# STUDIES ON THE FAUNA OF CURAÇÃO, ARUBA, BONAIRE AND THE VENEZUELAN ISLANDS: No. 3.

#### ZOOGEOGRAPHICAL REMARKS

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Much has been said of the geographical relations and the origin of the West Indian fauna, especially as to that of its vertebrates and mollusks. Mostly the islands off the Venezuelan coast, for the greater part within sight of the South American continent, remained out of question, although obvious differences between the fauna of Curação and that of the adjacent mainland were rather quickly noticed and its affinity towards the fauna of the Greater Antilles even emphasized (Bland, 1861; Baker, 1924).

Without going into the West Indian fauna as a whole, or the current theories that try to explain its distribution, an attempt is being made to find out what palaeogeographical indication is given by the fauna of the Leeward Group, by careful examination of the distribution of its mammals, reptiles, amphibians, fishes and mollusks, — these being the only groups, perhaps with exception of the birds, which are sufficiently well known to serve as a base for zoogeographical considerations. Biocoenoses were not studied, only the distribution of species and subspecies was taken into account. The biotopes usually being very small and scattered by many isolating factors formed by accidental circumstances, the fauna being very poor and the biology of the species practically unknown, it will be clear that we have to be unpretentious in our aim and very careful in our conclusions.

TABLE 12.  Distribution of the Mammals.	Morro de la Iguana Chiwo Angoletta Tamarindo Isla de Conejo Puerto Real La Pecha Morro Pando Blanquilla Tortuga Huespen Gran Roque Isla Larga Cayo de Agua Ave de Barlovento Ave de Barlovento Roine Klein Bonaire Klein Curaçao Curaçao Aruba Los Monges	Paraguaná N. Venezuela, Trinidad, N. E. Colombia other part of American continent other Antilles
Cebus margaritae Odocoileus gymnotis margaritae Odocoileus gymn. curassavicus Sylvilagus nigron. nigronuchalis Sylvilagus cumanicus margaritae Sylvilagus cumanicus margaritae Sylvilagus cumanicus avius Sciurus nesaeus Epimys norvegicus Mus musculus Oryzomys spec. Hesperomys? spec. Hesperomys? spec. Echimys flavidus Dasypus novemcinctus Peropteryx canina trinitatis Chilonycteris parnelli Mormoops meg. megalophylla Mormoops meg. megalophylla Mormoops megaloph, intermedia Micronycteris megalotis Glossophaga soricina Leptonycteris curasoae Phodotes tumid. tumidirostris Myotis nigricans Rhogeëssa minutilla Molossus major Molossus major Molossus pygmaeus Philander trinitatis venezuelae Marmosa mitis robinsoni		

<sup>×</sup> collected
0 from literature, very doubtful records omitted
7 doubtful

#### DISTRIBUTION OF THE SPECIES.

The evidence of the terrestrial mammals will be considered first. Of these 13 (16) species or subspecies are included in the present list. Three may be at once dismissed as being introduced by human agency, namely Epimys rattus, Epimys norvegicus and Mus musculus. Possibly Odocoileus gymnotis curassavicus should be added. The same subspecies is not unfrequently carried to Curação from northeastern Colombia and, furthermore, it may be concluded from the situation of the coral-limestones, that more than three-quarters of the island-area were certainly submerged in quaternary time, which probably precluded the survival of these animals.

It is doubtful what significance may be attached to the occurrence of the small Cricetine Hesperomys? (launcha aff.) on Aruba, since this genus is southern in range, none being found in northern South America. Also about the Oryzomys, of which only skull-fragments were found in the caves in Margarita and Curaçao, nothing can be said with certainty. Several members of this genus occur in Venezuela, but in the Antilles they appear to be known from Jamaica and St. Vincent only.

All other terrestrial species occur on the adjacent mainland or are represented by closely related forms. It is, of course, possible that some of them have been introduced by man, but there is no known evidence to support this supposition.

Turning to the bats, we find 12 species or subspecies recorded. On some islands local forms appear to have been developed, which phenomena was formerly emphasized by a still larger amount of "insular species". Well defined local forms are Leptonycteris curasoae and Mormoops megalophylla intermedia, both occuring in Curaçao and Aruba. Molossus pygmaeus, Phodotes tumidirostris and Rhogeëssa minutilla are probably not confined to these islands but are, as all other forms, common to the South American mainland and partly to the Caribbees. Chilonycteris parnelli occurs on the Greater Antilles and, furthermore, was once recorded from Venezuela.

Contrary to the former group, the lizards, of which 23(26) species or subspecies are listed, form a most conspicuous element in the island animal-world.

Among these, we know that the gekkos, which hide in or under the bark of trees, enter and abide in human habitations, are at times moved about fortuitously by human agency. On Curação and Aruba, the distribution of Gonatodes albogularis, which seems to be confined to the towns of Willemstad and Oranjestad, suggests recent introduction from the mainland. The occurrence of Gonatodes vittatus on Aruba gives, in this respect, also some ground for supposition, whilst the single museum-record of this species from Curação may be due to introduction or to inexact labelling.

It is not impossible that *Thecadactylus rapicaudus* owns its wide distribution through tropical America to fortuitous dispersal.

Another species which is reputed to be unsuitable for zoogeographical purposes is Iguana iguana iguana, not only common to South and Central America, but also widely, though very irregularly, distributed throughhout the West Indies. The iguanas are very good swimmers and often do not hesitate to plunge into the water when this is the only way of escape. Furthermore, they are often taken aboard the little coasters as fresh food supply, the legs fractured or tightly fastened round the body, and it may be freely assumed that

TABLE 13.  Distribution of the  Lizards.	Morro de la Iguana Chiwo Angoletta Tamarindo Isla de Conelo Pecha Isa Pecha Margarita Morro Fondeadero Morro Pando Blanquilla Tortuga Huespen Gran Roque Isla Larga Cayo de Agua Ave de Barlovento Ave de Sotavento (?) Bonaire Klein Curaçao Curaçao Aruba Los Monges	Paraguaná N. Venezuela, Trinidad, N. E. Colombia other part of American continent other Antilles
Gonatodes albogularis Gonatodes vittatus Gonatodes (? albogularis aff.) Gonatodes (? vittatus aff.) Gonatodes (? Cymnodact. aff.) Gonatodes (? Gymnodact. aff.) Gymnodactylus antillensis Phyllodactylus martini Phyllodactylus martini Phyllodactylus mülleri Phyllodactylus rutteni Thecadactylus rutteni Thecadactylus rutteni Thecadactylus rapicaudus Anolis lineatus Anolis bonairensis bonairensis Anolis bonairensis blanquillanus Iguana iguana iguana Tropidodactylus onca Tropidodactylus onca Tropidorus torquatus hispidus Ameiva bifrontata bifrontata Cnemidophorus lemn. lemniscatus Cnemidophorus lemn. nigricolor Cnemidophorus lemn. arubensis Cnemidophorus murinus murinus Cnemidophorus murinus murinus Cnemidophorus murinus ruthveni Gymnophthalmus lineatus Gymnophthalmus laevicaudus Tretioscincus bifasciatus	xxx xxx x	

X collected+ observed, not collected

<sup>0</sup> from literature, very doubtful records omitted ? doubtful

they, even in this condition, more than once escaped their fate. Still the smaller Venezuelan islands, Los Testigos excepted, probably possess rather independent populations, as their members often clearly show the phenomena of island-melanism.

