indicated. The two families of insectivores agree with the reptiles as to early date of entry, while the remaining mammals appear to represent at least two later immigrations. One is tempted to suppose a very early continental connection for amphibians and reptiles, insectivores, etc., and to recognize Matthew's argument that the remaining mammals are accidental. Geological conclusions based on zoogeographic evidence so fragmentary and contradictory are evidently of little real value.

One set of conclusions, however, from a general consideration of the fauna, seems well founded. This is my proposition (3), that the larger islands were connected at an early stage in the development of their fauna: that they have subsequently been separated, more probably by block-faulting than by any great change of level, that Porto Rico and the Virgin Islands were the last to be cut off, and that the Virgin Islands were connected with Porto Rico as recently as the Pleistocene.

The evidence of long isolation of the three western islands is plainly to be seen in the independent radiation which has taken place in the elements of their fauna. Bufo has evolved 5 species in Cuba, while Jamaica with no native toad, and Hispaniola with a single Bufo, have each produced 4 species of Hyla, independently, in the opinion of Dunn, who has lately examined the Jamaican species in detail. Dunn's conclusions are somewhat hesitatingly accepted by Noble (1927). Whether or not the radiation in Hyla has been independent, the fact that both Jamaica and Cuba have only a single species of *Ameira* while Hispaniola has 8, and 4 on the main island alone, certainly illustrates an independent evolution. Long separation is equally evident in the wealth of Cuban *Anolis* with no less than 3 related genera represented, *Norops, Chamæleolis* and *Deiroptyx*, equalling the number of species on the other three islands together. The Jamaican fauna, poor in some genera, has no less than 6 well-established species of *Sphærodactylus*, surely a sharp contrast with the 2 in all Central America !

Among the snake genera, *Tropidophis* has developed 4 species in Cuba, while *Epicrates* has 3 in Hispaniola, and an extra species on Mona. The Hispaniolan *Dromicus*, *Alsophis* and *Uromacer* fall in line with the other genera. The total impression of the herpetological fauna is plainly one of a fundamental unity, obscured only by the long evolution during subsequent isolation.

The fauna of the Lesser Antilles has been effectively contrasted by Anthony with that of the larger islands. His argument from the mammals that the animal population of the Lesser Antilles is fortuitous from South America and of relatively recent origin agrees exactly with my impression based upon the herpetological fauna. The fauna of Trinidad itself is far from rich in comparison with that of the mainland. Its reptiles and amphibians amount to about 80 species-almost all of them specifically identical with those of northern South America. This South American fauna disappears rather in proportion to distance from the mainland than in relation to size of landmass, for Tobago has 24 species with little endemism, Grenada 17 with about 4 endemic forms, St. Vincent 10 with 6 endemic. In the next four islands the fauna ranges only from 10 to 14 species, with 5 to 10 endemic forms. Endemic forms in the whole chain are very slightly differentiated from their very obvious relatives. The species may be grouped as mainland forms, with a haphazard distribution on the islands, endemic species of mainland genera, slightly differentiated, and endemic species of genera which range throughout the chain with vicariating forms from island to island. There is little or no "radiation," which is so marked a characteristic of the Greater Antilles. Examples of the haphazard distribution are afforded by Leptodactylus and Iguana, probably transported by the Indians as food animals, and by the snakes in general, though the faunæ in question may be imperfectly known, Leptotyphlops bilineatus, for example, occurring on Barbados and St. Lucia, Cloelia clelia on Grenada, St. Lucia and Dominica, although not recorded from the intervening

islands, St. Vincent and Martinique. The fer-de-lance skips Tobago, Grenada and St. Vincent, to appear only on St. Lucia and Martinique.

The northern group of twelve small islands, from Anguilla to Montserrat, has a fauna impoverished in genera, but rich in endemic species. Leptodactulus pentadactulus and Iguana iguana appear to represent Pre-Columbian introduction by natives. Eleutherodactylus martinicensis is recorded from five islands. Its status requires re-investigation. Tuphlops is known from St. Kitts and Antigua, the species doubtless undescribed. Leptotyphlops albifrons is reported only from Antigua. Its wide range and apparently haphazard arrangement seems to indicate a facility for fortuitous dispersal. Thecadactylus rapicaudus, widespread in the Lesser Antilles, is recorded from five of the northern islands. These irregular distributions contrast strongly with 3 endemic species of Sphaerodactylus on three islands, 7 Anolis on nine islands, and 8 Ameiva on ten islands. This portion of the fauna, which perhaps should include Alsophis, appears to represent an older nucleus, and I interpret its relations as representative of the uniformity of a typically oceanic fauna plus endemism induced by a considerable lapse of time.

