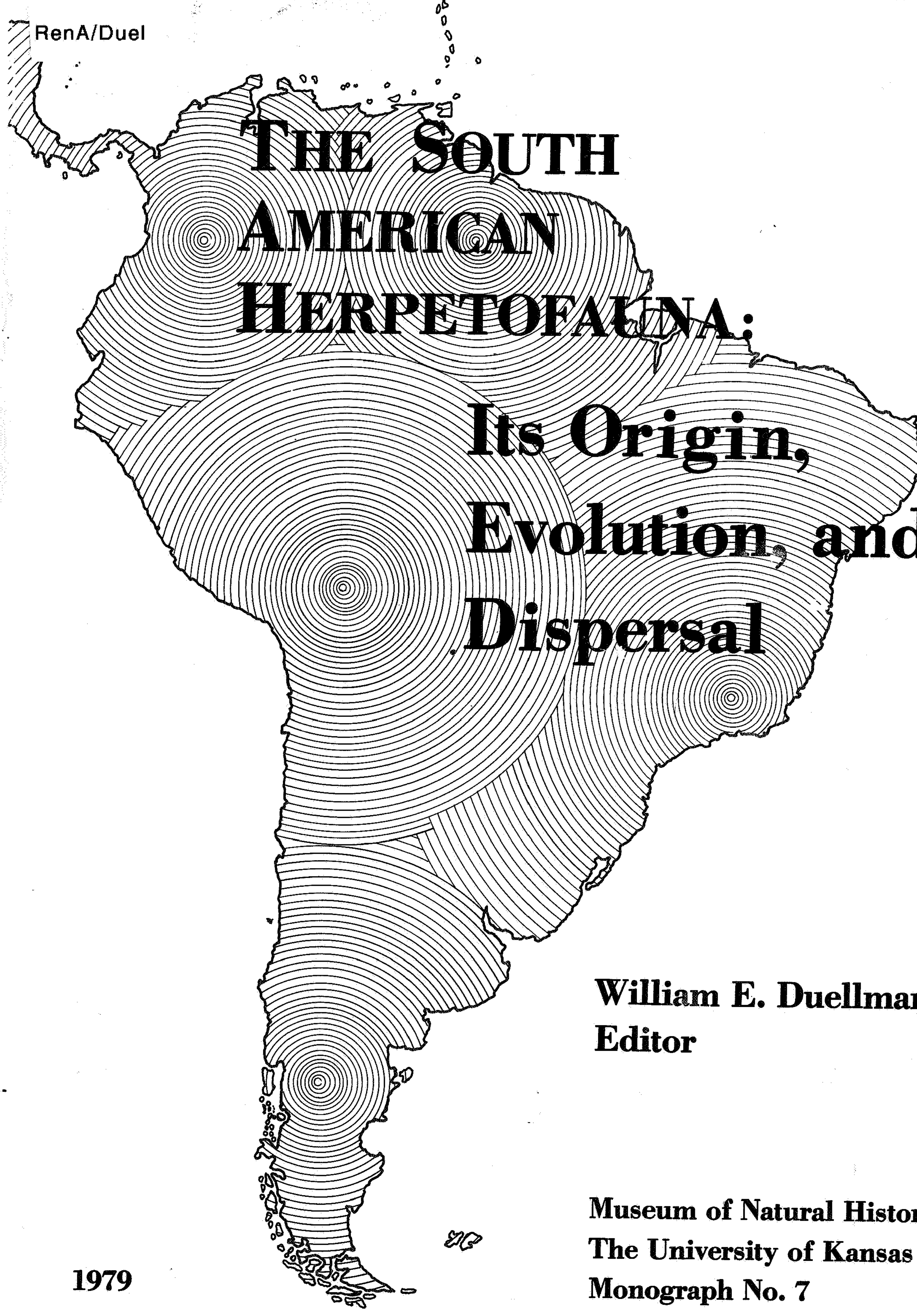

The South American Herpetofauna: Its Origin, Evolution, and Dispersal

William E. Duellman
Editor

Museum of Natural History
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THE SOUTH AMERICAN HERPETOFAUNA: ITS ORIGIN, EVOLUTION, AND DISPERSAL

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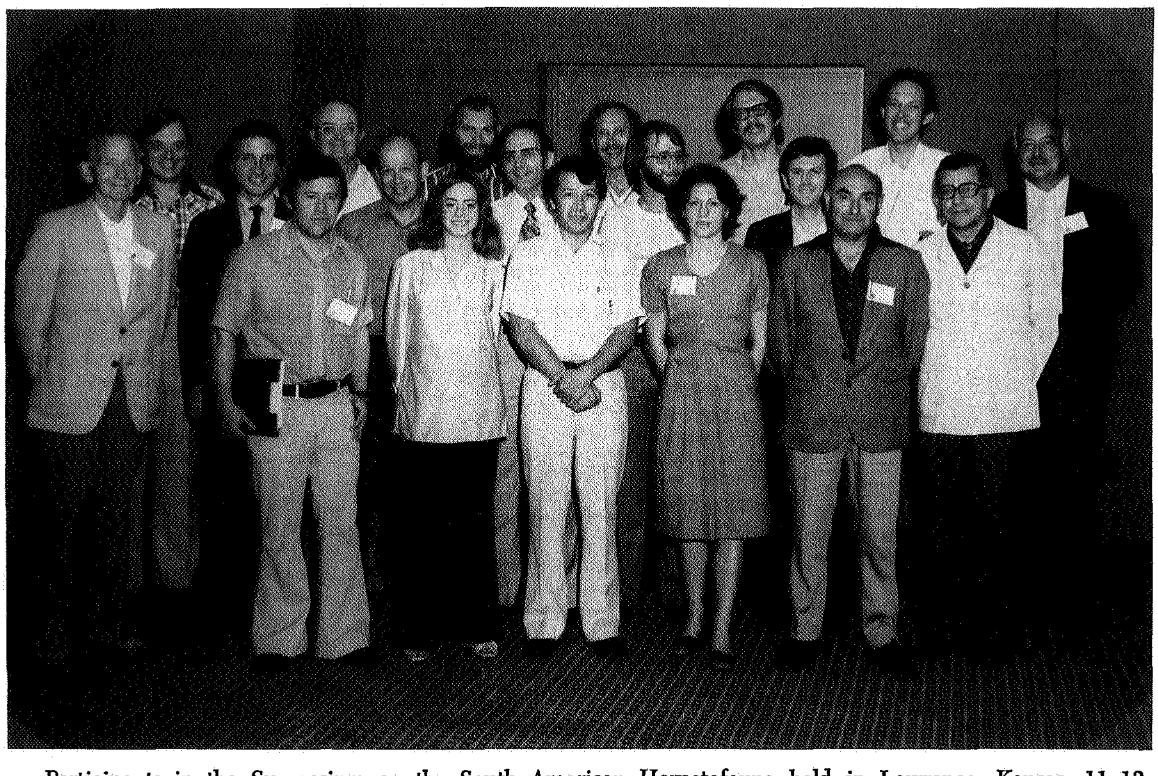
PREFACE

This volume is the result of a symposium of the same title held on 11–13 August 1977 in conjunction with the joint annual meetings of the Herpetologists' League and the Society for the Study of Amphibians and Reptiles at Lawrence, Kansas. I originally conceived the idea for such a symposium in August 1975 while returning from a 15-month sojourn in South America. My interactions with many South American biologists during that trip had convinced me that the time was appropriate for a thorough discussion of ideas and presentation of our existing knowledge of the South American herpetofauna. The initial response from colleagues was heartening, so during the following year the symposium was organized. Unfortunately, owing to various circumstances not all subjects were covered; obvious omissions in this volume are chapters on the South American-North American herpetofaunal relationships and the herpetofaunas of the Brasilian Highlands, the Atacama Desert, and the caatinga and campos cerrados of Brasil.

This volume is organized in much the same way as was the symposium, except that my introductory chapter provides an overview of the South American herpetofauna. Chapter 2 deals with the fossil record of amphibians and reptiles in South America, and Chapters 3 and 4 are concerned with the relationships of the South American herpetofauna with those of Africa and Australia. The Quaternary biogeography of the continent is the subject of Chapters 5–7. Treatments of regional herpetofaunas are found in Chapters 8–15, and the



Participants in the Symposium on the South American Herpetofauna held in Lawrence, Kansas, 11–13 August 1977. Front row (left to right): Alberto Veloso M., Beryl B. Simpson, Jaime E. Péfaur, Ana María Báez, José M. Cei. Second row: Lars Brundin, Thomas E. Lovejoy, Donn E. Rosen, Jürgen Haffer, Thomas H. Fritts, Ramón Formas, Raymond F. Laurent. Back row: William E. Duellman, James R. Dixon, Marinus S. Hoogmoed, John D. Lynch, W. Ronald Heyer, Michael J. Tyler, José M. Gallardo.

final chapter is devoted to the conservation of the herpetofauna.

I am grateful to the contributors to this volume for their scholarly efforts and for their patience and understanding while it was being produced. For their participation in the symposium, I thank the contributors and Lars Brundin, Thomas H. Fritts, W. Ronald Heyer, Jaime E. Péfaur, Donn E. Rosen, and Alberto Veloso M. Their enthusiastic participation contributed a high level of scholarly interaction, as well as much good cheer.

During the editing of this volume I called upon many colleagues to review manuscripts. The quality of the papers included herein benefited from reviews by Avelino Barrio, Lars Brundin, Richard Estes, Thomas H. Fritts, Steven Gorzula, W. Ronald Heyer, Philip S. Humphrey, Jean Lescure, Alan E. Leviton, John D. Lynch, Larry D. Martin, Braulio Orejas-Miranda, Jaime E. Péfaur, Alan H. Savitzky, Beryl B. Simpson, Linda Trueb, T. van der Hammen, Alberto Veloso M. and Richard G. Zweifel. The drawings for many of the papers were executed by Debra K. Bennett, Staff Illustrator of the Museum of Natural History at The University of Kansas. Jaime E. Péfaur translated many of the summaries and edited the Spanish of others. Linda Trueb's competent editorial review of the manuscripts is evident in their consistency and style. Rose Etta Kurtz retyped many pages of manuscript, and Rebecca A. Pyles painstakingly worked on the index. To all of these persons I owe a debt of gratitude for their endeavors in behalf of this volume.

Throughout the early phases of development and organization of the symposium, as well as during the production of this volume, Philip S. Humphrey, Director of the Museum of Natural History, has provided advice, encouragement and support. Ronald K. Calgaard, Vice Chancellor for Academic Affairs, and George R. Waggoner, Associate Vice Chancellor for International Programs, The University of Kansas, gave enthusiastic support for the symposium. Richard F. Treece of the Bureau of Conferences and Institutes coordinated the logistics of the meetings. Without their interest and aid the symposium and this volume would not have been possible.

Financial support for bringing together the participants in the symposium was generously provided by the National Science Foundation (DEB 76-16767), the World Wildlife Fund (WWF-US-71) and the Office of Academic Affairs, The University of Kansas. Support for the preparation of the index was provided by a grant from the General Research Fund of The University of Kansas.

William E. Duellman
Lawrence, Kansas
September 6, 1979

CONTENTS

10. The Herpetofauna of the Guianan Region

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Although this paper deals with a highland fauna, it is not limited to the reptiles and amphibians that occur at elevations of more than 1000 m. One of the main reasons for this is that "highlands" above 1000 m in the Guiana area are few and occupy only a very small part of the total area of the Guiana Shield. Another reason is that our knowledge of the herpetofauna at higher elevations in Guiana is still very fragmentary. These facts prompted me to deal with the herpetofauna of the entire Guiana Shield.

The coast of the Guianas was discovered in 1499 by Alonso de Ojeda and Amerigo Vespucci. After the discovery of the so-called "Spanish Main" or "Wild Coast," numerous expeditions tried to explore the interior in search of the fabulous El Dorado. Most famous of these adventurers was Sir Walter Raleigh, who undertook several expeditions into the interior of Guiana. Zoologically, these expeditions were of no importance whatsoever. From about the beginning of the 18th Century, zoological specimens, mainly from Surinam, started to reach Europe, and an important percentage of the species of reptiles and amphibians described by Linnaeus in 1758 originated from the Guianas. One of the first scientific explorers of the interior was Von Humboldt, who in 1801 visited the Río Orinoco and the Cassiquiare Canal (Gleason, 1931). In 1835 Sir Robert Schomburgk started his explorations in Guyana and adjacent countries in order to settle the frontiers. During these explorations, zoological collections were made that supplied a wealth of new data. Since Schomburgk's travels, an increasing number of scientific expeditions penetrated into the interior of lowland Guiana and it would lead us too far astray to try to deal with them here in any detail. I make an exception for the expeditions exploring the tepuis in Venezuela and Guyana, several of which even at the present day remain unvisited. The most renowned of these tepuis is Roraima with an altitude of 2810 m, discovered in 1838 by Robert Schomburgk and climbed for the first time in 1884 by Im Thurn and Perkins.