It should be noted that the fauna of all islands in question, which consist wholly of coral-rock, or are built up of sand and coral-debris, must have been introduced in comparatively recent time. In conformity with this, the known reptiles of Tortuga are identical with those of Orchila and other neighbouring islands, whilst the Cnemidophorus nigricolor, which inhabits the keys of Los Roques also occurs on Gran Roque and the adjacent island-groups. The Aves Islands have apparently derived their fauna from Bonaire as well as from the little islands to the East, but, besides this, the records of Tropidurus torquatus lispidus and Gymnophthalmus laevicaudus, not known from the neighbouring islands, point to introduction from the opposite mainland. As expected, the fauna of Klein Bonaire is the same as that of the main island, whilst the two species of Klein Curação are also to be found in Curação.

The doubtful species of Gonatodes, which occur on Los Hermanos, Orchila, Tortuga and Los Roques are probably local forms, about which as yet nothing can be said. The occurrence of Gymnodactylus antillensis, endemic to Curaçao, Bonaire and Las Aves, and once recorded from Orchila, is most interesting. On the mainland this genus is southern in range, no species being found in Venezuela or Colombia, whilst in the West Indian region one has been rarely found in the Caribbees.

In Phyllodactylus several species may be discerned, P. rutteni, P. martini and P. julieni, which are peculiar resp. to the region Los Hermanos-Los Roques, Bonaire-Curação and Aruba, whilst P. mülleri occurs on the mainland as well as on Margarita. The mutual relation of these species and their connection with other species is rather obscure, the more so because in other Antilles, specimens were found which were even considered identical with the species from Curação.

The anoles belong to two very different species: Anolis lineatus in Curação and Aruba, Anolis bonairensis bonairensis in Bonaire and probably Las Aves, Anolis bonairensis blanquillanus in Blanquilla and Los Hermanos. Here also, nothing can be said on the relationship to other species.

Tropidodactylus onca and Tropidurus torquatus hispidus have not been found West of Margarita, excepting a single record of the latter species from the Aves-Islands.

It is interesting that the widely distributed genus Ameiva does not occur on the islands between Margarita and Aruba. Most of the Antilles have been found to support a peculiar species; the Margarita-species, however, is not different from that of the opposite mainland, whilst that of the Testigos-Islands, although slightly different from the typical Ameiva bifrontata, is not considered to represent an endemic species or subspecies. On Aruba A. bifrontata has only been found in very limited numbers in the neighbourhood of Oranjestad, which suggest introduction from the adjacent continent.

In contrary to the former genus, Cnemidophorus is common to every island-group. Cnem. lemniscatus lemniscatus from the continent occurs on Margarita and the islands to its East and South; to this form Cnem. lemn. nigricolor, peculiar to the islands between Margarita and Bonaire, is very narrowly re-

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TABLE 14.  Distribution of the Snakes,  Crocodiles, Amphibians and  Fishes.	Morro de la Iguana Chiwo Angoletta Tamarindo Isia de Conejo Isia de Conejo Isia de Conejo Margarita Margarita Morro Pando Blanquilia Tortuga Huespen Gran Roque Isia Larga Cayo de Agua Ave de Barlovento Ave de Sotavento (1) Bonaire Klein Curaçao Curaçao Curaçao Aruba Los Monges	Paraguaná N. Venezuela, Trinidad, N. E. Colombia other part of American continent other Antilles
SNAKES Leptotyphlops albifrons Dromicus antillensis Leimadophis triscalis Leptodeira annulata Crotalus terrificus		.000 0 .x
CROCODILES Crocodylus intermedius		.0
AMPHIBIANS Pleurodema brachyops other species		.×
FISHES Cyprinodon dearborni Rivulus cylindraceus Rivulus hartii Mollienisia vandepolli Lebistes reticulatus Eleotris pisonis Awaous banana Agonostoma monticola		.X .000 .000 .000 .000

X collected
0 from literature, very doubtful records omitted
[Fishes according to L. F. de Beaufort (Amsterdam)]

lated. Cnem. lcmniscatus arubensis from Aruba shows some intermediate position between the first species and Cnem. murinus murinus from Curação and C. murinus ruthveni from Bonaire, which are generally considered as being the most primitive types of the genus.

The irregular distribution of Gymnophthalmus lineatus, Gymn. laevicaudus and Tretioscincus bifasciatus is very puzzling; all three are common to the mainland and are apparently lacking in the Antilles.

For completeness something must be said on the snakes, crocodiles, amphibians and fishes, although no detailed study of these groups could be made.

Firstly it should be noted that all the snakes observed in Margarita and the Testigos Islands, are also common to the mainland. One of these species, Drymobius boddaertii, was reported from Las Aves by Meek, 1910. Bonaire, Curaçao and Aruba are inhabited by different species, which are often widely distributed throughout tropical America.

Remains of an old and a very young specimen of Crocodylus intermedius from the Laguna de las Maritas, left little doubt as to its occurrence in Margarita.

Pleurodema brachyops, occurring in Margarita, Aruba and the neighbouring mainland, was accidently introduced in Curação about 1910, by sand from Aruba, used in building the Wilhelmina-wharf, Emmastad. In 1928 specimens were brought to Bonaire and soon afterwards were widely spread over this island. A Bufo and a Hyla occur in the more wooded central part of Margarita.

Lebistes reticulatus and Rivulus hartii are the only fishes in Margarita. The first has been observed in fresh and oligohaline water, the second even in rather strong mesohaline water. The distribution of Lebistes reticulatus has been strongly influenced by man, because of its general use as a destroyer of mosquito-larvae.

The other fishes of the Leeward Group are even less susceptible to salt water, perhaps with exception of Agonostoma monticola, whose occurrence in Pos Ariba, a oligohaline pond in central Curação, is most puzzling. It is curious, that the only species, which appears to be peculiar to the Leeward Group, Mollienisia vandepolli, often occurs in marine lagoons and in saltlakes, in water of more than 30 g Cl/l, together with Cyprinodon dearborni, the latter being the most hardy of all.

The snails, of which 58 species are listed, form a second conspicuous element of the island-fauna, which is zoogeographically of the highest interest.

All the 35 species occurring on Margarita are also known from the adjacent continent of South America, with exception of Subulina striatella which, however, is probably closely related to Subulina parana from Brasil. The scanty mollusk-fauna of the smaller islands E. and S. of Margarita also do not show any positive differences.

Contrary to this, the islands West of Margarita show a noticeable independency from the mainland-fauna. There is a high percentage of endemism, typical South American groups are absent or very scantily represented, and several Antillean groups form conspicuous components of the population.