The most obvious differences theoretically to be expected between continental and oceanic insular faunæ are (1) heterogeneity and (2) impoverishment in the oceanic islands. The presence of relict forms seems to me to be strong evidence of a land connection remote in time. Impoverishment may obviously occur in a continental fauna by extinction; and "fortuitous dispersal" may act as a screen allowing only certain forms to pass, so that extreme uniformity of fauna, instead of heterogeneity, may be a result of truly oceanic dispersal, as is to be seen in Polynesia, where island after island is inhabited by the same five species of lizards. Such uniformity is complicated by the age of the islands. It is thus curiously difficult to frame criteria whereby an insular fauna derived from land connection may be distinguished from one produced by "fortuitous dispersal."

# II, THE PORTO RICAN AND VIRGIN ISLAND FAUNA

Turning to the more detailed consideration of the Porto Rican fauna, it is interesting to note that important advances have been made in our knowledge of the amphibians and reptiles of this area since Stejneger's discussion of their origin and relations in 1904. The herpetological discoveries bearing directly on this problem have been (1) the description of *Ameiva wetmorei*, (2) the finding of *Bufo* and *Cyclura* on the outer Virgin Islands, (3) the discovery of fossil remains of *Cyclura* on St. Thomas and Porto Rico, (4) additions to the fauna of Hispaniola, especially the discovery of *Leptodactylus dominicensis*, (5) additions to the fauna of Porto Rico, especially *Alsophis antilleusis* and *Eleutherodactylus antilleusis*, which ally it more intimately to the fauna of the Virgin Islands, and (6) the elucidation of the relations of the Greater Antillean *Typhlops*. All of this new information has tended to emphasize the essentially Greater Antillean character of the Porto Rican fauna.

Stejneger divides the Porto Rican herpetological fauna into South American and Central American elements, including in the former the genera Ameira, Amphisbaena, Typhlops, Alsophis and Dromicus. These genera are all represented in Hispaniola, and their immediate presence in Porto Rico is amply accounted for by a union with Hispaniola. I have endeavored to show above that this apparent relation of the West Indian fauna with the South American is best explained by a land connection with Central America, when the time relations and larger outlines of faunal migration are considered.

Vaughan (1919, Bull, U. S. Nation, Mus., No. 103, pp. 547-612) has given an excellent résumé of the geological history of the West Indian area as far as known. In advocating the existence of former land connections with South and Central America, his paper cuts incisively into the more speculative maze of zoogeographic controversy. The only flaw is the fact that he appears to base his conclusions in part on zoogeographical data (p. 610), whereas I should like to accept them as a basis for zoogeography. For the present purpose however,—an examination of the immediate origin of the Porto Rican reptile and amphibian fauna,—the outline of the geologic history advanced by Vaughan is highly satisfactory, and it is possible to crystalize conclusions on the relations between Porto Rico and the Virgin Islands with each other and with Hispaniola into a more definite statement than has hitherto been possible.

According to Vaughan's physiographic history of the area in question, the Greater Antilles were joined to one another in late Miocene time, the resulting landmass including Porto Rico and the Virgin Islands as its easternmost extension. The scanty zoogeographic ties between the Virgin Islands and the Lesser Antilles exclude the presence of a contemporaneous land bridge to South America, or at least the continuation of any such bridge for a time commensurable with that of the union of the Greater Antilles. During the period of this uplift, the genera of reptiles and amphibians which may properly be regarded as "Greater Antillean" (through presence on three or more of the larger islands) acquired their distribution,