The first zoological collection ever made near any tepui was assembled there in 1842 by Richard Schomburgk. Other collections were made at the foot in the 1880's. The first herpetological specimens from the summit were secured by Quelch and McConnell in 1894. In 1898 they made a second expedition to the summit plateau. The material of these expeditions contained several new species. Boulenger (1895, 1900) studied them and described the frogs *Oreophrynella quelchii*, *O. macconnelli*, *Otophryne robusta* and *Hylodes marmoratus*, and the lizards *Neusticurus rudis* and *Euspondylus leucostictus*. Of these species, only the first and the last came from the summit of the mountain; the other species were collected at the base. The next zoological expedition, on a much larger scale and under the auspices of the American Museum of Natural History, visited Roraima in 1927–28, spending two weeks on the summit and about two months at the base (Tate, 1928, 1930a,b, 1932, 1939; Chapman, 1931). Among the material collected were several reptiles and amphibians. In 1971, 1973 and 1974 Roraima was visited again, this time by parties with herpetologists as members (Warren, 1973). Their collections contained many novelties.

In 1928 Mount Duida, at the western end of the series of tepuis, was explored zoologically. The expedition was the first that succeeded in climbing the mountain and spent three months at the summit. Among the herpetological material collected were the types of the teiid lizards *Pantodactylus tyleri* and *Arthrosaura tatei*, of the hylid frog *Stef-*

ania goini, and of the leptodactylid frog *Elosia duidensis*. In 1937–38 Auyantepui was zoologically explored. From 1938 until the present, considerable exploration took place in the tepui region, mostly ornithological and botanical, but as a by-product many herpetological specimens were collected, some of which at the time being new to science were described by Roze (1958a,b; Auyantepui, Chimantátepui), Rivero (1961, 1965, 1966, 1967a,b, 1968a–d, 1970, 1971; Duida, Marahuaca, Chimantátepui, La Escalera region and other tepuis) and Lancini (1968; Cerro Jauá). The most recent biological exploration of some large tepuis were the expeditions to Cerro Jauá and Sarisariñama in 1974 and to Cerro Yapacana in 1978. These were some of the rare expeditions in which herpetologists participated (Nott, 1975; Orejas-Miranda and Quesada, 1976). The herpetological results of these expeditions have not yet been published.

DELIMITATION AND DESCRIPTION OF GUIANA

Guiana is the area bordered by the Río Orinoco, the Cassiquiare Canal (connecting the Orinoco and Amazon drainages), and the Río Negro in the west, by the Rio Amazonas in the south and by the Atlantic Ocean in the north and the east. The area comprises three political units in their entirety, namely, Guyana, Surinam and French Guiana. Of Venezuela it comprises the Estado Bolívar and the Territorio Federal Amazonas, known under the common denomer Guayana. Of Brasil it comprises the Territorio do Amapá, the Territorio de Roraima and those parts of the states of Pará and Amazonas that are situated north of the Rio Amazonas and Rio Negro. Recently Lescure (1977) and Descamps et al. (1978) defined Guiana as the area bordered in the west by the Río Barama (Venezuela) and in the southeast by the Rio Araguari (Brasil). The southern border would be formed by the watershed between rivers emptying directly into the Atlantic Ocean and rivers belonging to the Amazonian drainage. In my opinion, this definition of Guiana is artificial and not in accordance with the biogeographical and geographical data (Fig. 10:1). The Serra Acarai and the Tumuc Humac Mountains, forming the divide between the French authors' Guiana and Amazonia apparently do form a geographical barrier for a number of endemic species (mainly frogs), but this is too small a proportion of the entire fauna to justify the definition of the Guiana area as they do. Far more species are spread on both sides of the divide and occur both in the Orinoco and Amazon Basin (Haffer, 1974; Müller, 1973). In a discussion of the Guiana herpetofauna I think it is better to take into consideration biogeographical data of the majority of the (herpeto)fauna being studied, rather than rely only on those of some endemic frogs. In that way the biogeographical definition of Guiana, as accepted here, agrees closely with the geographical, geological and climatological data. However, there are good grounds for considering the Guiana of the French authors as a subregion of the Guiana as here defined.

Geologically, this area is a unit known as the Guiana Shield (Gansser, 1954; Fittkau, 1974), of which small parts are situated west of the area as here delimited (Fig. 10:2). Along the edges, notably in the north, the east and the south, there are belts of alluvial deposits; however, the core is made up of pre-Cambrian metamorphic and igneous rocks. Together with the Brasilian Shield, it can be considered as part of the geological foundation of South America. Since Paleozoic times these shields have not been submerged. During the Mesozoic both shields were connected, for the Amazon was not yet present. During the Late Cretaceous the area was slightly uplifted and the first signs of the present Amazon Basin became visible. In the Tertiary there was a further uplift (Haffer, 1974). The higher, central parts of the Guiana Shield are covered with sandstone remnants of the Roraima Formation. Deposition of this sandstone took place in Proterozoic time, 1600–1800 m.y.b.p., as stream and delta deposits laid down in continental to epicontinental environments (Priem et al., 1973). After uplift, this formation covered the Guiana Shield as an extensive sandstone plateau or tableland, on which the early Guianan flora

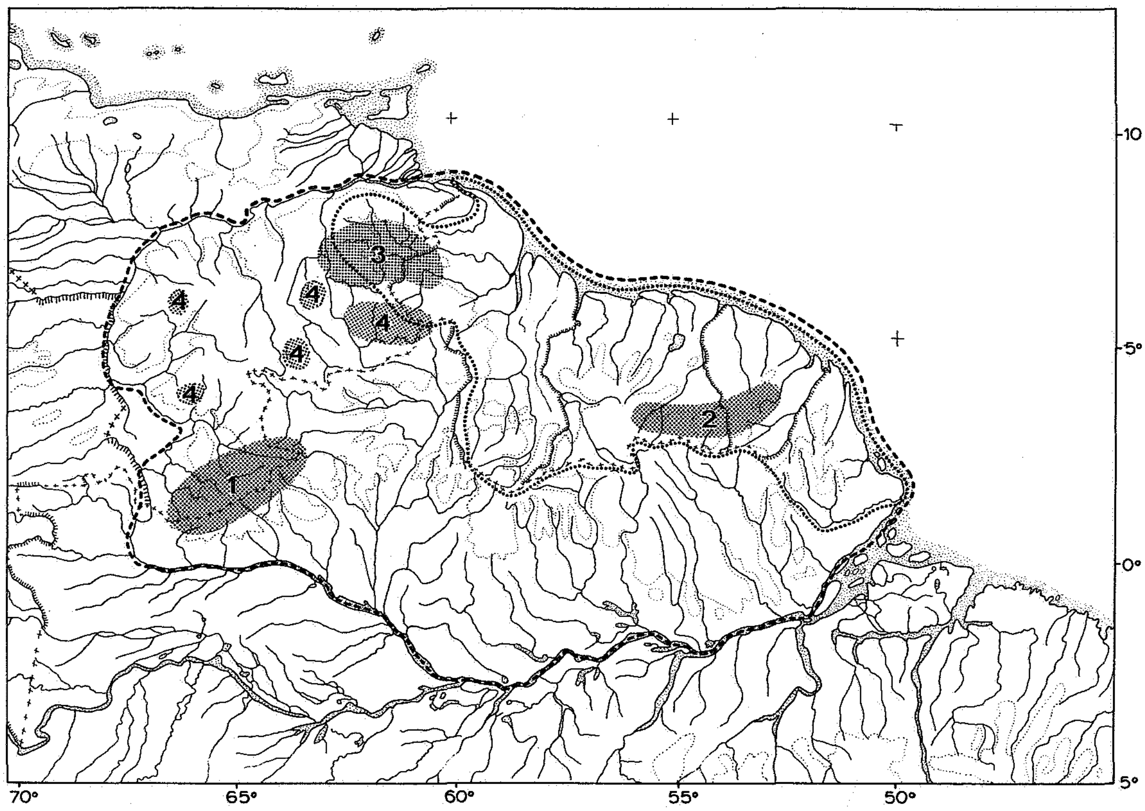


Fig. 10:1. Map of Guiana, showing the borders of the area as here defined (heavy broken line) and as defined by Descamps et al. (1978) and by Lescure (1977) (heavy dotted line). Presumed forest refugia are gray and indicated by numbers: 1 = Imerí Refuge, 2 = Guiana Refuge, 3 = Imataca Refuge, 4 = Tepui Refuges. The line of fine dots (in this and the following maps of Guiana) represents the 200 m contour line.

Mapa de la Guayana, mostrando los límites del territorio definido aqui (linea entrecortada gruesa) y el definido por Descamps et al. (1978) y por Lescure (1977) (línea gruesa punteada). Supuestos refugios forestales en gris, indicados con números: 1 = Refugio de Imerí, 2 = Refugio de Guayana, 3 = Refugio de Imataca, 4 = Refugios de Tepuyes. La línea punteada fina (en este y los siguientes mapas) representa la línea de contorno de 200 m.

developed (Maguire, 1970). During the Cretaceous and Tertiary uplift of the area, erosion shaped the present-day table mountains or tepuis. These mountains consist of layered, unfossiliferous, pink sandstones, with dolerite dikes and sills, reaching a maximum thickness of about 2400 m in Auyantepui in southeastern Venezuela and decreasing to 700 m in the Tafelberg in central Surinam (Haffer, 1974). At present, the Roraima Formation covers an area of about 450,000 km^2 and is spread over a total area of 1,200,000 km^2 in Venezuela, Guyana, Brasil and Surinam (Priem et al., 1973). The greater part of the Roraima sandstone is concentrated in the Gran Sabana region of Venezuela and the adjacent parts of Brasil and Guyana, with many isolated remnants in the western part of the Estado Bolívar and in the Territorio Federal Amazonas and two outlying remnants in eastern Guyana and in central Surinam (Bisschops, 1969; Priem et al., 1973) (Fig. 10:2). Some geologists (e.g., Priem et al., 1973:1677) are of the opinion that "It is impossible to decide whether occurrences represent erosional remnants of a once-continuous cover or sediments deposited in a number of isolated basins." However, most geologists and biologists regard the present-day sandstone mountains as remnants of a once-continuous sandstone cover. Also, one could imagine a combination of the possibilities, in which the western

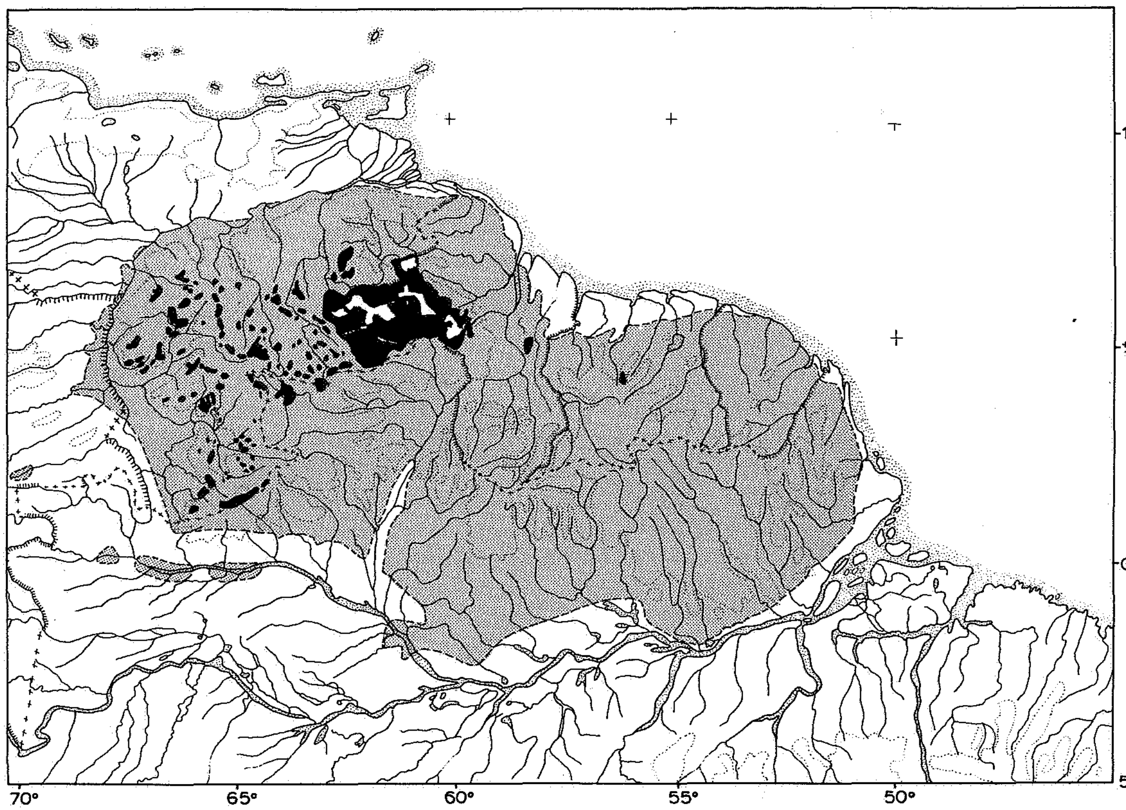


FIG. 10:2. Map of Guiana showing the extent of the Guiana Shield (gray area) and of the Roraima sandstone formation (black). The white areas in the sandstone represent gabbro (after Bisschops, 1969; Gansser, 1954; Priem et al., 1973).

Mapa de la Guayana mostrando la extensión del Escudo Guayaní (gris) y de la formación Roraima (negro). Las areas blancas en el gres de Roraima representan gabbro (según Bisschops, 1969; Gansser, 1954; Priem et al., 1973).