Physa cubensis, Lamellaxis gracilis, Lamellaxis micra, Drymaeus multilineatus and Liguus virgineus are certainly introduced by human agency; this probably is also the case with Caecilioides gundlachi, Luntia insignis and Ennea bicolor.

Lucidella lirata, Potamopyrgus parvulus, Planorbis circumlineatus, Gastrocopta barbadensis, Gastrocopta octonaria, Pupoides marginatus, Caecilioides conso-

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TABLE 15.  Distribution of the Snails.		Morro de la Iguana	Angoletta Tamarindo	Isla de Conejo	La Pecha Margarita	Morro Fondeadero	Morro Pando Blanquilla	Tortuga	Gran Roque	Cayo de Agua	Ave de Barlovento Ave de Sotavento (7)	Bonaire Klein Bonaire	Klein Curação	Aruba Los Monges	Paraguana N. Venez., Trinid., N.E. Col. other part of American cont. other Antilies
Alcadia dysoni Lucidella lirata Stoastomops walkeri Poteria translucida Cistulops raveni Tudora megacheilos Tudora rupis Tudora aurantia Tudora aurantia Tudora maculata Potamopyrgus parvulus Physa cubensis Planorbis circumlineatus Vaginulus linguaeformis Vaginulus linguaeformis Vaginulus spec. Succinea barbadensis Succinea gyrata Succinea gyrata Succinea tamsiana Succinea spec. Gastrocopta barbadensis Gastrocopta curacoana Gastrocopta geminidens Gastrocopta geminidens Gastrocopta octonaria Pupoides marginatus Bothriopupa tenuidens Caecilioides consobrina Caecilioides gundlachi Lamellaxis gracilis Lamellaxis micra Synopeas beckianum Subulina striatella Neosubulina gloynii Leptinaria lamellata Luntia insignis Spiraxis blandi Thysanophora crinita Thysanophora plagloptycha Thysanophora plagloptycha Thysanophora plagloptycha Thysanophora plagloptycha Thysanophora vanattai Guppya gundlachi Guppya molengraaffi Habroconus ernsti Scolodonta starkei Bulimulus constrictus		· · · · · · · · · · · · · · · · · · ·	××××××××××××××××××××××××××××××××××××××	×	· · · · · · · · · · · · · · · · · · ·		······································	× × × × × × × × × × × × × × × × × × ×	· · · · · · · · · · · · · · · · · · ·			×····×××·×···×··×··×··×··×···×········	.>>> .>>> .>>> .>> .>> .>> .>> .>> .>>	···×··································	
Brachypodella raveni Microceramus bonairensis Streptaxis glaber Ennea bicolor	• •		• • •				.×	×		• •	• •		•	<b>※:</b> :×:	×:::: :×0:0 :0:0

brina, Synopeas beckianum, Thysanophora crinita and Drymaeus virgulatus are common to the adjacent mainland and are often widely spread; in certain cases their discontinuous distribution on the western islands of the Leeward Group arouses the suspicion of fortuitous dispersal. On Aruba Oxystyla maracaibensis appears to be entirely subfossil. The genus Succinea is very imperfectly known and is therefore excluded from further consideration.

The element which appears to be peculiar to the Leeward Group is confined to Bonaire, Curaçao and Aruba, with two exceptions which may be first considered. Spiraxis blandi has been described in 1873 from Los Roques, after a single specimen; anatomy unknown. Though this record, at first suggests an affinity to the Greater Antilles, a strong similarity to Pseudosubulina (= Spiraxis) decussata from the mainland should be noted. Microceramus bonairenis has been found in a more or less subfossil state on the peninsula of Paraguaná, which denotes the possibility of the occurrence of living specimens in this, and perhaps also other calcareous regions of the continent. The specimens from Blanquilla and Tortuga are probably subspecifically separable from those of the Dutch Islands, which also show some slight differences.

Two genera, Stoastomops and Cistulops, three subgenera, Bonairea, Neosubulina s.s. and Cerion s.s., and 12 species are, as far as known, endemic to Curaçao, Aruba and Bonaire. Of these Guppya molengraaffi was found only on the Seroe Christoffel, the region which approaches nearest to the rainforest of Antilles and Scuth America, inhabited by closely allied species. The other are all more or less xerophytic and generally show a marked preference for limestone-rock. Tudora megacheilos, Tudora aurantia, Gastrocopta curacoana, Neosubulina gloynii and Cerion uva invade the more heavily wooded parts in the higher hills of non-calcareous rock, but they are much rarer in these places than on limestone in apparently more arid conditions. A similar type of habitat has been studied in the neighbouring islands and in different places on the adjacent northcoast of South America.

It is most noticeable that in the mollusk-fauna of Curaçao, Aruba and Bonaire an obvious Antillean element may be observed. Cerion is practically limited to the Bahamas and the Greater Antilles, occurring in subfossil state as far South as St. Croix. Microceramus is another Antillean genus which reaches the mainland of North America, but is apparently lacking in most of the Lesser Antilles and in the mainland of South America, with exception of Paraguaná. Stoastomops and Cistulops also appear to have their nearest relatives on the Greater Antilles. The Chondropominae are a characteristically Antillean group, although they reach the mainland in many places around the Caribbean Sea and the Gulf of Mexico. On the other hand the members of this group appear to be most closely related to those of northern South America.

The genus Neosubulina is known only from the Dutch islands of the Leeward Group and northern South America, while Brachypodella raveni belongs to the mainland group of the genus. The relation of Gastrocopta curacoana is uncertain, and also about that of Thysanophora vanattai, the type of the subgenus Hojeda H. B. Baker, nothing can be said with certainty.

As already fully discussed by H. B. Baker, 1924, Curação can be divided into several faunal areas. Most distinct is the area of the Tafelberg Santa Barbara, which is, above all, characterized by the presence of *Tudora megacheilos pilsbryi* and *Tudora rupis rupis*. The other areas are less marked. Their boundaries generally correspond with the sunken valleys which cut up the limestone rim into a series of quite isolated ridges.

#### AFFINITIES OF THE FAUNA.

The known M a m m a l s of the Leeward Group consist of 25 (28) species or subspecies. One half of these (50%) are common to the South American mainland and, partly, also to the other Antilles. A few species (10%) are known to be introduced by human agency. — The other forms (40%) are local species or subspecies which are represented on the adjacent mainland by narrowly related forms and do not belong to any peculiar Antillean genus or species.

The known Lizards of the Leeward Group consist of 23 (26) species or subspecies. One half of these (50%) are common to the South American mainland and, for a very small part only, also to the other Antilles. A single species is supposed to be introduced by human agency. — The other forms (50%) are local species or subspecies which, for the greater part, are not represented on the adjacent mainland by narrowly related forms and do not obviously belong to any peculiar Antillean genus or species. — The species and subspecies which are peculiar to the Leeward Group, are confined to the islands West of Margarita; this region may be divided in smaller areas which possess a more or less different faunistical character: Los Hermanos-Blanquilla, Orchila-Tortuga, Los Roques, Bonaire, Curaçao, Aruba.