In order to connect the Virgin Islands with Porto Rico, no great degree of emergence is necessary, as they are separated by water not exceeding twenty fathoms in depth. St. Croix is included in the same way. with no greater amount of emergence, because its present separation by greater depths of water is believed to be due to faulting. The water between Porto Rico and Santo Domingo is much deeper (reaching 318 fathoms), but still shallow in comparison with the depths to the north and south. Even for this connection, however, the amount of emergence necessary is no greater, for there is important evidence of faulting, as I have shown elsewhere (1926). The earthquakes of October, 1918. which caused great damage to the cities of Mayagüez and Aguadilla, on the west coast of Porto Rico, were probably caused by adjustments in this faulted area. The sharp truncation of the eastern end of Santo Domingo doubtless represents another fault line. Point Jiguero and Desecheo Island appear to represent the older period of mountain-making of the general Hispaniolan-Porto Rican axis, (i. e., an Eocene or Lower Oligocene connection) while Mona Island, almost exactly half way between the southwest corner of Porto Rico and Saona Island, and topographically almost exactly similar to Saona, may be a remnant of the Upper Miocene (or later?) land bridge itself. The rapid undercutting of the north and east sides of Mona now in progress indicates a considerable recent reduction of its area. The date of the faulting which separated Porto Rico from Santo Domingo is placed in the Pliocene by Vaughan (p. 611)), and the separation of St. Croix from Porto Rico probably took place during the same period, but perhaps at a later date. It is likely that Porto Rico and the remaining Virgin Islands were separated by a submergence in the Pliocene, but they were reunited in the Pleistocene, perhaps by the withdrawal of the water for the continental ice sheets, to form a "Greater Porto Rico" to which the common fauna of the islands now separated corresponds. The present configuration of Porto Rico and the Virgin Islands is (geologically) extremely The very evident peneplanation of the greater part of the recent. mountain area at a height between 1500 and 2000 feet appears to date at least from the early Tertiary, and implies long-continued existence as a land area.

The interpretation of the existing faunal relations of Porto Rico, in the light of the geological hypothesis, becomes relatively simple. The fauna of the Virgin Islands stands in the same relation to the Porto Rican as does that of Porto Rico to the Hispaniolan. The degree of difference in each case corresponds to the relative length of time since their respective separations, and the degree of impoverishment to their relative areas.

The fauna of the Virgin Islands consists of 22 species, of which 2, *Iguana iguana rhinolopha* and *Thecadactylus rapicaudus*, belong to genera foreign to Porto Rico. The iguana was probably introduced by man; the gecko probably is a fortuitous arrival. Of the remaining 20 species, 11 are identical with Porto Rican forms:

- 1. Leptodactylus albilabris
- 2. Eleutherodactylus antillensis
- 3. Sphaerodactylus macrolepis
- 4. Hemidactylus mabouia
- 5. Anolis cuvieri
- 6. Anolis cristatellus

- 7. Anolis stratulus
- 8. Anolis pulchellus
- 9. Ameiva exsul
- 10. Mabuya sloanii
- 11. Alsophis antillensis

The remaining 9 species are directly related to Porto Rican species and are for the most part simply vicariating forms:

Virgin Islands	Porto Rico
1. Bufo turpis	Bufo lemur
2. Eleutherodactylus lentus	Eleutherodactylus richmondi
3. Anolis acutus	Anolis poncensis (?)
4. Cyclura pinguis	<i>†Cyclura portoricensis</i> (?)
5. Ameiva polops	Ameiva wetmorei
6. Amphisbaena fenestrata	Amphisbaena caeca
7. Typhlops richardii	• Typhlops platycephalus
8. Dromicus exiguus	Dromicus stahli
9. Alsophis sancti-crucis	Alsophis portoricensis

Examined more in detail the chief questions which require discussion are: (1) the impoverishment of the Virgin Island fauna, in which many species of Porto Rican *Eleutherodactylus* and *Anolis* are unrepresented, while *Celestus, Epicrates* and *Pseudemys* are entirely wanting; (2) the apparently haphazard distribution of *Bufo, Anolis cuvieri* and *Cyclura;* (3) the position of St. Croix in relation to the other islands and Porto Rico, and (4) the origin of the species common to several of the Virgin Islands but absent in Porto Rico.

The absence of forms may be explained as original or secondary. The discovery of the remains of recently extinct Cyclura in both Porto Rico and St. Thomas, coupled with the presence of living Cyclura on Mona and Anegada, obviously indicates that in this genus a process of extinction is taking place. The same factor probably accounts for the isolated

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occurrence of a *Bufo* on Virgin Gorda and of *Anolis cuvieri* on Tortola. The absence of *Celestus* and of *Anolis gundlachi* and *Anolis krugi*, may indicate, on the other hand, that these forms never reached the Virgin Islands. There is no reason to believe that, if the whole land area were elevated 150 or 200 feet and so reunited, the species which now avoid the coastal plain in Porto Rico would be able to reach the Virgin Islands. The fact that of the entire Virgin Island fauna only *Eleutherodactylus lentus* is related to "coffee belt" species in Porto Rico indicates that this factor has probably operated as an important one in the past.