Roraima Formation once formed a continuous cover and the two outlying areas in Demerara and Surinam could have been deposited in isolated basins. However, decisions on this subject should be reached by geologists, although perhaps biologists may contribute to the solution. In this paper I adhere to the view that the tepuis are remnants of a once-continuous formation. It seems useful to state that the arch of sandstone tepuis in southern Colombia, west of the Río Orinoco, and ending quite close to the Andes in the Sierra de Macarena, is not of the same as the Roraima Formation (Lescure, 1977). This sandstone is much younger and probably represents a deposition of erosional products of the Roraima Formation (Haffer, 1974; Paba-Silva and Van der Hammen, 1960). These tepuis probably arose by "Block faulting in conjunction with the Andean uplift toward the end of the Tertiary and at the beginning of the Pleistocene" (Haffer, 1974).

The Guiana Shield consists of an elevated portion in the west, rising from sea level to well over 1000 m in relatively extensive areas. This portion bears the sandstone tepuis of which the highest attain a height of 2810 m (Mount Roraima) and 3014 m (Serra de Neblina). These tepuis are mostly flattopped, with perpendicular cliffs several hundred meters high separating the plateau summits from the talus formed by the accumulation of erosional products at the base of the cliffs (Figs. 10:3–4).

The western part is separated from an eastern elevated part by a depression formed by the river systems of the Rio Branco and the Essequibo River, which may be connected

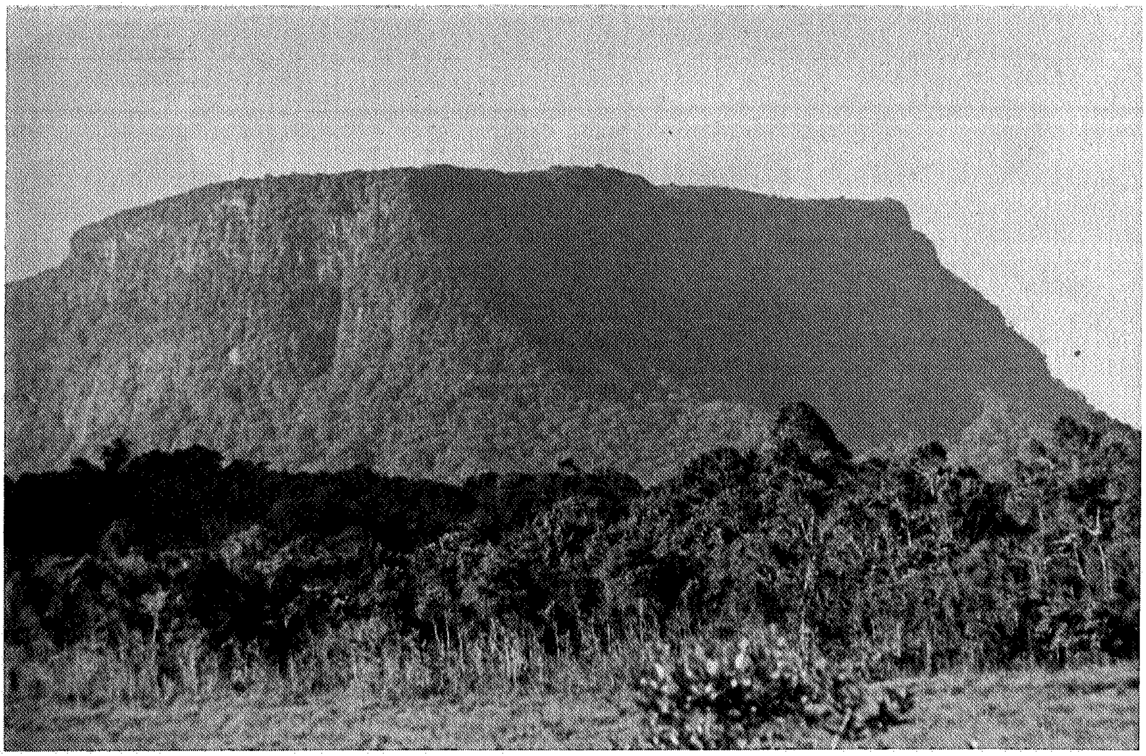


FIG. 10:3. The Tafelberg in Surinam, the easternmost remnant of the Roraima formation. Note the flat top, the steep, bare upper reaches of the flanks and the sloping talus covered with forest.

La Montaña Tafelberg en Surinam, el residuo más oriental de la formación Roraima. Observase la cumbre aplanada, las flancos escarpados y rasos en su parte superior y el talud inclinado y cubierto de selva.

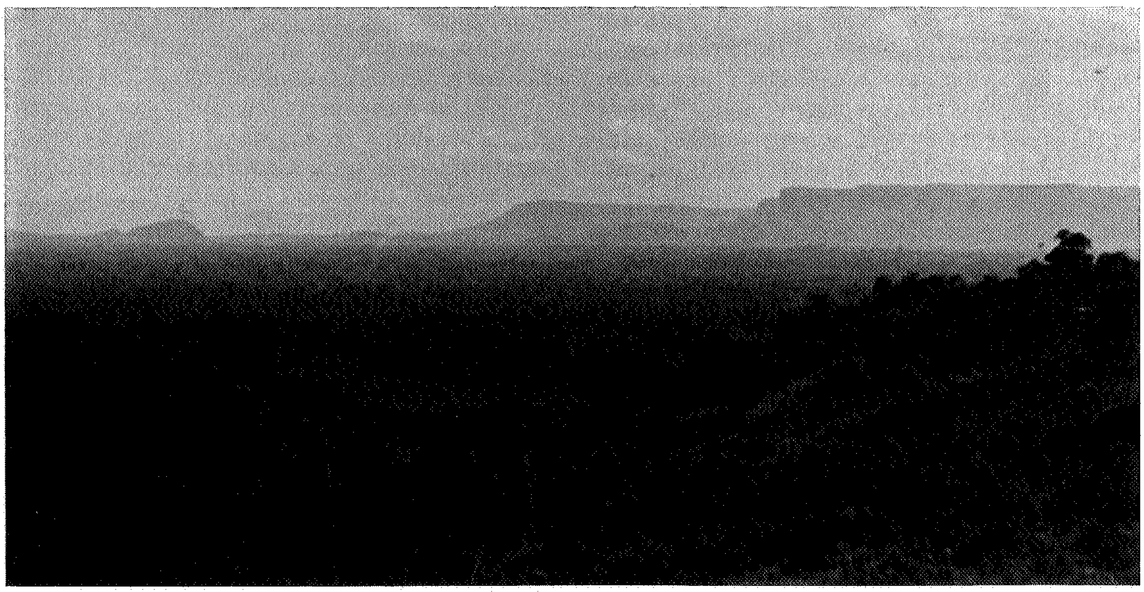


FIG. 10:4. View of several tepuis south of El Manteco, Estado Bolívar, Venezuela.

Vista de algunos tepuyes al sur de El Manteco, Estado Bolívar, Venezuela.

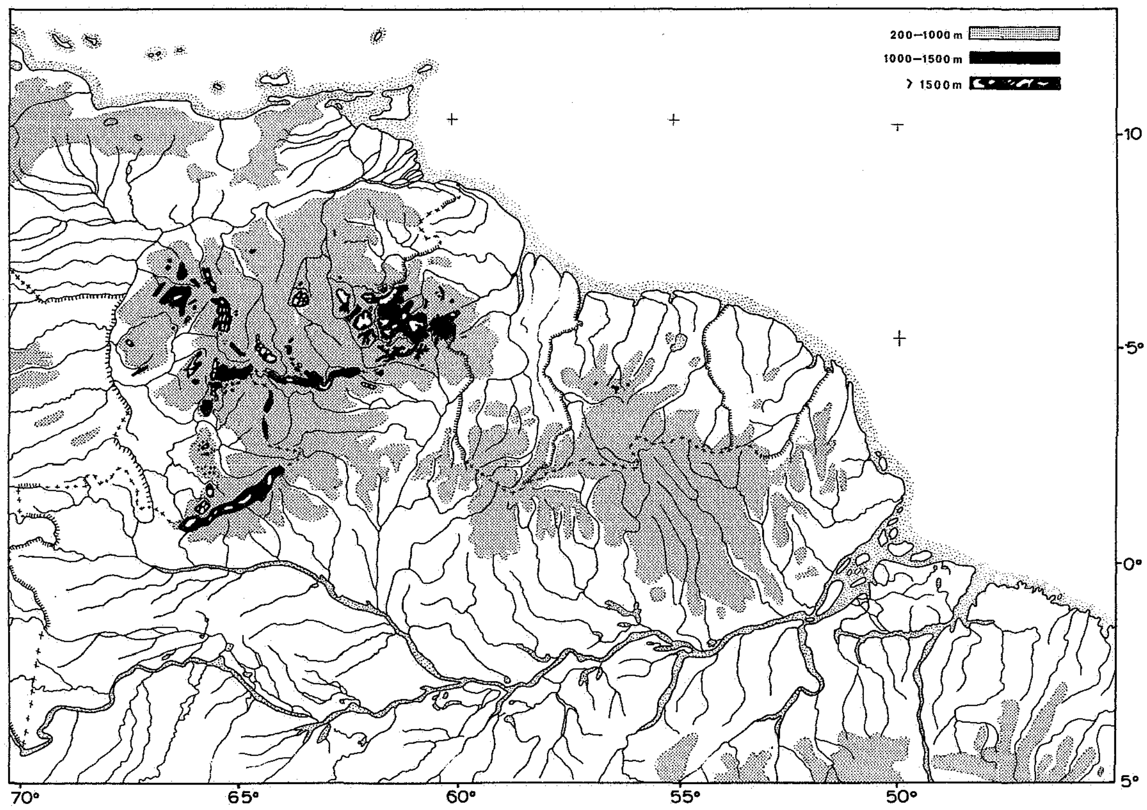


FIG. 10:5. Map of Guiana with the contour lines of 200, 1000 and 1500 m (after Mayr and Phelps, 1967). *Mapa de la Guayana con líneas de contorno de 200, 1000 y 1500 m (según Mayr y Phelps, 1967).*

during the rainy season when large areas are inundated. The eastern part is much lower than the western one, reaching a maximum height of 1280 m (Julianatop) in central Surinam. From the divide between the Amazon Basin and rivers flowing north to the Atlantic Ocean (nowhere over 1000 m high), the country gradually slopes down to sea level. Thus, although the topography of eastern Guiana may be rather rugged, with many mountain ranges and valleys separating them, the area hardly ever exceeds 1000 m. In western Guiana, the topography is more or less the same, but on a higher level, with the consequence that more extensive areas are over 1000 m. However, superimposed on the Guiana Shield in this region are sandstone tepuis that may reach elevations of almost 3000 m (Fig. 10:5). The Guiana Highlands are also known as Pantepui.

The greater part of the area is covered by tropical rainforest, but savannas also play an important role. In the western and northwestern portion of the shield there are savannas more or less continuous with the llanos of central Venezuela. In the three Guianas there is a band of coastal savannas on white sand, reaching from Georgetown in the west to Cayenne in the east. East of Cayenne and in Amapá the white sand is absent and some extensive swamps in that region are dry savannas in the dry season. In Amapá this coastal belt is bordered on the west by a belt of cerrado—savanna with isolated trees. Isolated, extensive savanna complexes of the cerrado type are present (Hills, 1969) in southwestern Guyana (Rupununi), in southeastern Venezuela (Gran Sabana) and on the border between Surinam and Brasil (Sipaliwini/Paru savannas). Smaller, isolated savannas occur in Surinam and in Venezuela both on the Roraima sandstone and on other substrates (Fig. 10:6). On the higher points, starting at about 800 to 1000 m, cloud forest occurs with

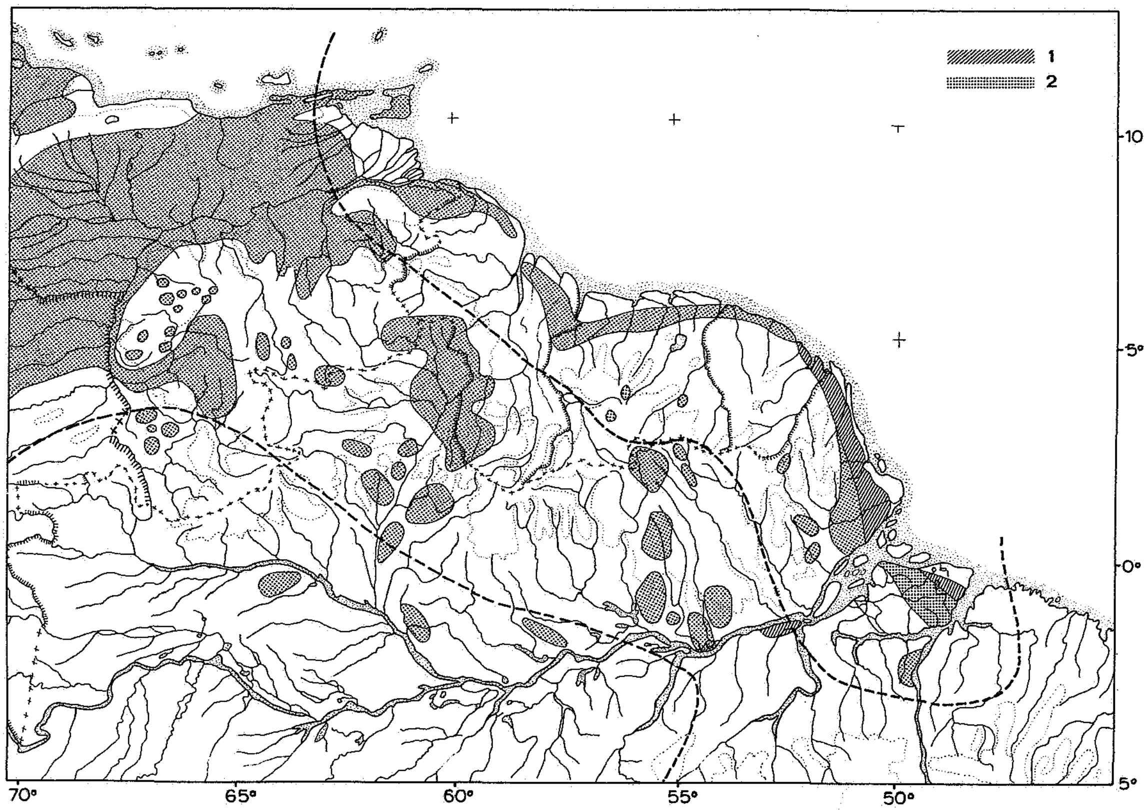


FIG. 10:6. Map of Guiana showing the distribution of forest and savannas. Forested areas white, savannas gray, inundated savannas hatched. The zone with lower rainfall (cf. Fig. 10:7) has been indicated with heavy broken lines (after Hills, 1969; Müller, 1973; Oldenburger et al., 1973; Prance, 1973; Romariz, 1974 and personal field data).