The Snakes, Amphibians and Fishes which inhabit Margarita and Los Testigos are probably all mainland-species. Those which occur in the other islands, are for the greater part also common to South America. The only species which appears to be peculiar to Curaçao, Aruba and Bonaire, is a fish, by no means confined to freshwater only, which is represented on the mainland by rather closely related forms.

The known Mollusks of the Leeward Group consist of 58 (60) species. Three quarters of these (75%) are common to the South American mainland and, for nearly their half, also to the other Antilles. A few species are supposed to be introduced by human agency. — The other forms (25%) are local species

which, for the greater part, are not represented on the adjacent mainland by narrowly related forms and, in a few cases, belong to peculiar Antillean genera. — The species which are peculiar to the Leeward Group, are practically confined to the islands Bonaire, Curaçao and Aruba; each island possessess a somewhat different faunal character. Bonaire and Klein Bonaire together forming the most distinct of all areas. — Margarita, and the islands to its East and South, have a fauna which shows no differences to that of the adjacent mainland, whilst the islands to its West apparently have a somewhat closer relationship with that of Curaçao.

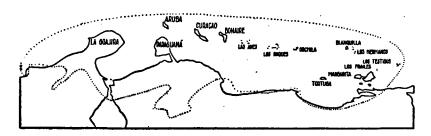


Fig. 21 The Leeward Group. — The punctuated line indicating the isolated dry region along the northcoast of South America, with a rainfall of less than 680 mm a year.

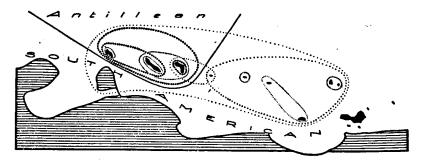


Fig. 22 Affinities of the older elements in the fauna of the Leeward Group. —
The punctuated lines indicating the areas of endemic species.

MAMMALIA Cebus margaritae Odoccolleus gymnotis margaritae Odoccolleus gymnotis curassavicus Sylvilagus cumanicus margaritae Sylvilagus cumanicus margaritae Sylvilagus cumanicus margaritae Sylvilagus cumanicus avius Sylvilagus nesaeus Sylvilagus nesaeus Sedurus nesaeus S
Brachypodella raveni

<sup>×</sup> own observation 0 from literature

<sup>-</sup> closely related form
same genus, no closely related form
doubtful

## Isla de Caribes (1/3 km²) Lizards 6. Snakes 1.

The fauna shows no differences to that of the adjacent mainland.

> Coche (50 km<sup>2</sup>) Lizards 3. Amphibians 1.

The fauna shows no differences to that of the adjacent mainland.

# Cubagua (26½ km²) Lizards 3.

The fauna shows no differences to that of the adjacent mainland.

# Margarita (850 km²)

Mammals 17(18). Lizards 8. Snakes 6. Amphibians 3. Fishes 2. Mollusks 34(36).

The fauna shows no obvious differences to that of the adjacent mainland. The species or subspecies which appear to be confined to this island are closely related to mainland-forms and might hardly deserve special denomination.

Only known from Margarita: Cebus margaritae (not verified), Odocoileus gymnotis margaritae, Sylvilagus cumanicus margaritae, Sciurus nesaeus (not verified), Echimys flavidus (not verified), Rhogeessa minutilla (not verified).

# Los Testigos (5 islands: $3\frac{1}{2}$ km<sup>2</sup>) Mammals 2. Lizards 6. Snakes 1. Mollusks 8.

The fauna shows no obvious differences to that of the adjacent mainland. The subspecies which appears to be confined to these islands is closely related to mainland-forms and hardly deserves special denomination.

Only known from Los Testigos: Sylvilagus cumanicus avius.

Los Frailes (2 islands: 1 km<sup>2</sup>) Lizards 5. Mollusks 1.

The fauna shows no obvious differences to that of the adjacent mainland.

## Los Hermanos (2 islands: $2\frac{1}{2}$ km<sup>2</sup>) Lizards 6, Mollusks 1(2).

The fauna shows some obvious differences to that of Margarita and the adjacent mainland and is very closely related to that of Blanquilla.

Only known from Los Hermanos: Gonatodes (? Gymnodactylus aff.). Only known from the Leeward Group: Phyllodactylus rutteni, Anolis bonairensis blanquillanus, Cnemidophorus lemniscatus nigricolor.

# Blanquilla (45 km<sup>2</sup>) Lizards 4. Mollusks 5(6).

The fauna shows some obvious differences to that of the adjacent mainland and is closely related to that of the neighbouring islands.

Only known from the Leeward Group: Phyllodactylus rutteni, Anolis bonairensis blanquillanus, Cnemidophorus lemniscatus nigricolor. Microceramus bonairensis (incl. Paraguaná)

### Tortuga (140 km<sup>2</sup>) Lizards 4. Mollusks 2.

The fauna shows some obvious differences to that of the adjacent mainland and is closely related to that of the northern islands.

Only known from the Leeward Group: Gonatodes (? albogularis aff.), ? Phyllodactylus rutteni, Cnemidophorus lemniscatus nigricolor, Microceramus bonairensis (incl. Paraguana).

# Orchila (25 km<sup>2</sup>) Lizards 4 Mollusks 3

The fauna shows some obvious differences to that of the adjacent mainland and is closely related to that of the neighbouring islands.

Only known from the Leeward Group: Gonatodes (? albogularis aff.). Gymnodactylus antillensis (not verified), Cnemidophorus lemniscatus nigricolor.

## Los Roques (3 islands: 1½ km²) Lizards 4. Fishes 1. Mollusks 2.

The fauna shows some obvious differences to that of the adjacent mainland and is closely related to that of the neighbouring islands.

Only known from Los Roques: Gonatodes (? vittatus aff.), Spiraxis blandi (not verified). Only known from the Leeward Group: Phyllodactylus rutteni, Cnemidophorus lemniscatus nigricolor.

# Las Aves (2 islands: $\frac{1}{2}$ km<sup>2</sup>) Lizards 6. Snakes 1.

The fauna shows a few obvious differences to that of the adjacent mainland and is related to that of the neighbouring islands.

Only known from the Leeward Group: Gymnodactylus antillensis, ? Anolis bonairensis bonairensis (not verified), Cnemidophorus lemniscatus nigricolor.

## Bonaire (265 km<sup>2</sup>)

Mammals 2. Lizards 7. Snakes 1. Amphibians 1. Fishes 4. Mollusks 17.

Klein Bonaire (7 km<sup>2</sup>)

Lizards 5. Amphibians 1. Mollusks 10.

The fauna shows several obvious differences to that of the adjacent mainland and is rather closely related to that of Curaçao. The occurrence of Cerion, Stoastomops and Microceramus suggests some relationship with the fauna of the Greater Antilles, while Anolis bonairensis and Tudora also might represent an Antillean element; this Antillean affinity is, however, rather insignificant when compared with the much closer relationship to the South-American mainland-fauna.