The mere fluctuation in size of these islands has an important influence on the rain fall and humidity (and evaporation), i. e., the most important climatic factors affecting the fauna. The complete submergence of an islet would not be necessary to exterminate the greater part of its fauna, and it is a differential extermination of this nature which I believe to be the chief cause of the impoverishment of the Virgin Island fauna, and possibly of the West Indian fauna in general.

St. Croix presents something of a problem. The Amphisbaena fenestrata from that island should be compared again with specimens from St. Thomas, and with A. caeca. Anolis acutus, Ameiva polops and Alsophis sancti-crucis are decidedly less closely allied to Porto Rican species than are the species from St. Thomas and even the outermost of the northern Virgin Islands. On the other hand, Ameiva polops indicates a relationship with the arid district of Porto Rico. If the "Greater Porto Rico" at any time included St. Croix, that area must have belonged to the extended arid district, which influenced distribution in the "Greater Porto Rico" exactly as it does in the present. The separation of St. Croix in Pliocene time by faulting (as suggested by Vaughan) doubtless excluded it from union with Porto Rico in the Pleistocene, while a Pleistocene (Glacial period) connection of the other Virgin Islands with Porto Rico seems highly probable.

Three species—*Eleutherodactylus lentus, Amphisbaena fenestrata* and *Dromicus exiguus*—are common to two or more of the Virgin Islands and are absent from Porto Rico. Their development may be explained as due to a differentiation of the fauna of the lower-lying eastern end of the "Greater Porto Rico," or to differentiation during the hypothetical Pliocene separation.

The Porto Rican herpetological fauna differs from that of Hispaniola chiefly in the absence of the following genera.\*

<sup>\*</sup> Ocdipus is excluded from the Hispaniolan fauna pending verification of its occurrence. Dunn regards the Haitian origin of Peter's Ocdipus infuscatus as mythical.

- Hyla
   Gonatodes
   Aristelliger
   Leiocephalus
   Hispaniolus
   Chamaelinorops
- 7. Wetmorena

- 8. Sauresia
- 9. Tropidophis
- 10. Uromacer
- 11. Hypsirhynchus
- 12. Ialtris
- 13. Crocodylus

Seven of these, Chamaelinorops, Hispaniolus, Wetmorena, Sauresia, Uromacer, Hypsirhynchus and Ialtris are confined to Hispaniola, while the other six are found in Cuba and Jamaica and for the most part in Central America. An extensive impoverishment of the fanna of Porto Rico is obviously its most conspicuous characteristic. Recent extinction may well be admitted as a considerable factor in this impoverishment, in view of the discovery of the remains of an extinct Porto Rican Gyclura as well as by analogy with the extinction of the mammalian fauna. This may be due to two factors, the restriction of habitat formations due to increased cultivation, and the changes in climate due to past emergence and submergence. On the other hand, the much greater altitudes of the mountains of Hispaniola, and the great diversity of habitat conditions of that island, of which perhaps the most remarkable is the stratification of the vegetation on the mountains, makes it highly probable that a number of forms have developed in situ, and had not acquired a sufficient range before the separation of Porto Rico to reach it, even if the habitat conditions of the intervening area were not unfavorable. If the late Miocene uplift was not extensive, and if Mona Island is a remnant of the actual land connection via Saona and southwest Porto Rico, the habitat conditions of the land-bridge must have been such as to prevent the spread of many forms. It is more difficult to explain the differences in the development of such genera as Sphaerodactylus, Celestus, Ameiva and Epicrates, which have several species on Hispaniola and only one on Porto Rico.

It is possible that Hispaniola was broken up into several islands during the Miocene, as is indicated by the Miocene deposits which compose the plain between the Central Sierra and the Monte Cristi Range, and by the "through valley" of the saline lakes to the southwest.