Mapa de la Guayana mostrando la distribución de selva y sabana. Selva en blanco, cerrado en gris, campo rayado. La zona menos lluviosa (cf. Fig. 10:7) se ha indicado con una línea entrecortada gruesa (según Hills, 1969; Müller, 1973; Oldenburger et al., 1973; Prance, 1973; Romariz, 1974 y observaciones personales).

thick layers of mosses covering the trees, shrubs and the ground. This is especially so on the talus of many of the tepuis. The plateau summits of the smaller tepuis have only a shallow layer of soil, which is insufficient to support forest; thus, the vegetation is low, often savannalike. The plateau summits of the larger (more extensive) tepuis is more diversified, and in some places a sufficiently deep layer of soil has accumulated to support moderately high forest; however, in other places there is only sparse vegetation (Chapman, 1931; Gleason, 1931; Maguire, 1945, 1955, 1970; Mayr and Phelps, 1967; Tate, 1928, 1930a,b, 1932, 1938a,b, 1939; Tate and Hitchcock, 1930).

The climate of the region under discussion is characterized by two dry and two rainy seasons per year. Their duration and the period of the year in which they fall are somewhat variable, and at higher elevations the distinction between dry and rainy seasons may be hardly evident, but in general this division holds true for the greater part of the area. Within the area a wide zone with distinctly lower rainfall extends northwest-southeast connecting the llanos of Venezuela with the caatinga and cerrado region of central Brasil (Figs. 10:6–7). Within this zone, which roughly covers the extreme southwestern part of Surinam, southern Guyana, southeastern Venezuela and the Guianan part of Pará, the annual rainfall is 2000 mm or less. To the northeast and to the southwest the

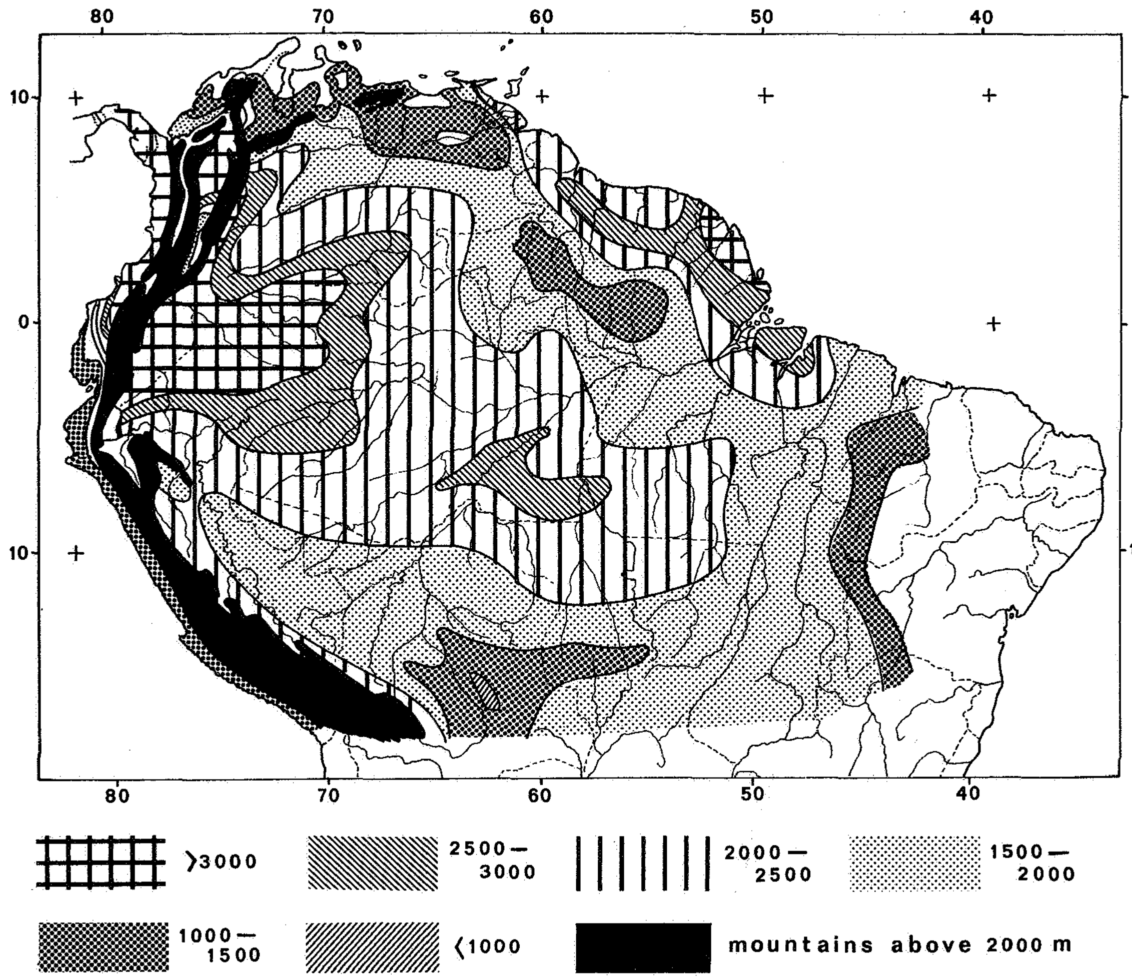


FIG. 10:7. Rainfall (mm) distribution in northern South America (after Prance, 1973; Reinke, 1962). *Distribución de la lluvia (mm) que cae anualmente en la parte norte de la América del Sur (según Prance, 1973; Reinke, 1962).*

annual rainfall increases, reaching maxima of over 3000 mm in northeastern French Guiana and coastal Amapá and of some 2500 to 3000 mm in the upper Orinoco region (Reinke, 1962; Prance, 1973). Mean annual temperatures are between 24° and 27°C in the lowlands and decrease with increasing altitude.

During the last few years it has become increasingly clear that Pleistocene and Holocene climatic changes had a profound influence on the vegetation of northern South America, especially in Amazonia and adjacent regions. It is presumed that during dry climatic phases the rainforest disappeared from large stretches of the Amazon Basin and was restricted to refuges, mostly along its periphery (Brown et al., 1974; Haffer, 1969, 1974, this volume; Vanzolini, 1970a). Inversely, during the wet climatic phases the rainforest spread again from the refugia and the savanna vegetation and fauna retreated into refuges. Of importance in this connection are the Guiana, Tepui and Imerí forest refuges of Haffer (1969, 1974); the Guiana (forest), Pantepui (montane forest) and Roraima (savanna) centers of Müller (1973); and the Guiana, Imataca and Imerí refuges of Prance (1973), all of which are situated within the limits of the area considered here (Fig. 10:1). The aforementioned belt with a lower precipitation played an important role in the distribution of plants and animals during the different climatic periods. At present, the savanna complexes of interior Guiana are situated in this belt (Fig. 10:6). However, during dry climatic phases probably much larger areas of it were covered with savanna, thereby providing a dispersal route for savanna inhabitants, either to the north or to the south, and at the same time forming a barrier to east-west dispersal of forest inhabitants. On the other hand, both areas with higher rainfall, adjacent to this dry belt, are thought to be the areas where forest refuges were situated during arid phases—to the northeast the Guiana refuge, to the southwest the Imerí refuge. During wet climatic phases, the forest spread from these refuges and invaded the savanna belt, fragmenting it into several isolated savanna complexes, as is the case today (Fig. 10:6). The montane forests covering the slopes of the tepuis in southern Venezuela can be regarded as isolated occurrences of rainforest on places with favorable climatic conditions (high elevation, high rainfall) generally having unfavorable climatic, and possibly edaphic, conditions (Gran Sabana area). These forests, which are different from the tropical lowland rainforests, probably were only connected with the lowland forests during very wet climatic phases. Although Müller's concept of the Guiana center is much wider (and based on several different groups) than Haffer's, Prance's and others' Guiana refuge, I think we can synonymize the two without problems; the same is true for the Pantepui center and the Tepui refuge. There is no parallel in Müller's concepts of Haffer's and Prance's Imerí refuge. The Imataca refuge, which was postulated by Prance (1973) for plants is only substantiated further by data from butterflies (Brown et al., 1974) (Fig. 10:8).

HERPETOFAUNA

Although since 1894 quite a substantial number of reptiles and amphibians has been collected from the sandstone tepuis, only a small part of it was collected by herpetologists. This partly explains our scant and fragmentary knowledge of these groups. Thorough herpetological exploration of the tepui region, starting with the now easily accessible La Escalera region in eastern Venezuela, probably will provide us with many interesting finds. Because our present knowledge is so fragmentary, it is often difficult to decide whether a certain species is really restricted to one tepui or not. The available data permit some zoogeographical conclusions, but those regarding the so-called endemics certainly have to be drawn with much reserve.

Presently a total of 408 species of reptiles and amphibians is known to occur in the Guiana region (Table 10:1, Appendix 10:1). Seventy-six species are represented by 108 subspecies, which raises the number of species-group taxa for the region to 440. The herpetofauna of Guiana can be allocated to eight groups, which in turn can be partly subdivided.

1. Endemic in Guiana region:
   A. Highland (over 1000 m)—18 amphibians, 9 reptiles.
   B. Lowland (below 1000 m)—74 amphibians, 50 reptiles.
2. Amazonian:
   A. Periferal along western and northern margin of basin—10 amphibians, 19 reptiles.
   B. With disjunct populations in upper Amazonia and near the mouth of the Amazon—2 amphibians, 1 reptile.
   C. Species of Amazon Basin occurring on southern edge of Guiana and along eastern margin, where they may reach French Guiana—3 amphibians, 11 reptiles.
   D. Widespread Amazonian, occurring throughout greater part of Guiana—39 amphibians, 62 reptiles.
3. Widespread species (distribution extending from México or Central America over entire cis-Andean tropical South America): 12 amphibians, 35 reptiles.
4. Species reaching their eastern distribution limit on the Guiana Shield, from Central America, northwestern South America or upper Amazonia: 11 amphibians, 17 reptiles.

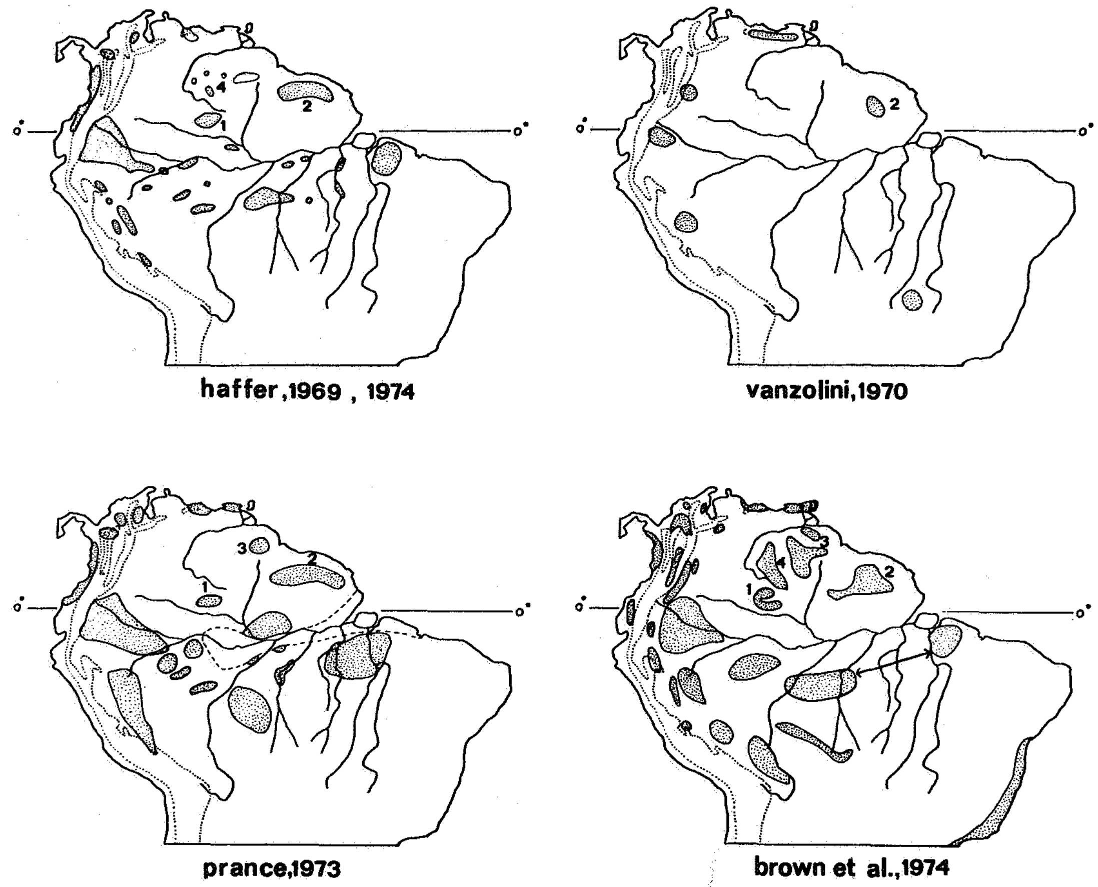


FIG. 10:8. Location of forest refugia during arid periods according to several authors; numbers as in Fig. 10:1.
Situación de los refugios de selva durante los períodos secos según algunos autores; los numeros como en la Fig. 10:1.