Only known from Bonaire: Anolis bonairensis bonairensis (? incl. Las Aves), Cnemidophorus murinus ruthveni, Stoastomops walkeri, Tudora aurantia, Tudora maculata. Only known from the Leeward Group: Gymnodactylus antillensis, Phyllodactylus martini, Mollienisia vandepolli, Gastrocopta curacoana, Neosubulina gloynii, Cerion uva, Brachypodella raveni, Microceramus bonairensis (incl. Paraguaná).

# Curação (425 km²)

Mammals 11(13). Lizards 8(9). Snakes 2. Amphibians 1. Fishes 4. Mollusks 27.

Klein Curação (11/4 km²)

Lizards 2.

The fauna shows several obvious differences to that of the adjacent mainland and is rather closely related to that of Bonaire and Aruba. The occurrence of Cerion, Cistulops and Microceramus suggests some relationship with the fauna of the Greater Antilles,

while Tudora also might represent an Antillean element; this Antillean affinity is, however, rather insignificant when compared with the much closer relationship to the South-American mainland-fauna.

Only known from Curaçao: ? Odocoileus gymnotis curassavicus, Phodotes tumidirostris tumidirostris (not verified), Molossus pygmaeus, Cnemidophorus murinus murinus, Tudora megacheilos pilsbryi, Tudora rupis rupis, Tudora rupis muskusi, Tudora rupis grandiensis, Tudora rupis hatoensis, Guppya molengraaffi. Only known from the Leeward Group: ? Sylvilagus nigronuchalis nigronuchalis, Mormoops megalophylla intermedia, Leptonycteris curasoae, Gymnodactylus antillensis, Phyllodactylus martini, Anolis lineatus, Mollienisia vandepolli, Cistulops raveni, Tudora megacheilos megacheilos, Gastrocopta curacoana, Neosubulina gloynii, Cerion uva, Brachypodella raveni, Microceramus bonairensis (incl. Paraguaná).

## Aruba (173 km<sup>2</sup>)

Mammals 5. Lizards 10. Snakes 2. Amphibians 1. Fishes 1. Mollusks 19.

The fauna shows several obvious differences to that of the adjacent mainland and is rather closely related to that of Curação. The occurrence of Cerion, Cistulops and Microceramus suggests some relationship with the fauna of the Greater Antilles, while Tudora also might represent an Antillean element; this Antillean affinity is, however, quite insignificant when compared with the much closer relationship to the South-American mainland-fauna.

Only known from Aruba: Phyllodactylus julieni, Cnemidophorus lemniscatus arubensis, Thysanophora vanattai. Only known from the Leeward Group: ? Sylvilagus nigronuchalis nigronuchalis, Mormoops megalophylla intermedia, Leptonycteris curasoae, Anolis lineatus, Mollienisia vandepolli, Cistulops raveni, Tudora megacheilos megacheilos, Gastrocopta curacoana, Neosubulina gloynii, Cerion uva, Brachypodella raveni, Microceramus bonairensis (incl. Paraguaná).

# Paraguaná

The fauna shows no obvious differences to that of the neighbouring part of the mainland. The occurrence of *Microceramus* suggests some relationship with the fauna of the Greater Antilles, while *Tudora*, which occurs in other parts of Venezuela, also might represent an Antillean element.

# La Goajira

The fauna shows no differences to that of the neighbouring part of the mainland.

#### PALAEOGEOGRAPHICAL CONCLUSIONS.

In the fauna of the Leeward Group three elements may be discerned: 1. a southern, modern element; 2. a southern, older element; 3. a northern, still older element.

- 1. The "southern, modern element" consists of species common to the South American continent or having closely related mainland-forms. This element cannot be distinctly separated from a "more widely spread, modern element", consisting of species of unknown origin. The fauna of Margarita and the islands to its South and East is wholly composed of this element, which is probably fortuitously scattered over the other islands. This very strongly suggests the existence of a well-wooded land-connection between the continent and Margarita in quaternary time. The scanty fauna of Cubagua, Coche, Los Frailes and Los Testigos is not contradictory to a similar supposition.
- 2. The "southern, older element" consists of endemic species of presumably South-American origin (e.g. Phyllodactylus, Cnemidophorus, Neosubulina, Brachypodella). It forms a considerable part of the island-fauna West of Margarita. This strongly suggests a long geographical isolation of this region, probably even since late-tertiary time. The region probably was soon scattered. It is possible that Bonaire, the most distinct of all areas, was loosened before the connection between, other islands was dissolved (Werner, 1925). The Venezuelan Islands, in general, were populated from the East, the Dutch Islands from the West.
- 3. The "northern, still older element" consists of endemic species of presumably Antillean origin (e.g. Stoastomops, Cistulops, ? Tudora, Cerion). It forms a noticeable part of the fauna of Bonaire, Curação and Aruba (Baker, 1924). This suggests a land-connection with a territory inhabited by an ancient Antillean fauna, possibly as early as middle-tertiary time. There is little to indicate that this Antillean fauna inhabited parts of the South-American continent, although it is not impossible that a thorough study of the northern coast may bring a number of these "relics" to light. At the moment it seems to be more probable that these presumable traces of Antillean element in the

northern part of South America intruded from the north, along the same way which brought the "southern, older element" to the island-region, or that possibly it entered this country via Central America since pliocene time.

The flora of Margarita is identical in appearance with that of the adjacent mainland. Although more than 30% of the 644 plants reported from Margarita in 1909 (Johnston), were not known from the continent at that time, it may be concluded from later investigations that a large part of them certainly occurs on the mainland. The flora of Margarita appears to be wholly composed of a southern, modern element, which is mixed with species more widely spread throughout tropical America. This strongly suggests the existence of a land-connection between the continent and Margarita in quaternary time. The scanty flora of Cubagua, Coche, Los Frailes and Los Testigos is not contradictory to a similar supposition.

The flora of the Venezuelan Islands West of Margarita shows some differences with that of the adjacent mainland, in having a few species, which appear to be peculiar to the Leeward Group, in common with the Dutch Islands. The islands show rather obvious differences. There are little data for palaeogeographical conclusions.

The flora of Bonaire, Curação and Aruba shows some obvious differences with that of the adjacent mainland (Boldingh, 1914). There is a rather high percentage of endemism. It has a noticeable affinity with that of the other Antilles; this, however, appears to be rather insignificant if compared with the much closer relationship of the South-American mainland-flora. The islands show some differences. This suggests a rather long geographical isolation of the region, a former land-connection with South America and, possibly, another land-connection explaining Antillean affinities.

A topographical classification, based on the depth of the sea, agrees with our faunal experiences, as Margarita and the islands to its South and East are lying in a shallow sea and are not separated from the mainland by much deeper water as in the case of the other islands. In this unstable region, other conclusions on topographical data are hardly to be expected. Aruba is separated by a narrow channel of not more than 200 m deep from the shallow mainland-waters; this situation does not correspond with the considerable differences in the fauna of this island and that of the continental-coast.