Only two species are common to Porto Rico and Hispaniola, one of which, *Hemidactylus mabouia*, is a house-gecko and plainly fortuitous, while the other, *Mabuya sloanii*, requires critical study. I have seen no Hispaniolan specimens. The number of species which are closely related on the two islands is large:

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# SCHMIDT, AMPHIBIANS OF PORTO RICO

#### Hispaniola Porto Rico Bufo gutturosus 1. Bufo lemur Leptodactylus dominicensis 2. Leptodactylus albilabris 3. Eleutherodactylus portoricensis Eleutherodactylus auriculatoides 4. Eleutherodactulus richmondi Eleutherodactylus weinlandi Sphaerodactylus difficilis 5. Sphaerodactylus macrolepis 6. Anolis cuvieri Anolis ricordii 7. Anolis cristatellus Anolis cybotes Anolis semilineatus 8. Anolis pulchellus 9. *†Cyclura portoricensis* Cuclura cornuta 10. Celestus pleii Celestus sp. 11. Ameira ersul Ameiva vittipunctata 12. Ameira metmorei Ameira lineolata Amphisbaena weinlandi 13. Amphisbaena caeca 14. Typhlops platycephalus Typhlops sp. 15. Epicrates inornatus Epicrates striatus 16. Dromicus stahli Dromicus parvifrons 17. Alsophis portoricensis Alsophis melanichnus 18. Pseudemys stejnegeri Pseudemys palustris

The Mona Island species, especially *Cyclura stejnegeri* and *Epicrates* monensis, add important links to this relation.

The remaining Porto Rican species, mostly *Eleutherodactylus* and *Anolis*, which are clearly more closely related to other forms in the Greater Antilles than to South American or Lesser Antillean species, may be regarded as the individual development of the Greater Antillean fauna on Porto Rico, whose mountains occupied a relatively isolated position during any land connections that may have existed, certainly since the early Tertiary.

The general conclusion is that the herpetological fauna of the "Greater Porto Rico" is simply an impoverished Greater Antillean fauna. Its resemblances to the fauna of Hispaniola are due to land connection, the date of which is placed by geologists in the Upper Miocene. The differences between the Porto Rican and Hispaniolan faunas are due: (1) to a process of extinction still continuing: (2) to the isolated position of Porto Rico at the eastern end of the land mass, the babitat conditions of the supposed land-bridge being unsuited to the spread of many forms; (3) to the differentiation of specifically Porto Rico being a center of differentiation for autochthonous forms, as I suppose those of Hispaniola to have been, and (b) during post-Phiocene time, since the separation of Porto Rico from Hispaniola.

# Order TESTUDINATA

## Emydidae

## Pseudemys Gray

Each of the islands of the Greater Antilles is inhabited by a species of fresh-water turtle belonging to the genus *Pseudemys*. This genus has a large development in Eastern North America and in Central America.

## Pseudemys stejnegeri, sp. nov.

## Text Figs. 51 and 52

Emys rugosa Stahl, 1882, Fauna Puerto-Rico, p. 68.—Garman, 1887, Proc. Amer, Philos, Soc., Vol. XXIV, p. 286.

Clemmys decussata Peters, 1876, Monatsber. Akad. Wiss. Berlin, p. 705.— Gundlach, 1881, Anales Soc. Españ. Hist. Nat., Vol. X, p. 307.

Pscudcmys palustris Stejneger, 1904, Rept. U. S. Nation. Mus., 1902, p. 710, Figs. 179-186.

Type locality.—San Juan, Porto Rico.

Distribution.—Recorded only from Caguas, San Juan. Desengaño (Cartagena Lagoon) and Guanica Lake.

*Diagnosis.*—A *Pseudemys* closely allied to the *Pseudemys palustris* of Jamaica and Hispaniola, from which it is distinguished by smaller size and by having the axillary and fifth marginal shields usually not in contact.

*Type.*—U. S. N. M. No. 25642, San Juan, Porto Rico. Adult female collected by the U. S. Fish Commission "Fish Hawk" Expedition.

Description of type.—<sup>1</sup> "Shell moderately convex, the height being more than one-half the greatest width; length of carapace less than two and a half times the height of the shell and about one and one-third times its greatest width; carapace faintly keeled and with longitudinal wrinkles crossed by radiating ridges, which are especially strong on the anterior costals; nuchal narrow; first vertebral shield urceolate, anterior and posterior sutures of same length; lateral sutures of second, third, and fourth vertebrals much longer than the anterior and posterior sutures; vertebrals much narrower than costals; posterior margin of carapace slightly serrate, each of four posterior marginals on each side being faintly emarginate; carapace broader behind than in front, the posterior marginals flaring out considerably; plastron less than twothirds and more than one-half the greatest width of the carapace; the posterior lobe a trifle wider than the anterior, its length much less than

<sup>&</sup>lt;sup>1</sup> Quoted from Stejneger, 1904, p. 711.