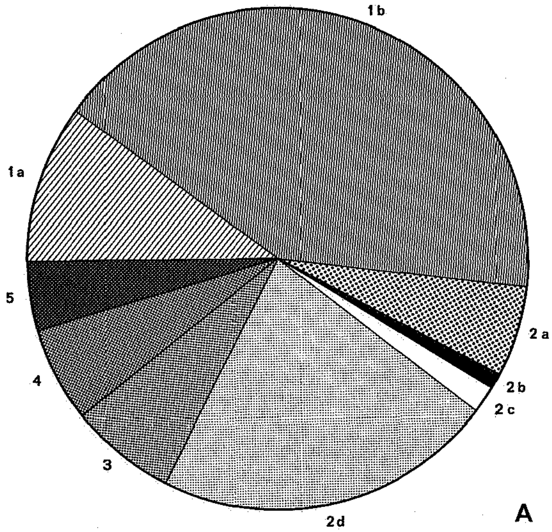
5. Species from southeastern or central Brasil reaching Guiana, mostly not farther than French Guiana, some reaching Surinam or even Venezuela: 8 amphibians, 13 reptiles.
6. Cosmopolitan species: 0 amphibians, 6 reptiles.
7. Species imported from the Caribbean region: 1 amphibian, 4 reptiles.
8. Species with limited or uncertain distributions that may occur in the region: 0 amphibians, 3 reptiles.

The last three groups in the tabulation above are of no importance in the following considerations. The five cosmopolitan species of sea turtles and one species of cosmopolitan gecko are of no importance here. It is evident that the imported species do not need further attention. Of the three species in the last group, it has not been established beyond doubt that they occur in the Guiana region. Thus, there remain five important groups, totaling 177 amphibians and 217 reptiles, that reflect the complicated history of the Guiana herpetofauna and that are dealt with in detail later.

Considerable differences exist between the percentages of reptiles and amphibians in five different groups and subgroups (Fig. 10:9, Table 10:2). These groups are highland (1A) and lowland (1B) endemics, disjunct (2B) and widespread (2D) Amazonian, and wide-

TABLE 10:1.—Composition of the Guianan Herpetofauna. The columns contain the total numbers of species in a given family that inhabit the Guianas and the numbers of species that are endemic to the Guianas.

Family	Species Total	Species Endemic
Anurans		
Pipidae	2	1
Dendrobatidae	15	9
Ranidae	1	--
Leptodactylidae	38	12
Bufonidae	17	8
Hylidae	75	43
Pseudidae	2	--
Centrolenidae	7	6
Microhylidae	8	4
Total Anurans	165	83
Caecilians		
Rhinatrematidae	2	2
Typhlonectidae	2	1
Caeciliidae	9	6
Total Caecilians	13	9
Total Amphibians	178	92
Chelonians		
Cheloniidae	4	--
Dermochelyidae	1	--
Kinosternidae	1	--
Testudinae	2	--
Emydidae	1	--
Pelomedusidae	4	--
Chelidae	5	--
Total Chelonians	18	--
Crocodilians		
Crocodylidae	1	1
Alligatoridae	4	--
Total Crocodilians	5	1
Snakes		
Anomalepidae	2	1
Leptotyphlopidae	8	4
Typhlopidae	4	1
Aniliidae	1	--
Boidae	5	--
Dipsadidae	6	1
Colubridae	91	20
Elapidae	9	2
Crotalidae	6	--
Total Snakes	132	29
Lizards		
Gekkonidae	13	4
Iguanidae	18	3
Scincidae	1	--
Teiidae	33	16
Total Lizards	65	23
Amphisbaenians		
Amphisbaenidae	10	6
Total Amphisbaenians	10	6
Total Reptiles	230	59
Total Amphibians and Reptiles	408	151



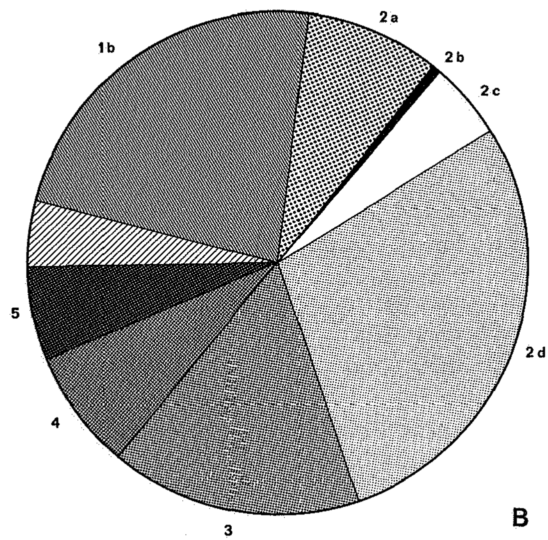


FIG. 10:9. Proportion of the total numbers of species accounted for by each group; numbers of groups as in Table 10.2. A = amphibians, B = reptiles.

Porcentaje que representa cada grupo del número total de especies; números de grupos como en la Tabla 10:2. A = *anfibios,* B = *reptiles.*

spread (3). Both in the widespread Amazonian and in the generally widespread species the percentage of reptiles is distinctly higher than that of amphibians; moreover, in the species reaching their eastern distribution limits in Guiana (4), and in the species com-

TABLE 10:2.—Composition of the Guianan Herpetofauna.
The columns contain the total number of species having a certain distribution and the percentage this group forms of the total number of species in the Guianan Region.

Type of distribution	Amphibians Number	Amphibians Percentage	Reptiles Number	Reptiles Percentage	Total Number	Total Percentage
1. Endemics						
A. Highland	18	10.17	9	4.15	27	6.85
B. Lowland	74	41.81	50	23.04	124	31.47
		51.98		27.19		38.32
2. Amazonian						
A. Periferal	10	5.64	19	8.75	29	7.36
B. Disjunct	2	1.12	1	0.46	3	0.76
C. Basin	3	1.69	11	5.06	14	3.55
D. Widespread	39	22.03	62	28.57	101	25.63
		30.48		42.84		37.30
3. Widespread	12	6.77	35	16.12	47	11.92
4. Reaching eastern limit	11	6.21	17	7.83	28	7.10
5. From SE. or C. Brasil	8	4.51	13	5.99	21	5.32
Subtotal Guiana Region	177	99.95	217	99.97	394	99.96
6. Cosmopolitan	–		6		6	
7. Imported from Caribbean	1		4		5	
8. Uncertain distribution	–		3		3	
	178		230		408	

ing from the southeast (5), the percentage of reptiles is slightly higher than that of amphibians. In my opinion, this is the clue to the explanation of the differences observed. It is a reflection of the greater mobility of reptiles, as compared with the more sedentary habits of amphibians, which are restricted by their mode of reproduction. As there is a strict dependence on the kind of water (standing or running, large or small body of water), which for most species is very specific, this further restricts the possibilities for amphibian dispersal. Also species that have direct development on land are still dependent on water in the form of a high humidity. This explains the high endemism of this group in Guiana and also the higher percentage of disjunct Amazonian species of amphibians (Lynch, this volume). In all cases, the amphibians did not have the chance to expand their ranges far beyond the region of origin or from that of isolation during one of the climatic phases. Reptiles, given the same time and being independent of water for their reproduction, had a much greater rate of dispersal and either spread beyond the borders of Guiana (and thus ceased to be endemics of that region) or closed the gap between disjunct populations of one species.

I consider those species having distributions that do not, or hardly, exceed the borders of Guiana to be endemics. This is a fairly large area. Among the endemics several subdivisions can be recognized; the one between highland and lowland endemics will be discussed later. The other subdivision is between local and wide-ranging endemics, but this is partly artificial and mainly reflects our fragmentary knowledge of the species considered to be local.

Altitudinal Distribution

Of the indubitably native species only 55 (31% of total amphibians) species of frogs and 38 (18% of total reptiles) species of reptiles (lizards and snakes) (Appendix 10:1) occur at elevations of more than 1000 m. No caecilians, crocodilians, chelonians or amphisbaenians are known from above 1000 m. Of the species occurring over 1000 m, 37 frogs and 29 reptiles also occur below 1000 m, which leaves 18 frogs (10% of total) and 9 reptiles (4% of total) restricted to elevations of more than 1000 m. All of these are highland endemics, restricted to the western part of the Guiana Shield.

Highland endemics.—Most of these species have restricted distributions, usually consisting only of the summit or talus slopes of one or a few adjacent tepuis (Figs. 10:10–11). As stated before, this either reflects our fragmentary knowledge of the herpetofauna of the Guiana Highlands, or these distributions are real and the comparable habitat on other tepuis is occupied by a related species. However, this has only been documented (and poorly so) for the endemic frog genus *Stefania*.

The bufonid genus *Oreophrynella* from Roraima and Auyantepui is considered to be a specialized derivative from the general atelopodid stock and to have evolved in isolation since the Early Tertiary or the Cretaceous (McDiarmid, 1971). The same is true for the microhylid frog *Otophryne* (not an altitudinal endemic), composed only by *O. robusta* with two subspecies—one restricted to high elevations on Chimantátepui, the other occurring in the greater part of interior Guiana at elevations of 200 to 1666 m. Like *Oreophrynella*, *Otophryne* also shows a combination of primitive, derived and unique characters. This is most easily explained by assuming that these frogs were subject to a long evolution in isolation on the sandstone formation, probably since the Cretaceous or Early Tertiary; the invasion of tropical lowland Guiana by *Otophryne* may be considered as secondary. According to Lynch (pers. comm.), the leptodactylid frog *Hylodes duidensis* belongs to an undescribed genus of the tribe Eleutherodactylini. Its relations are not clear, but it may have developed on the Guiana Shield as a highland derivative of the eleutherodactyline stock. *Stefania* is an endemic, egg-brooding hylid frog genus clearly related to the northern Andean *Cryptobatrachus*. According to Rivero (1970), these frogs can be divided into the *Stefania goini* group, with two species, and the *Stefania evansi* group with five species (and three undescribed ones). One member of the *goini* group occurs on Mount Duida in the west, the other on Chimantátepui in the east. One member of the *evansi* group occurs on Cerro Marahuaca and the others on the eastern part of the Roraima Formation. The distribution of the members of these species groups can be explained most easily by assuming that the genus *Stefania* arose from hylid stock in the Guiana Highlands, probably prior to the Oligocene. Initially, the stock split into two groups, which during the most recent uplift of the area in Mio-Pliocene times became isolated on several tepuis and since differentiated into the several species now composing the two species groups. The occurrence of *Stefania evansi* in lowland areas may be regarded, as in *Otophryne*, as being secondarily, induced by the Pleistocene climatic changes, which lowered the general temperature of the area by about 3°C (Van der Hammen, 1974).

Species showing a slight degree of Andean relationships are members of the frog genera *Centrolenella* and *Eleutherodactylus*, and of the colubrid snake genus *Atractus*; all three genera probably evolved in or near the Andes, either in the foothills or in the lowlands, and subsequently spread to the east. However, the endemic altitudinal species belonging to these genera have no direct relations with Andean species and probably are altitudinal forms derived from lowland species. The matter is slightly different for the species of *Euspondylus*, a genus of teiid lizards of Andean origin, members of which live at medium to high altitudes in the Andes from Perú to Venezuela; two species reached the higher altitudes of the Guiana Shield, possibly during a time of Pleistocene climatic depression. The altitudinal endemics of the tree frog genus *Hyla* all apparently are related to lowland species groups.