From a geological point of view all the islands, with exception of Margarita, Cubagua, Coche and possibly Tortuga, belong to the Antillean province, differing markedly from northern and middle Venezuela by lacking geosynclinal development of tertiary deposits. On most of these islands abyssal and, partly also, hypoabyssal rocks are found, derived from a quartzdioritic magma, clearly differing from the rocks of the Caribbean coastrange. It is possible that the peninsulas of Paraguaná and La Goajira belong to the same province.

The greater part of Paraguana and La Goajira was submerged in early quaternary or pliocene time. The fauna, as far as known, does not suggest a long geographical isolation of the archipelagos which must have represented the mountainous region of these peninsulas.

Cubagua, Tortuga, Los Roques with exception of El Gran Roque, Las Aves, Klein Bonaire and Klein Curaçao, wholly consist of quaternary coral-rock or are built up of sand and coral-debris. According to this, the fauna is composed of the same species which occur in the neighbouring islands or on the mainland,

It might be assumed that the submarine plateau, from which Margarita, Cubagua, Coche, Los Frailes and Los Testigos arise, was above sea level in early pleistocene time. During this period the schisty bases of Coche and southern Macanao were eroded, on which afterwards, probably in connection with a positive change of the sea level, the detritus-masses were deposited, now-adays covering this region as well as Cubagua and a part of the Araya-peninsula. An upheaval, in connection with a considerable and still continuing differential movement followed, and a part of the sediment was again removed, giving Margarita, Coche

and Cubagua their present shape. The modern, continental fauna of Margarita and Los Testigos fully complies with this notion of geological history in later time.

Practically no data exist from which we can derive any idea of the palaeogeography of the island-region between Margarita and Bonaire. Blanquilla is still limestone-capped at its eastern side, but there is no indication that this older formation of coral-rock extended over the whole island. In Los Hermanos, Orchila and the Gran Roque no older limestone occurs. These islands may be remnants of a large stretch of land, according to the general exposure of ancient rocks, implying a strong denudation. The steep slopes of the smaller islands and the considerable depth of the sea in their immediate vicinity suggest strong tectonical movements in subrecent time. According to the fauna, it is not likely that a direct or indirect land-connection with the mainland existed in quaternary time.

In Bonaire, Curaçao and Aruba, a positive change of sealevel in early quaternary time, by which the greater part of the islands was submerged, caused a deposition of limestone upon the denuded and abraded older rocks. After that, a slight upwarping of the limestone took place and the coral-rock of the central part, with underlying rocks, were largely removed. Afterwards there were several slow changes in level, both in a positive and in a negative way and some tectonical movements, continuing until the present time. Roughly estimated from the situation of these limestone-beds, more than 4/5 of each island-area were under sea in early pleistocene time. According to the fauna it can be taken for granted that Bonaire, Curaçao and Aruba were not wholly submerged.

From geological indication, the most recent land-connection with a large stretch of land in the South is of uppermost cretacic age, when the Soebi Blanco-conglomerates and the Midden Curaçao-beds were deposited. Small areas of upper-eocene limestone prove that in older tertiary time the former landconnection had disappeared and the region was wholly submerged. From the younger Tertiary practically nothing is known. An upwarping

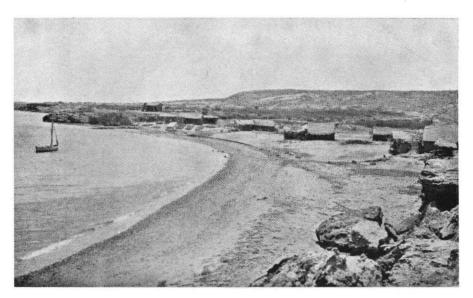
of the island-region followed, probably in the Lower-Oligocene, whilst in northern Venezuela sediments of enormous thickness were deposited, the northern post-eocene geosyncline ending not far from the present northcoast.

According to our zoogeographical knowledge, this island-region was probably above sea-level since middle-tertiary time, successively connected with a stretch of land towards the North, inhabited by the ancient Antillean fauna, and with the South American continent towards the West or Southwest. Afterwards the region was thoroughly scattered, forming the present territory of Curaçao, Aruba, Bonaire and the Venezuelan Islands.

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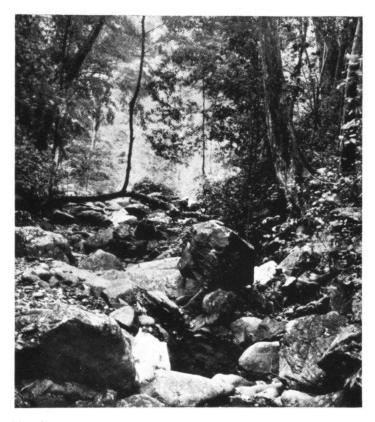
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I a Ranchería at the northern coast of Cubagua. The island is flattened and consists of limestone. The scanty vegetation is chiefly composed of scattered shrubs of Croton flavens, Opuntia caribaea and Opuntia Wentiana. (Stat. 9 and 129 are situated in a small gully to the right)



Ib Looking northward from the peninsula of Puerto Santo towards the Morro de Puerto Santo (100 m), E. of Carúpano. The rocks consist chiefly of crystalline schists. The peninsula is covered by a considerable growth of shrubs with much Agave Cocui; the Morro has a scanty grassy plantcovering with scattered Lemaireocereus griseus. (see Stat. 125—126)



II a The Río del Valle, Margarita, just above the Toma de Agua, with large boulders of antigorite-rock. On Margarita this rather luxuriant vegetation is confined to the higher and more protected parts of the Cerros de Copey.

(Stat. 144, near Stat. 26)



II b Looking northward across the valley of the Rio Asunción, towards the Cerros de Matasiete (600 m), an outcrop of granitic rocks in Margarita.

(Stat. 137 is situated in the background to the left)



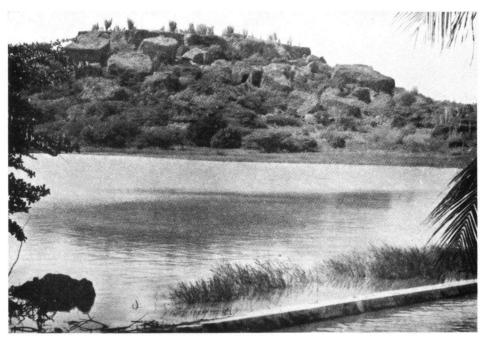
III a The Morro Grande of Tamarindo (200 m), seen from the Morro de la Iguana, Los Testigos. The islands are build up of granitic rocks. The foreground with a conspicuous growth of Cereus margaritensis. (see Stat. 157 and Stat. 162—163)



III b The Morro Grueso (180 m), seen from the Morro Fondeadero, Los Hermanos. The foreground consists of hornblende-rock and is covered with guano; showing conspicuous specimens of Lemaireocereus griseus. (see Stat. 169)



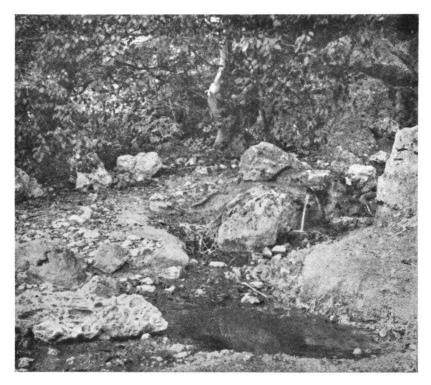
IV a Limestone terraces between Fontein (1.) and Rooi Onima (r.), at the northcoast of Bonaire. Approximate height of lowest-terrace (in foreground), lower, higher and highest-terrace resp. 8, 20, 50 and 80 m. Vegetation with conspicuous Cereus repandus.