the width of the bridge; abdominal suture longest, equaling those of the pectorals and femorals together; humeral suture shortest; gulars projecting, cut off square anteriorly; plastron slightly emarginate behind; axillars and inguinals large, latter largest; head moderate; snout short, pointed, feebly projecting; upper jaw with a very slight median notch, no cusps; jaws feebly denticulated; alveolar surface broad, with a deep notch behind on the median line; symphysis of mandible as broad as one-half the longest diameter of the orbit; digits connected with broad webs. Color (in alcohol) of carapace above nearly uniform tawny olive; plastron yellowish, with obscure dusky symmetrical sinuous markings all over; top of head without markings; yellowish lines narrowly

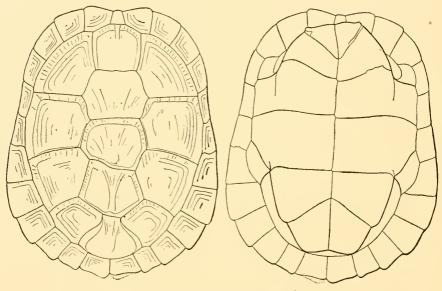


FIG. 51.—Carapace and plastron of *Pscudemys stejnegeri*. (From Stejneger.) One-half natural size.

edged with blackish on sides and under surface of head and neck, one from the nostrils crossing the upper jaw obliquely and ending abruptly at the posterior angle of the mandible, another from above the nostrils, crossing the eye of the lower posterior edge of the orbit, and thence obliquely down and backward to the corner of the mouth, continuing backward under the tympanum down the side of the neck; two fainter lines, one between the two just described and one above the transocular line, crossing the tympanum; a line on the symphysis of the mandible bifurcating on the chin and a third median line originating on the chin a short distance behind the fork, the three continuing parallel down the under side of the neck; two similar but wider lines on the upper side of the fore legs and two on the under side of the hind legs."

# DIMENSIONS

	mm,
Length of carapace	232
Width of carapace anteriorly	150
Width of carapace posteriorly	170
Height of shell	95
Width of anterior plastral lobe	90
Width of posterior plastral lobe	-93,
Width of bridge	$\mathbf{SS}$
Width of head	

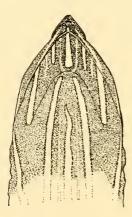
It must be added that the relation between the axillary and fifth marginal shields in this specimen is the normal one, i. e., that they are widely separated by a suture of the fourth marginal with the pectoral, as is illustrated in Stejneger's figure of another specimen, reproduced here (Fig. 51).

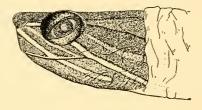
Remarks.—Stejneger makes the comment with reference to this turtle that "There are indications at hand that there may be some constant differences between those inhabiting the different islands, but the material at my disposal is not sufficient to warrant an attempt to separate them." I have seen nineteen Porto Rican specimens and thirteen Hispaniolan, but I have nevertheless hesitated at separating the Porto Rican specimens as a distinct species. I feel that there are now certain indications at hand that there are two forms of this turtle in Hispaniola, which lack of material prevents me from distinguishing; and this uncertainty as to the Hispaniolan forms does not clarify the relations of the Porto Rican species. The character chosen as distinctive, the contact of the axillary shield with the fifth marginal or its exclusion from the fifth marginal by a contact of the fourth marginal with the pectoral shield is a trivial one. The specimens examined vary in this respect as follows:

Localities	Axillary reaching 5th marginal	Not reaching 5th marginal
Porto Rico	0	15
Hispaniola	11	2
Cuba	11	1
Jamaica		0

In the series of paratypes—U. S. N. M. No. 25643, 25644 and 25653, A. M. N. H. No. 15186, and F. M. N. H. No. 12476-12489 inclusive (the latter ex Danforth collection)—the length of the carapace of the type is not exceeded. The extremes of the Danforth series are 100-179 mm., the average 124 mm. Three Hispaniolan specimens measure 232, 234 and 241 mm., and I have seen much larger specimens at Monte Cristi. Additional information as to the adult size of Porto Rican specimens is, however, much to be desired.

Fowler has discussed the color dimorphism in this species in some detail, and Danforth comments on it as follows: "There is a popular idea that there are two species, a green and a black one, but I have seen intergrades between the two." This feature of the Porto Rican species is unknown in the Hispaniolan *Pseudemys*.