Riolama, a monotypic, endemic teiid lizard genus restricted to the summit of Mount Roraima, is known only from the type specimen. Presumably it is related to *Leposoma* and its relatives, but its history is not clear. It may have evolved from lowland microteiids by isolation on a sandstone tableland prior to the Oligocene, as was probably the case in *Stefania*. The colubrid snakes *Liophis* and *Thamnodynastes* occur in lowland Amazonia and Guiana, but they seem to be of southern Brasilian origin and to have evolved into several altitudinal species in Guiana. The nearest relative of the iguanid lizard, *Tropidurus bogerti*, is *T. torquatus hispidus* (R. Etheridge, pers. comm.), a member of a species or

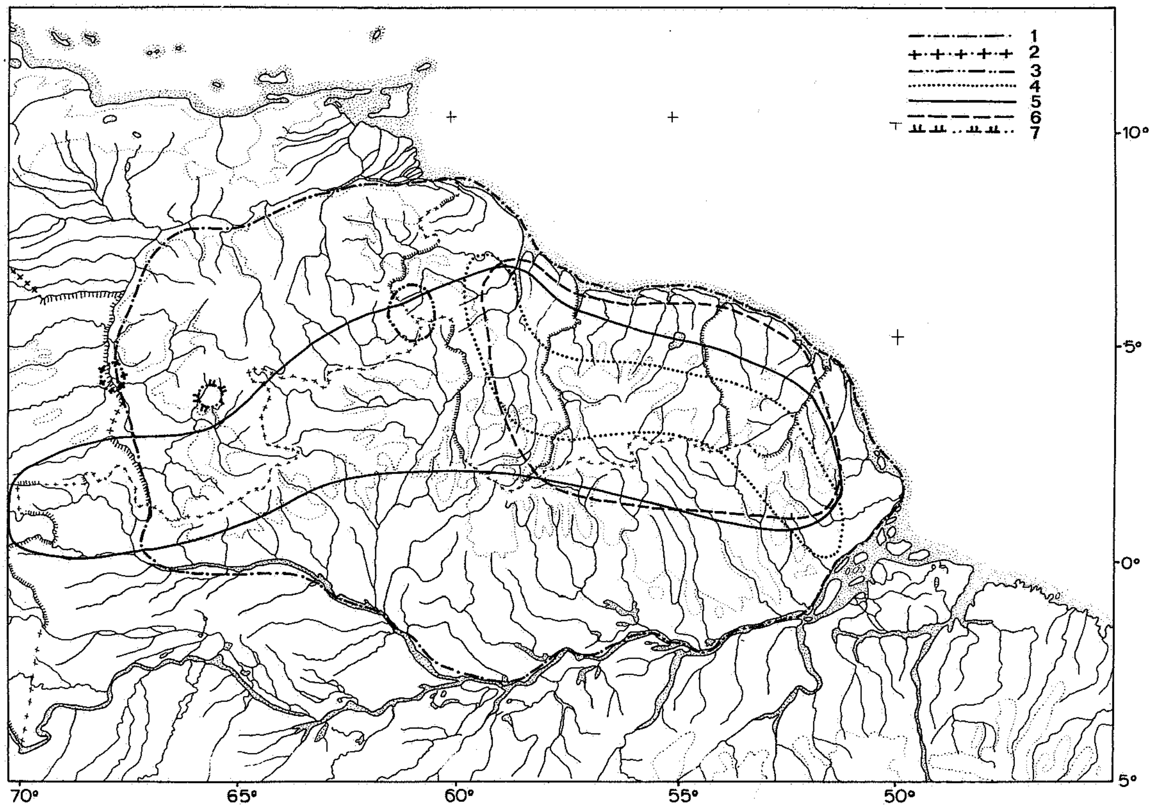


FIG. 10:10. Distribution of some endemic species within Guiana.
Distribución de algunas especies endémicas en la Guayana.
1 = *Hyla multifasciata.* 2 = *Aparasphenodon venezolanus.* 3 = *Bufo nasicus, Hyla sibleszi, Hyla lemai.* 4 = *Hyla ornatissima.* 5 = *Otophryne robusta.* 6 = *Allophryne ruthveni.* 7 = *Hyla ginesi, Stefania goini, Stefania marahuaquensis, "Hylodes" duidensis.*

species complex, which may be of southeastern Brasilian origin. The few altitudinal endemic subspecies all have evolved by isolation at higher altitudes from lowland relatives of different origins.

Attempts to explain the origin of the fauna of Pantepui have been based on the distribution of birds (Chapman, 1931; Haffer, 1974; Mayr and Phelps, 1967), mammals (Tate, 1939), frogs (Rivero, 1965) and snails (Haas, 1957). Because of different dispersal abilities and different geological ages of the groups concerned, these studies came to different conclusions. For instance, birds supposedly were able to reach Guiana from the Andes by (simply stated) flying from one mountain with suitable climate to the next. This possibility doesn't exist for the other groups. The distribution of the endemic Guianan herpetofauna can be explained with the aid of the following theories.

1. The Mountain Bridge Theory as presented by several authors (Todd and Carriker, 1922; Haas, 1957) apparently is useless, because there is no geological evidence for a connection of southern Venezuela with the Andes. As has been pointed out, the sandstone mountains (Sierra de Macarena) in southern Colombia are not the remnants of such a bridge.
2. The Plateau Theory, starting from the assumption that "a more extensive tableland probably did exist on the Guayana shield during the Mesozoic and Tertiary, prior to an intensive erosional dissection" (Haffer, 1974:163) is useful to explain the presence of several

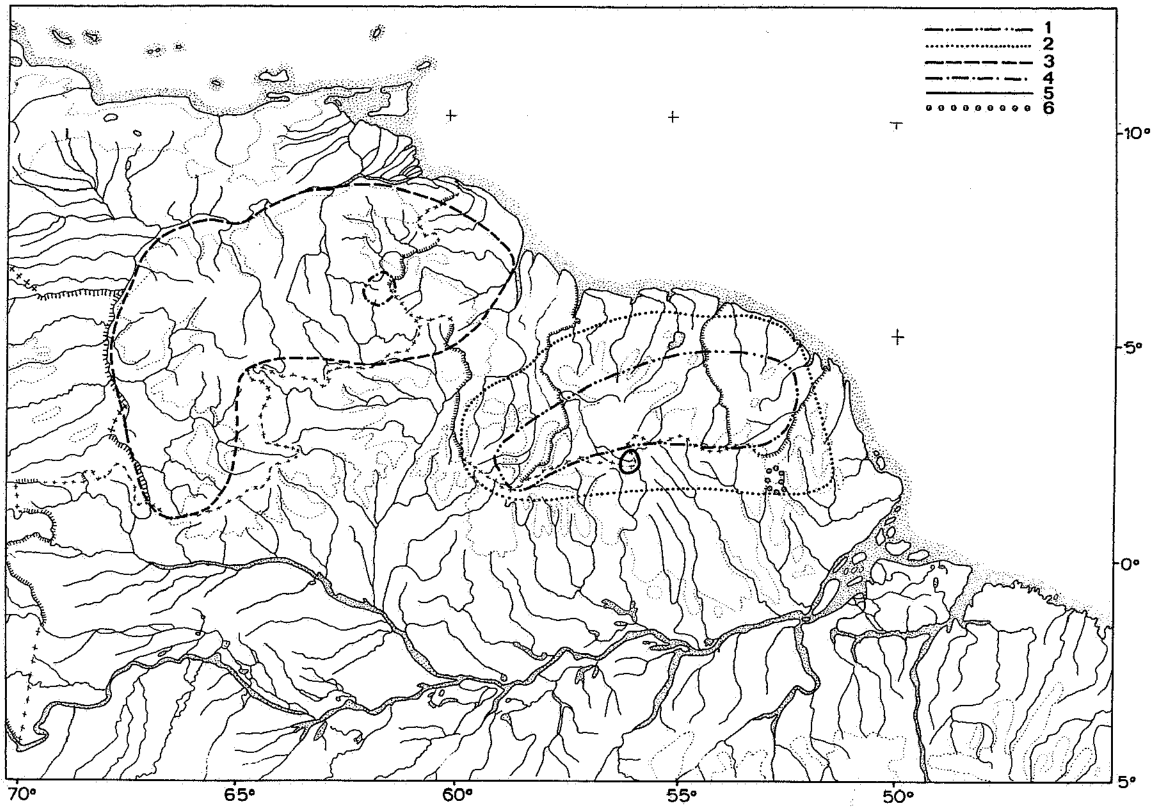


FIG. 10:11. Distribution of some endemic species within Guiana.
Distribución de algunas especies endémicas en la Guayana.
1 = *Hyla proboscidea.* 2 = *Dendrobates tinctorius.* 3 = *Dendrobates leucomelas.* 4 = *Hyla rodriguezi, Stefania scalae, Eleutherodactylus pulvinatus.* 5 = *Dendrobates azureus.* 6 = *Phyllobates pulchripectus, Amapasaurus tetradactylus.*

relicts, such as the frogs *Oreophrynella* and *Otophryne*. A slightly modified version, starting with the assumption that the Roraima Formation underwent orogenic movements that shaped it into a mountain range before erosion graded it into a plateau, which in turn was uplifted and eroded into its present shape, serves well to explain the distribution of the genus *Stefania* (Rivero, 1970).

3. The Modified Cool Climate Theory departs from the assumption that during the glacial periods of the Pleistocene, the lowlands between the Andes and Guiana, and within the Amazonian basin had a cooler climate. This indeed was true, the temperature of the lowlands having been about 3°C lower than at present (Van der Hammen, 1974), but this was not sufficient to make the lowlands subtropical instead of tropical, as had been assumed formerly (Chapman, 1931; Tate, 1939). However, it may have facilitated the dispersal of certain organisms, because all life zones on mountains shifted to lower altitudes, thus creating suitable habitats for subtropical organisms in places where they were formerly absent. These still widely-separated, subtropical habitats could have been of importance for birds. The distribution of amphibians and reptiles apparently related to Andean taxa could not have gone only via those "stepping stones" but most likely through the lowlands at times of cooler temperatures.

4. The Habitat Shift Theory assumes that part of the fauna of Pantepui was derived from tropical lowland elements that changed their habitat preference. It serves to explain the distribution and occurrence of the majority of the taxa living at higher elevations. They either differentiated in situ after invasion of the highlands by a lowland ancestor (most highland endemics) or are themselves widely distributed in the lowlands surrounding Pantepui and apparently have wide ecological amplitude.
5. The Distance Dispersal Theory, which assumes that the Guiana Highlands were colonized from distant sources by island hopping, is of no use in explaining the distribution of the herpetofauna, although it seems to be useful for partly explaining the distribution of flying organisms (mainly vertebrates) (Mayr and Phelps, 1967).

Lowland endemics.—The lowland endemics are a rather mixed group, containing species restricted to elevations below 1000 m and species occurring from sea level to well above 1000 m. Several species occur from about sea level to a maximum of 2400 m. In a number of cases [*Neusticurus tatei, N. racenisi, N. rudis* (all three teiid lizards), *Stefania evansi* (hylid frog), *Otophryne robusta* (microhylid frog)] they clearly evolved on part of the sandstone plateau and secondarily invaded the tropical lowlands. Others, like *Dendrobates steyermarki* (poison-arrow frog), *Hyla ginesi, H. benitezi, H. kanaima, H. lemai, H. sibleszi, Stefania marahuaquensis, S. woodleyi* (hylid frogs) and *Euparkerella* sp. "A" (leptodactylid frog), have narrower elevational distributions, occurring only from about 600 to 1500 m. They also probably evolved at higher altitudes and secondarily invaded the adjacent lowlands, but apparently their ecological tolerance is not so great as that of the species in the first group. The remaining species occurring above 1000 m are actually lowland species, having arisen in tropical lowlands and from there extended their range by moving up onto the sandstone plateau, often to the base of the tepuis, sometimes even to the summit.

Dendrobates steyermarki known from an isolated sandstone mountain in western Venezuelan Guiana is most closely related to Andean species of the *Dendrobates minutus* group (Silverstone, 1975). This is the only Guianan lowland species showing such a link and probably this is a relict of a formerly more widespread group, which became isolated from the main body of the group when temperatures increased during one of the Pleistocene climatic phases.

Euparkerella, with recent representatives living at low to high elevations in areas periferal to the Amazon Basin (Roraima, Andes of Ecuador and Perú, southeastern Brasil), is represented by one endemic species. Its distribution may be explained by assuming that the presently known species are the survivors of a genus that once occupied a more extensive range, covering the entire Amazon region and adjacent territories. When the range of the genus became discontinuous is not clear, but tentatively we may place that event in the early Pleistocene. It was probably caused by the evolution in the Amazon Basin of new groups of litter-adapted frogs.

There are five (monotypic) lowland endemic genera [*Allophryne* (hylid frog), *Rhinatrema* (caecilian), *Peltocephalus* (pelomedusid turtle), *Amapasaurus* (teiid lizard) and *Mesobaena* (amphisbaenian)], of which only *Allophryne, Rhinatrema* and *Peltocephalus* have more or less extensive ranges. *Amapasaurus* is restricted to a small area in eastern Guiana and *Mesobaena* to western Guiana. The ranges of the first four genera and of many endemic species coincide with that of the postulated Guiana Forest Refuge (Haffer, 1969, 1974; Lescure, 1975, 1977) or with parts of it (Figs. 10:10–11). Therefore, it seems possible that these genera arose in this refuge during the early Pleistocene. The same holds true for most of the other lowland endemic species, but here we might date the specific diversification as late Pleistocene.