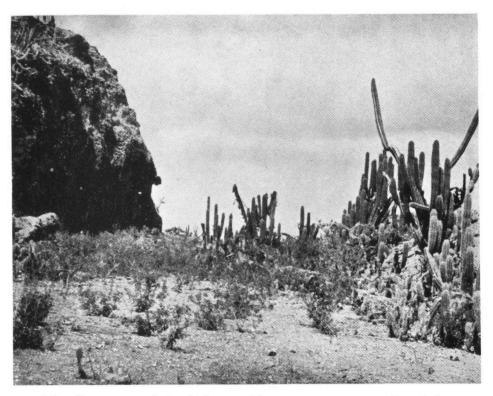
IV b Tanki Onima, Bonaire, after the rainy season. The valley of Onima has been dammed for agricultural purposes; after rains the accumulated water covers large areas which are later drying up. The isolated table-mountain, the Kaumati (43 m), shows the crumbling of the elevated coral-limestone plateau by removal of the underlying rock. (Stat. 46, near Stat. 194)



Va Pos Jatoe Largoe, one of the numerous places in the limestone-plateau of southern Bonaire, where the cavern-water is made accessible by roof-collapse. (Stat. s.n.)



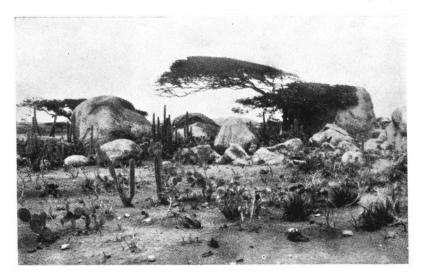
Vb Bron Wandongo, at the foot of the escarpment of the higher corallimestone terrace of Hato, Curaçao. A short iron pipe transmitting the spring-water to a small pool with Najas guadalupensis; trees of Hippomane Mancinclla in the background. (Stat. 76—76A and Stat. 220)



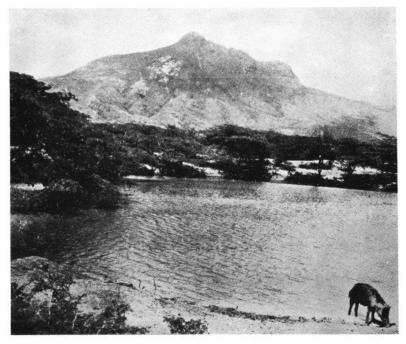
VI a Escarpment of the higher coral-limestone terrace near San Pedro, Curação. A vegetation with Croton flavens, Lemaireocereus griseus and Opuntia Wentiana predominating. (Stat. 226)



VI b Rooi Bringamosa, a river-bed in the diorite-landscape of central A r u b a, holding some water; looking northeastward towards the diabase-hill Arie Kok (186 m). (Stat. 103)

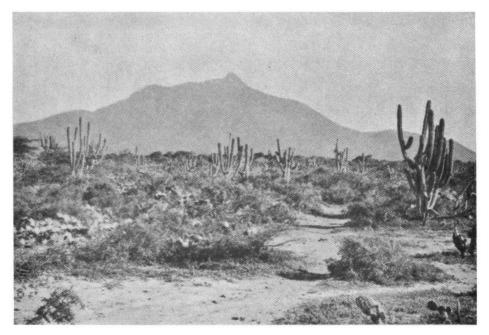


VII a Exfoliated diorite-blocks, West of the Hooiberg, Aruba. The vegetation is confined chiefly to Jatropha gossypifolia, Opuntia Wentiana, Lemaireocereus griseus and Aloe vera; the dividivi-tree has been greatly deformed by the eastern tradewind.



VII b Looking northward across the Estanque de Santa Ana, towards the Cerro de Santa Ana (abt. 800 m), Paraguaná. (Stat. 110)

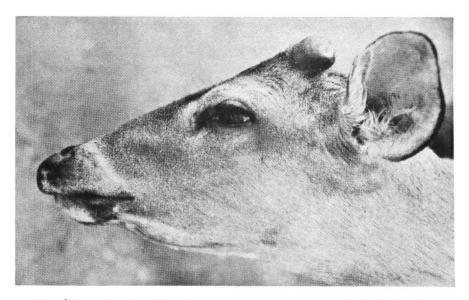
#### TAB. VIII



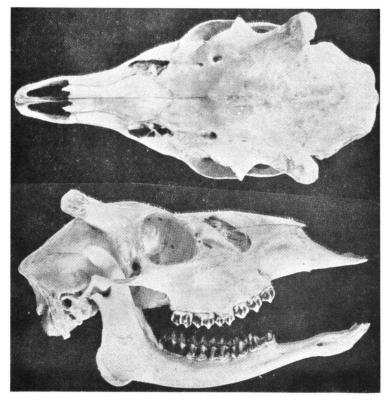
VIII & Looking southward towards the Cerro de Santa Ana, an outcrop of gabbroid-rock, dominating the peninsula of Paraguaná. The mountains are encircled by a rather high limestone-plateau which, in this locality, is covered by thorny shrubs, Opuntia Wentiana and conspicuous Lemaireocereus griseus.