F16. 52.—Head of *Pseudemys stejneyeri* from below and from side, to show color-pattern. (After Stejneger.)

*Habits.*—Nothing is known of the habits of this species except for the observations of Danforth (1925), which I quote: "By April they were laying eggs. For that purpose they come out on land at night, and the natives choose that time to hunt them with the aid of lights. They are sold in the markets for food. These turtles are only rarely seen sunning themselves."

# A HAND-LIST OF THE AMPHIBIANS AND REPTILES OF THE VIRGIN ISLANDS

In view of the fact that the Virgin Islands are frequently visited by naturalists en route for other localities, I have drawn up a table of the known distribution of the species, and added artificial keys and notes on some of the questions of interest which remain for investigation, in the hope that they may be found useful.

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	Porto Rico.	Vieques.	Culebra.	St. Thomas.	St. John.	Tortola.	Jost Van Dyke.	Virgin Gorda.	Anegada.	St. Croix.
Bufo turpis								x		
Leptodactylus albilabris	X	X	X	X		X	х		X	X
Eleutherodactylus antillensis Eleutherodactylus lentus	X	X	Х	XX		X				x
Hemidactylus mabouia	x			x						
Thecadactylus rapicaudus				X						x
Sphaerodactylus macrolepis	x	x	X	X		X		Х	X	X
Anolis cuvieri	Х	X	1			X				
Anolis cristatellus	X	X	X	X	Х	Х	Х	Х	X	X
Anolis stratulus	X	X	X	X		X	X		-	
Anolis pulchellus Anolis acutus	X	X	X	X		Х	Х	Х	Х	X
Iguana iguana				x						
Cyclura pinguis									x	
Ameiva exsul	x	X	X	X	х	X		X	X	x
Ameiva polops										X
Amphisbacna fenestrata				X	Х					X
Mabuya sloanii	X		X	X	х		X			XX
Typhlops richardii Dromicus exiguus	X	x	x	X	x					
Alsophis antillensis	х	X		X	X			x	x	
Alsophis sancti-crucis										x
Total No. Species 22	12	10	10	16	6	8	5	6	7	13

DISTRIBUTIONAL LIST OF THE AMPHIBIANS AND REPTILES OF THE VIRGIN ISLANDS

# Notes on Herpetology of the Virgin Islands

## I. Amphibians.

1. Bufo turpis Barbour. Readily recognized as the only toad in the islands. Known only from a single specimen collected on Virgin Gorda by James Lee Peters in 1915. Additional specimens for further comparison with the Porto Rican toad are much to be desired.

2. Leptodactylus albilabris (Günther). General aspect frog-like. Barbour has called attention to apparent differences in specimens from St. Croix, and suggests that the species is adapting itself to burrowing habits there.

3. Eleutherodactylus antillensis (Reinhardt & Luetken). Coloration variable, usually uniform grayish brown, the concealed surface of the thighs reticulated with black.

4. Eleutherodactylus lentus (Cope). The uniformly mottled colora-

tion and the light dorsolateral lines readily distinguish this species. Its note is undescribed, and its breeding habits are quite unknown.

II. Reptiles.

1. *Hemidactylus mabouia* (Moreau de Jonnès). It is difficult to understand why this introduced form has not become more common. It may be looked for at night on the walls of buildings near electric lights.

2. Thecadactylus rapicaudus (Houttuyn). It is not known whether this species has become established in St. Thomas and St. Croix.

3. Sphaerodactylus macrolepis Günther. The range of variation in size of dorsal scales should be determined for Virgin Island specimens, for comparison with the data given above for the Porto Rican series.

4. Anolis cuvieri Merrem. The giant Anolis is recorded only from Tortola. It may be extinct even there, as there is no recent record. It might be looked for on St. John.

5. Anolis cristatellus Duméril & Bibron. The common Anolis of fence posts and open brush.

6. Anolis stratulus Cope. Often associated with A. cristatellus but a little more arboreal in its habits in Porto Rico. It should be looked for on St. Croix.

7. Anolis pulchellus Duméril & Bibron. Also associated with A. cristatellus, this species is readily recognized by its more slender body and longer tail. Another species (Anolis richardii Duméril & Bibron) with a slender body, keeled ventral scales and the occipital scale in contact with the scales bordering the orbits, was described from Tortola. Special search by Mr. Peters, who explored the outer Virgin Islands for the Museum of Comparative Zoology, failed to re-discover this species. Anolis krugi, another closely allied species, might be looked for in the more shaded and moist localities on St. John.