Endemic subspecies of species not endemic to Guiana probably arose during one of the more recent (late Pleistocene or Holocene) dry or wet climatic phases occurring in northern South America.

A few of the lowland endemics occurring in western Guiana, mainly around the headwaters of the Río Orinoco, seem to strengthen Haffer's view of an Imerí forest refuge. These endemics include one monotypic genus (*Mesobaena*, amphisbaenian), eight species [*Aparasphenodon venezolanus* (tree frog), *Dendrobates leucomelas* and *D. steyermarki* (poison-arrow frogs), *Atractus insipidus*, *Helicops hogei*, *Liophis canaima* (all colubrid snakes), *Phyllodactylus dixoni* (gekkonid lizard), *Crocodylus intermedius* (crocodile)] and three subspecies [*Hydrops triangularis venezuelensis*, *Leptophis ahaetulla copei* (both colubrid snakes), *Micrurus surinamensis nattereri* (elapid snake)]. A similar situation is known in birds, with one endemic genus and nine endemic species (Haffer, 1974). Assuming a similar divergence rate for the organisms involved, this seems to point to at least three arid phases during which the forest fauna was isolated in this Imerí forest refuge.

Different patterns of distribution exist in Guiana. The endemic species are not evenly distributed throughout the area. As has been noted in the section on altitudinal distribution, all altitudinal endemics are restricted to the western part of the Guiana Shield, the area west of the Essequibo-Río Branco Depression. The ranges of most of the species that supposedly originated on the higher parts of the sandstone area do not extend far beyond; only a few reach the Essequibo River in the east. Exceptions, like the microhylid frog, *Otophryne robusta*, and the teiid lizard, *Neusticurus rudis*, extend their ranges beyond the Essequibo River. The Essequibo-Río Branco Depression seems to have been a barrier to the eastward distribution of a number of species, mainly Pantepui species. On the other hand, it was a barrier to the westward distribution of a number of species. The effect of this barrier is evident from the ranges of lowland endemics (Fig. 10:11). Of the 74 endemic species of lowland amphibians (Table 10:2, Appendix 10:1) 18 (24%) occur on both sides of the Essequibo-Río Branco Depression, 32 (43%) only occur east of the depression, and 24 (32%) only occur west of it. Of the 50 endemic species of lowland reptiles (Table 10:2, Appendix 10:1) 18 (36%) occur on both sides of the Essequibo-Río Branco Depression, 17 (34%) only occur east of the depression, and 15 (30%) only occur west of it. The picture changes distinctly when the altitudinal endemics also are considered. In that case the number of amphibians restricted to the western part of Guiana becomes 42 and the corresponding number of reptiles 24. The percentages change accordingly, for amphibians respectively 18 (22%), 32 (39%) and 42 (51%); for reptiles respectively 18 (31%), 17 (29%) and 24 (41%). Among the widespread endemics the proportion of reptiles is considerably higher than that of amphibians; in both the western and eastern endemics the proportion of amphibians is higher than that of reptiles, reflecting the greater mobility of reptiles. When only the lowland endemics are considered, the percentage of amphibian species restricted to the east is distinctly higher than that of species restricted to the west, in reptiles it is only slightly higher. This probably reflects the greater importance of the Guiana Refuge for amphibians, as compared to the importance of the Imerí Refuge. For reptiles, both refuges apparently were equally important. Why the Guiana Refuge was more important for amphibians than for reptiles remains a matter of conjecture. However, possibly it results from the greater dependence of amphibians on water and moist habitats. Thus, isolation in different refuges was more severe for amphibians than for reptiles; reptiles restricted to different forest refuges probably came into contact earlier than the amphibians, thus diminishing the possibilities of having attained reproductive incompatibility. Maybe it was simply a matter of size, the Guiana Refuge having been larger (and therefore possibly harboring more species) than the Imerí Refuge. Perhaps both factors played a role.

The Essequibo-Río Branco Depression also served as a route for lowland Amazonian species invading the northern part of Guiana.

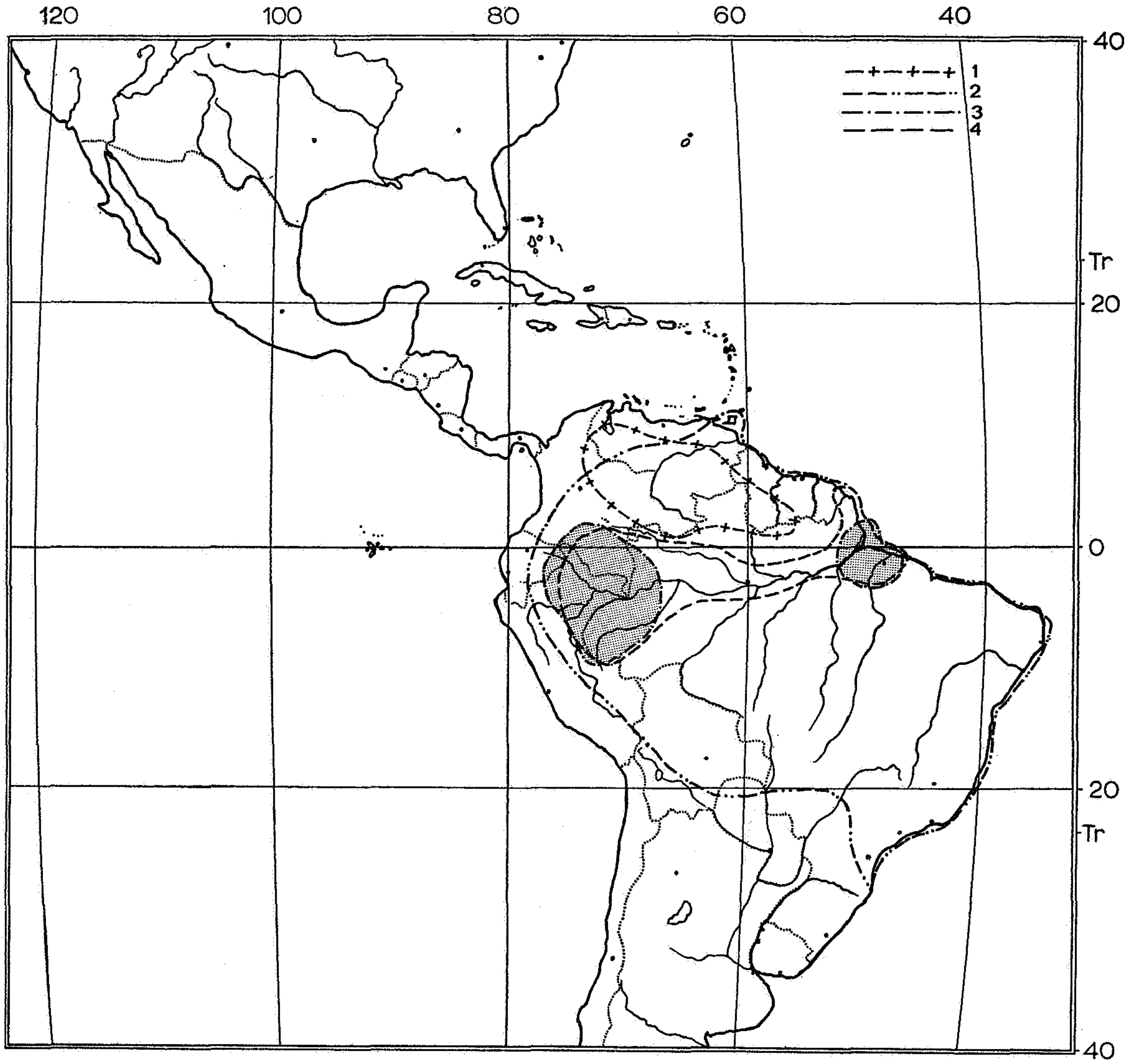


FIG. 10:12. Distribution of species belonging to the groups 2–5 (Table 10:2, Appendix 10:1).
Distribución de especies pertenecientas a los grupos 2–5 (Tabla 10:2, Apéndice 10:1).
1 = *Pseudopaludicola pusilla* (group 4). 2 = *Hyla geographica* (group 2d). 3 = *Lepidoblepharis festae* (group 2b). 4 = *Crocodilurus lacertinus* (group 2c).

Amazonian Species

I do not treat the other groups (Figs. 10: 12–13) in the detail that I have done for the Guiana endemics, because they are dealt with by Dixon, Lynch, and Rivero-Blanco and Dixon (this volume).

A few species reach parts of Guiana because of certain hydrological features. The occurrence in Guyana of the aquatic Amazonian species *Melanosuchus niger* (the black caiman) and *Chelus fimbriatus* (the matamata) apparently is the result of the rainy season connection between the Río Branco and the Essequibo River via the flooded Rupununi Savanna. The occurrence of these species in eastern French Guiana can be explained in a similar way, because the extensive coastal swamps and inundated savannas in Amapá, during the rainy season form an unbroken connection between the Amazon and the Oyapoc, Approuague and Mahury basins. In

FIG. 10:13. Distribution of species belong to the groups 2–5 (Table 10:2, Appendix 10:1).
Distribución de especies pertenecientas a los grupos 2–5 (Tabla 10:2, Apéndice 10:1).
1 = *Lysapsus limellus* (group 5). 2 = *Lysapsus limellus laevis* (group 5). 3 = *Hyla senicula melanargyrea* (group 5). 4 = *Leptodactylus rhodomystax* (group 2a). 5 = *Phrynohyas venulosa* (group 3).

Surinam no such connections occur between the Corantijn or Marowijne river systems and the Amazon Basin; this explains the absence of these two species in that country.

Other species of the Amazon Valley apparently succeeded in reaching eastern French Guiana but did not penetrate farther west. The distribution of a few species with disjunct populations in upper Amazonia and near the mouth of the Rio Amazonas (Table 10:2, Appendix 10:1, Fig. 10:12) is correlated with areas of high rainfall (over 2500 mm) (Fig. 10:7) and may have been caused by the most recent arid phase, which apparently ended 2000 years ago and caused a separation of the upper and lower Amazonian forests (and the animals living in them) (Haffer, 1974). A number of these species are distributed in an arciform area from Bolivia along the eastern foot of the Andes to the Guianas. This arc can be termed the Amazonian Arc. Lescure (1977) called the northern part of this arc (Serra do Navio to Loreto, Perú) the Roraima Arc, because he believed that all sandstone in this region belonged to the Roraima Formation. As pointed out before, this is not the case. However, the existence of an arciform distribution pattern in several reptiles and amphibians seems to be real (Fig. 10:13). For at least one species, the toad *Bufo guttatus*, this pattern apparently is caused by its being saxicolous. It is nearly always found associated with rocks; the geological nature of these rocks apparently is not important, as it may consist of either granite or sandstone. The absence of this species in central Amazonia is understandable, because in that area rocks are absent; only alluvial material is present. A number of Guianan endemics [*Otophryne robusta* (Fig. 10:10), *Leptodactylus rugosus*], which formerly were thought to be restricted to the northern part of the arc because of their close association with sandstone, now have been found associated with other types of rocks as well. For most of the species having the periferal or Amazonian Arc distribution it is not possible to explain simply their absence from central Amazonia. Possibly the presence of close relatives or other ecological competitors there is the most important reason.

Widespread Species

Most of the species in this group apparently had their origin in Amazonian South America; from there they dispersed into southern Central America (Fig. 10:13); a few are of Central American origin and dispersed into South America. One example of this last subgroup is the teiid lizard *Cnemidophorus l. lemniscatus*, occurring from Honduras to the mouth of the Amazon. This species occurs only along the coast in Guiana. The fact that this species is still extending its range along the lower Amazon (Vanzolini, 1970b) and that it does not occur in the far interior of the Guianas indicate that it is a recent immigrant from the northwest. The presence of forests in southern Surinam and French Guiana, was a barrier to the dispersal of *C. l. lemniscatus* (a savanna inhabitant) into the large inland, edaphic savannas in the Sipaliwini/Paru area. Fluctuation of the size of the forests, thereby at times forming a barrier between the inland and coastal savannas, was responsible for the isolation of the inland savannas; lizards living there are distinctly different from the populations of the same species in savannas farther north (Hoogmoed, 1973).

Species Reaching the Eastern Limit of Their Distributions on the Guiana Shield

Some of these species are of Central American origin, others of upper Amazonian, or coastal Venezuelan origin. A number of them are savanna inhabitants that just reach the western part of the Guiana Shield, where the llanos extend east of the Río Orinoco (the leptodactylid frog *Ceratophrys calcarata*). A few leptodactylid frogs (*Physalaemus pustulosus*, *Pleurodema brachyops*) reach the Rupununi Savanna, one leptodactylid frog (*Pseudopaludicola pusilla*) just reaches the Sipaliwini Savanna in Surinam (Fig. 10:12), and one tree frog (*Hyla rostrata*) so far has only been found in the vicinity of El Dorado (Venezuela) and possibly near Cayenne (French Guiana). All of these species have been dealt with in other sections.