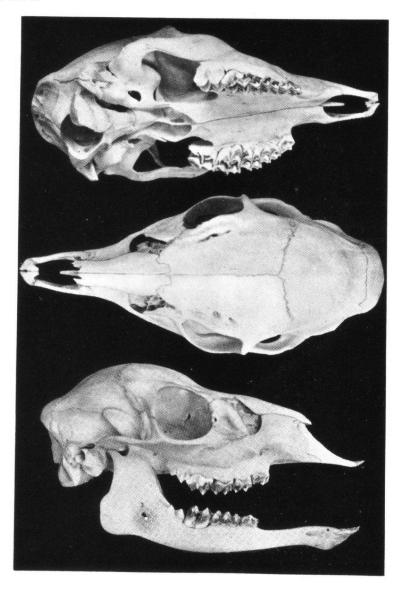
VIII b The Rio Calancala near San Antonio, a very shallow river South of the peninsula of La Goajira. Indians are loading a canoe with dividivi for transport to Rio Hacha. (Stat. 115)



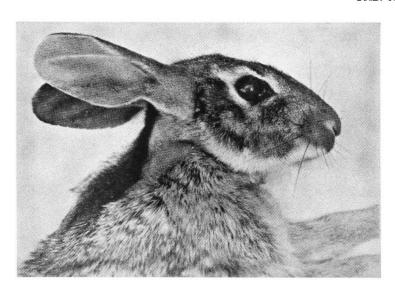
IX a Head of adult Odocoileus gymnotis curassavicus with shedded antlers, Curação. (Odoc. 5, holotype; just after death)

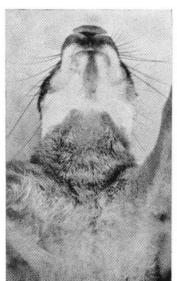


IX b Skull of adult male Odocoileus gymnotis curassavicus, Curação, from above and from the right. (Odoc. 5, holotype)



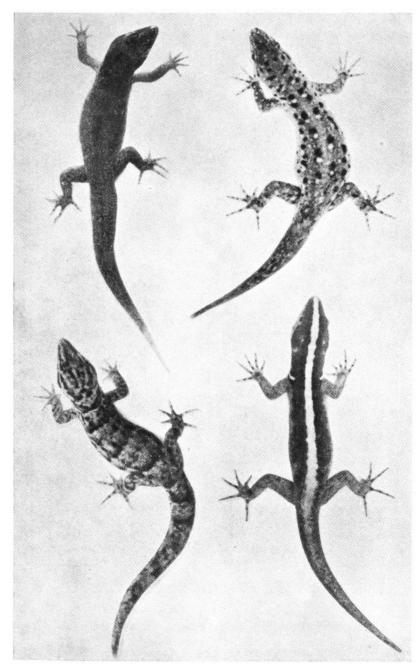
X Skull of nine months old female Odocoilcus gymnotis curassavicus, Curação, from below, from above and from the right. (Odoc. 2, paratype)



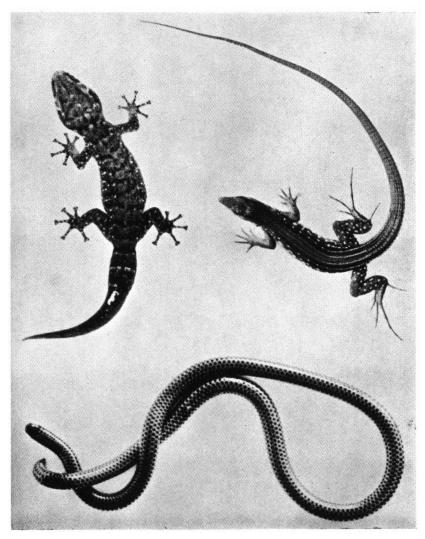




XI Head of Sylvilagus nigronuchalis nigronuchalis from Falcón, Aruba, from the right, from below and from above, showing the deep black nape. (topotype; just after death)



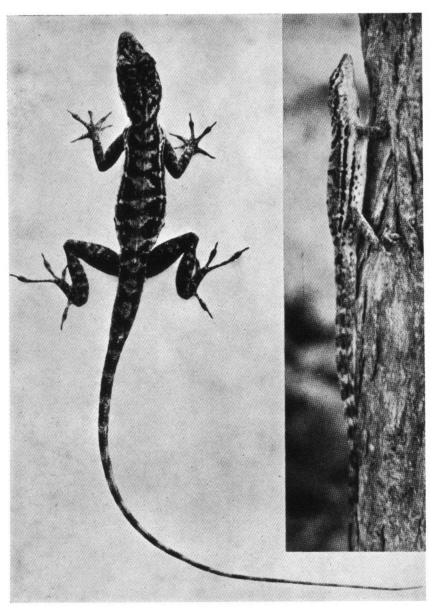
XII On the left: Gymnodactylus antillensis from Bronswinkel, Bonaire: above the male with grey body and orange-red head, below the female. On the right: Gonatodes vittatus from Oranjestad, Aruba; above the female, below the male. (from life,  $\times$  ca  $^{5}/_{3}$ )



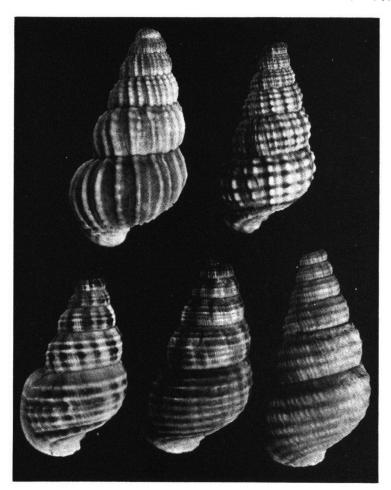
XIII Above on the left: Phyllodactylus julieni from Baca Morto, Aruba. (from life,  $\times$   $^{7}/_{6}$ )

Above, on the right: Cnemidophorus lemniscatus arubensis from Oranjestad, Aruba. (from life,  $\times$   $^{2}/_{3}$ )

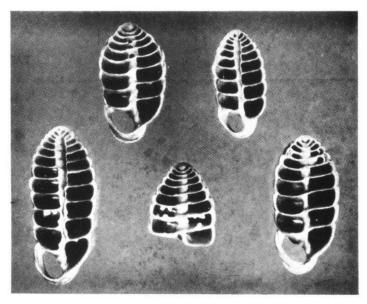
Below: Leptotyphlops albifrons from Lima, Bonaire, silver coloured. (from life,  $\times$  2)



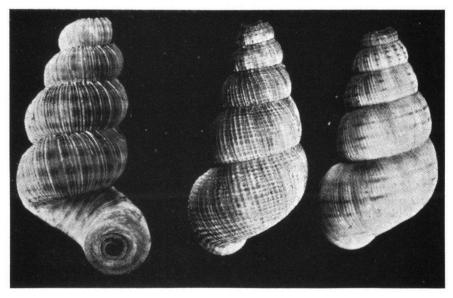
XIV Anolis lineatus from Hato, Curação, from above (nat. size) and from the right, same specimen. (from life)



XV Above, from left to right: Tudora rupis muskusi, St. 242A, and Tudora rupis grandiensis, St. 225. Below: Tudora rupis rupis, 2 specimens, St. 206, and Tudora rupis hatoensis, holotype, St. 217; all from Curação. (X 7/2)



XVI a Cerion uva from Curação; from left to right, 1–3 St. 220, 4–5 St. 242. Whorls in cross-section, showing structure of axis, axial-lamellae, parietal-tooth and the occurrence of parietal and palatal-teeth in young specimens.  $(\times^{5/3})$ 



XVI b From left to right: Tudora maculata from Bonaire, St. 190. ( $\times$  10) Tudora aurantia from Bonaire, St. 197 and St. 184, showing sculpture-differences. ( $\times$   $^{7}/_{2}$ )