8. Anolis acutus Hallowell. Related to Anolis pulchellus but confined to St. Croix, this species has not recently been recorded. It should be compared with Anolis poncensis of the arid district in Porto Rico for possible relationship.

9. Iguana iguana (Linné). This species is much used for food in many localities, which probably accounts for its introduction in St. Thomas. It does not appear to have become well established, but Barbour records a specimen of *iguana* from Water Island, near St. Thomas, in 1917.

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10. Cyclura pinguis Barbour. Known from a single specimen secured on Anegada by Mr. Peters. It should be further compared with the extinct Cyclura mattea Miller, from St. Thomas.

11. Ameiva exsul (Cope). Apparently exterminated in St. Thomas by the mongoose, the ground lizard is still found on the adjacent Water Island.

12. A meiva polops Cope. Known only from the type from St. Croix. It should be looked for on the tops of the limestone hills, in the same habitat as that of A. wetmorei of Porto Rico.

13. Amphisbaena fenestrata Cope. This species may be looked for wherever there is tillable soil. Specimens from St. Croix should be compared with those from St. Thomas for possible differences.

14. *Mabuya sloanii* (Daudin). A rare species. Virgin Island specimens have a somewhat different coloration from those of Porto Rico.

15. Typhlops richardii Duméril and Bibron. This burrowing blind snake can usually be secured through people who are cultivating or plowing. A series from both St. Thomas and St. Croix would be of interest for comparison with the Porto Rican specimens described above.

16. Dromicus exiguus Cope. This species like L. stahli of Porto Rico, may prove more abundant than is believed to be the case. It probably is found in similar situations.

17. Alsophis antillensis (Schlegel). Formerly abundant on St. Thomas, now apparently rare.

18. Alsophis sancti-crucis (Cope). The present status of this species on St. Croix is unknown. It was not found by Noble or Ruthven, who visited the island in 1914.

# ARTIFICIAL KEYS TO THE SPECIES

## I. Frogs and Toads

1. {	Skin rough; head with bony ridgesBufo turpus Skin smooth; head without bony ridges 2
2.	Tips of digits not at all dilated; thigh with dark crossbarsLepodactylus albilabris Tips of digits slightly or considerably di- lated; thighs mottled, not barred 3
	Tips of digits slightly dilated; belly smooth; back mottled
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II. Lizards and Snakes	
1. {Limbs well developed	
2. {No eyelids; skin soft, often broken in catching; digits more or less dilated 3 Eyelids present; skin firm: digits dilated or not	
Digits dilated only at tip, with circular plate beneath; skin covered with over- lapping scales; size small, less than three inches	5
Digits broadly dilated, with transverse lamellae beneath: skin of back covered with granular scales not overlapping; adults larger, exceeding three inches 4	
<ul> <li>Slender terminal joint bearing claw be- yond the expanded portion of digitsIIcmidactylus mabouia</li> <li>4. No slender terminal join on digits: claw concealed in slit between expanded sides of digits</li></ul>	
5. {Digits dilated, with slender terminal joint beyond dilation	
6. Scales on back (closely examined) consist of larger seales entirely surrounded by smaller granules	
7. {Ventral scales keeled: dorsal scales more or less enlarged in vertebral region 8 {Ventral scales smooth	
<ul> <li>Enlarged occipital scale (largest median scale on head behind orbits) separated from enlarged scales bordering orbits by one or more seales</li></ul>	
Back with four or five well-defined trans- verse spots: throat fan of male uniform orange	

10.	Under side of body covered with large plates in regular longitudinal and trans- verse series
11.	(Eight rows of ventral plates
12.	No dorsal fold or crest
13.	Dorsal crest continuous
14.	Seve concealed beneath skin15 Eve distinct
	Body covered with overlapping scalesTyphlops richardii Skin divided into small rectangular seg- ments, arranged in regular ringsAmphisbacna fcnestrata
16.	No pits at tips of scales; dorsal scales in 19 rows; ventral plates 134-146; sub- caudals 79-86Dromicus exiguus A pair of distinct pits or pores near tip of each scale17
	Dorsal scales in 17 rows; ventral plates 191-195; subcaudals 145-147Alsophis sancti-crucis Dorsal scales in 19 rows; ventral plates 170-189; subcaudals 116-144Alsophis antillensis

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