Species From Southeastern or Central Brasil Reaching Guiana

Most of the species from southeastern or central Brasil reaching Guiana do not extend farther west than French Guiana or Surinam (Fig. 10:13); only seven [*Hyla x-signata* (tree frog), *Leptodactylus fuscus* (leptodactylid frog), *Pseudis paradoxus* (pseudid frog), *Phrynops geoffroanus* (chelid turtle), *Liophis miliaris* (colubrid snake), *Coleodactylus meridionalis* (gekkonid lizard), and *Tropidurus torquatus* (iguanid lizard)] reach Venezuela. The majority, if not all, of these species are inhabitants of savannas or open swamps, and their distributions are closely associated with those habitats. Apparently these species are recent immigrants from the southeast that either used the savanna corridor (central and northeastern Brasil to southeastern Venezuela) during the last arid phase (about 2000–3500 years ago), when the greater part of this area was covered with a cerradolike vegetation, or they used the open swampy coastal area of Amapá. Most of these species have not differentiated and when they have, the subspecies occurring in the Guianas is identical with the one in northeastern Brasil. The exceptions are the bufonid *Melanophryniscus moreirae*, and the pseudid frogs, *Pseudis paradoxus* and *Lysapsus limellus*, all of which have endemic subspecies in Guiana. The last two species may have reached Guiana during an earlier dry phase and probably along a different route (from Rio Tapajós via Rio Negro and Rio Branco to the north). Furthermore, *Pseudis paradoxus* reaches the western part of Guiana, whereas in Guiana *Lysapsus limellus* is only in the western part (Fig. 10:13).

ANALYSIS OF GEOGRAPHIC DISTRIBUTION

For three groups (frogs, lizards and snakes) data are sufficient to permit an attempt of comparison with localities outside the Guianan Region. However, data were scarce and comparisons for frogs only could be made with the Belém region (Crump, 1971), for lizards with Belém (Crump, 1971; Da Cunha, 1961) and Iquitos (Dixon and Soini, 1975), and for snakes only with Iquitos (Dixon and Soini, 1977). All data have been compiled in Tables 10:3–8. In these tables the total number of species in each locality is on the diagonal from upper left to lower right. The number of species common to each combination of regions is to the right and above the diagonal with the totals. To the left and below the diagonal are the Faunal Resemblance Factors (FRF) as computed for each combination of regions, using the formula (Duellman, 1965, 1966):

$$FRF = \frac{2C}{N_1 + N_2}$$

where N_1 and N_2 are the numbers of species occurring in any two given regions and C is the number of species common to the two regions compared. The computations were made both for forest- and savanna-inhabiting species.

The data for frogs (Tables 10:3–4) show that among forest inhabitants there is a distinctly higher resemblance between the anuran faunas of eastern Guiana (Guyana east of the Essequibo River, Surinam, French Guiana, and northern part of Amapá) and of the Brasilian part of Guiana (Guiana Region south of divide) than between both of

TABLE 10:3.—Comparison of Rainforest Frog Faunas of Different Regions in Northeastern South America.

	Species in Common			
FRF	Western Guiana	Eastern Guiana	Brasilian part Guiana	Belém
Western Guiana	**76**	41	31	14
Eastern Guiana	0.51	**83**	42	22
Brasilian part Guiana	0.52	0.67	**43**	19
Belém	0.28	0.40	0.58	**23**

TABLE 10:4.—Comparison of Savanna Frog Faunas of Different Regions in Northeastern South America.

	Species in Common			
FRF	Western Guiana	Eastern Guiana	Brasilian part Guiana	Belém
Western Guiana	**36**	23	20	13
Eastern Guiana	0.69	**31**	19	13
Brasilian part Guiana	0.69	0.72	**22**	12
Belém	0.51	0.46	0.65	**15**

TABLE 10:5.—Comparison of Rainforest Snake Faunas of Different Regions in Northern South America.

	Species in Common			
FRF	Western Guiana	Eastern Guiana	Brasilian part Guiana	Iquitos
Western Guiana	**80**	65	53	54
Eastern Guiana	0.78	**85**	54	53
Brasilian part Guiana	0.75	0.74	**60**	46
Iquitos	0.65	0.62	0.63	**84**

TABLE 10:6.—Comparison of Open Formation Snake Faunas of Different Regions in Northern South America.

	Species in Common			
FRF	Western Guiana	Eastern Guiana	Brasilian part Guiana	Iquitos
Western Guiana	**19**	14	11	4
Eastern Guiana	0.75	**18**	12	5
Brasilian part Guiana	0.68	0.77	**13**	4
Iquitos	0.33	0.43	0.44	**5**

TABLE 10:7.—Comparison of Rainforest Lizard Faunas of Several Regions in Northern South America.

	Species in Common									
FRF	Paramaribo	Cayenne	Lely Mountains	Alto Maraca	Iquitos	Bolívar	Belém	Brasilian part Guiana	Eastern Guiana	Western Guiana
Paramaribo	**20**	17	13	11	16	18	17	20	20	20
Cayenne	0.77	**24**	14	10	15	18	19	22	24	22
Lely Mountains	0.62	0.61	**22**	14	16	18	16	21	22	22
Alto Maraca	0.56	0.47	0.68	**19**	14	13	14	19	19	18
Iquitos	0.51	0.45	0.49	0.45	**43**	19	23	25	25	24
Bolívar	0.69	0.64	0.67	0.51	0.51	**32**	18	24	27	32
Belém	0.68	0.70	0.62	0.57	0.63	0.55	**30**	28	28	25
Brasilian part Guiana	0.66	0.68	0.67	0.64	0.60	0.66	0.80	**40**	34	35
Eastern Guiana	0.59	0.73	0.69	0.63	0.59	0.73	0.78	0.83	**41**	37
Western Guiana	0.59	0.61	0.63	0.54	0.53	0.81	0.64	0.80	0.84	**47**

TABLE 10:8.—Comparison of Savanna Lizard Faunas of Several Regions in Northern South America.

	Species in Common									
FRF	Paramaribo	Cayenne	Lely Mountains	Alto Maraca	Iquitos	Bolívar	Belém	Brasilian part Guiana	Eastern Guiana	Western Guiana
Paramaribo	**3**	3	0	0	0	3	2	3	3	3
Cayenne	1.0	**3**	0	0	0	3	2	3	3	3
Lely Mountains	0	0	**0**	0	0	0	0	0	0	0
Alto Maraca	0	0	0	**0**	0	0	0	0	0	0
Iquitos	0	0	0	0	**0**	0	0	0	0	0
Bolívar	0.35	0.35	0	0	0	**14**	2	4	6	14
Belém	0.80	0.80	0	0	0	0.25	**2**	2	2	2
Brasilian part Guiana	0.85	0.85	0	0	0	0.44	0.66	**4**	4	4
Eastern Guiana	0.66	0.66	0	0	0	0.60	0.50	0.80	**6**	6
Western Guiana	0.35	0.35	0	0	0	1.0	0.25	0.44	0.60	**14**

those areas and western Guiana (Guyana west of Essequibo River, Venezuelan Guayana). This could be explained by the barrier function of the Essequibo-Rio Branco Depression. On the other hand, the resemblance between the forest anuran fauna of Belém as compared to the other regions, shows a steady decrease towards the west. We see quite a different picture when comparing the savanna anuran faunas. Here the resemblance between eastern Guiana and the Brasilian part of Guiana is only negligibly higher than that between both of those areas and western Guiana. The resemblance between Belém and the Brasilian part of Guiana is in the same category as that between the three areas of the Guiana Region among themselves. However, the resemblance between Belém and both eastern and western Guiana is distinctly lower. Although 13 of the 15 species known from Belém occur throughout western and eastern Guiana, the resemblance factor is low because these species only are a fraction of the much larger savanna anuran fauna there, which contains a fairly high proportion of local endemics (which still may prove to be more widespread) and a number of species reaching their eastern distribution limits in Guiana. Thus, it can be concluded that for savanna-inhabiting frogs there are no barriers within Guiana and, for that matter, scarcely any barriers towards areas surrounding Guiana. For forest-inhabiting frogs there is a distinct barrier within Guiana, formed by the Essequibo-Rio Branco Depression and also, the forest anuran fauna is distinctly separated from that to the southeast. However, these conclusions are based only on data from four areas (three of which chosen with a certain bias) and therefore should be treated with much reserve, although they do confirm the picture that emerged from a first study of distribution maps. These findings for the anuran faunas can be most easily explained by assuming that the Essequibo-Rio Branco Depression not only served as a connection (and dispersal route for aquatic species) between Guiana and Amazonia, but also was the area that retained its savanna vegetation longest, as still indicated by the presence of large savanna areas in the border region of Guyana and Brasil and in the coastal area near the mouth of the Essequibo River. Thus, this area formed an efficient barrier to the dispersal of forest frogs; at the same time, it formed a dispersal route for savanna frogs. This situation apparently lasted until fairly recently, until under the influence of an increasingly wet climate the forests in the Guiana and Imerí refuges started to expand and met in the Essequibo-Rio Branco Depression. This explains why many forest species have their eastern or western distribution limits at the Essequibo-Rio Branco Depression. Several species that apparently were associated with one of the refuges in the region succeeded in crossing the depression, but this could have taken place only recently when the savanna vegetation was substituted by forest.

Comparison of the snake and lizard faunas of several localities gives quite a different picture. The data for forest-inhabiting snakes (Table 10:5) show that there is a great resemblance between different parts of the Guiana Region and that the resemblance with the forest snake fauna of Iquitos is fairly good, but distinctly lower than within Guiana. The data suggest a gradual transition within Guiana from west to east and also from Iquitos to Guiana, but owing to lack of data from intermediate localities this last hypothesis cannot be proved. Only five snakes inhabiting open formations are found in the Iquitos area; all of these are either associated with open aquatic or edge situations. Real savanna species are absent, because no suitable habitat is available in the region (Dixon and Soini, 1977). When comparing these snakes (Table 10:6) with the open formation species of Guiana, it is clear that the resemblance between Iquitos and the three parts of Guiana is small. Within Guiana there is a lower degree of resemblance between the snake faunas of western Guiana and the Brasilian part of Guiana, but this is caused by the presence in western Guiana of several species reaching their eastern distribution limits there and in the Brasilian part of Guiana of species reaching their northern distribution limits there, and of species that are known only from the Amazon Basin. However, the data for snakes again are based only on four areas.

The lizards and amphisbaenians ("saurians") appeared to offer the best possibilities for a faunal analysis, because there were several places from which representative samples seemed to be present (Tables 10:7–8). However, upon closer examination, it soon turned out that the data were not very reliable. This holds true for the forest lizards and amphisbaenians of Lely Mountains, Paramaribo, and Alto Maraca (Amapá). When compared with the entire region of which they are part, respectively eastern Guiana (twice) and the Brasilian part of Guiana, they show resemblance factors of only 0.69, 0.59 and 0.64, respectively. These are hardly more, or even lower, than their respective resemblance factors with the lizard fauna of Belém (0.62, 0.68 and 0.57). For Cayenne the situation seems to be better; when compared with eastern Guiana it shows a resemblance factor of 0.73, but here we should keep in mind that the total number of species reported from this locality also contains old records that possibly refer to specimens that were shipped from Cayenne but actually did not occur there. From the remaining data it is clear that there is a diminishing resemblance westward between the rainforest lizard faunas of Belém and Guianan areas. Within Guiana the resemblance is high, and nowhere is a clear break apparent. The resemblance factor between Belém and Iquitos is slightly higher than that between Iquitos and the different parts of Guiana. Resemblance between Iquitos and western Guiana is smaller than that with the Brasilian part of Guiana. This apparent reversal of expected resemblances is the result of the influence of Amazonian species in the Brasilian part of Guiana and in eastern Guiana. Apparently there is a fairly well-developed barrier southwest of Guiana, separating the lizard faunas of Guiana and upper Amazonia. Again, our knowledge of areas intermediate between Iquitos and Guiana is poor, and the conclusions must be regarded as preliminary. When comparing the savanna lizard faunas of different regions (Table 10:8) we get a very different picture. There is no resemblance with Iquitos, where this category of lizards is completely absent. The agreement between Belém and the different Guianan areas diminishes westward, and there seems to be a break between western Guiana on the one hand and eastern Guiana and the Brasilian part of Guiana on the other. Upon closer examination, this apparent break is caused completely by the presence in western Guiana of a number of altitudinal endemics and of western species just reaching their eastern limits in Guiana. When these species (forming 60% of the savanna lizard fauna) are excluded, there are no breaks for the remaining general savanna lizards within Guiana, neither with Belém. The only break is between Iquitos and Guiana, and this can be completely explained by the absence of suitable savanna habitat in upper Amazonia. As for savanna-inhabiting frogs, the Essequibo-Rio Branco Depression formed no barrier to that part of the savanna inhabitants that had been in the area relatively long. For a number of local savanna endemics it seems to act as such, mainly because those endemics did not have the chance to expand their area of distribution.

On the basis of the data presented in Tables 10:3–8 it can be concluded that for forest inhabitants Guiana seems to be a real herpetogeographic entity, well separated from surrounding areas to the southwest and the southeast. Within the area, the Essequibo-Rio Branco Depression forms a barrier for the distribution of a number of eastern forest species to the west and of western forest species to the east. No such function is present for savanna inhabitants that, with the exception of local endemics, are spread throughout the area. There is no separation to the southeast for savanna-inhabiting species, which consequently show a great resemblance with the savanna fauna of northeastern Brasil.

The data do not present any evidence for the recognition of a Guiana Region as defined by Lescure (1977); distinct breaks between eastern Guiana and the Brasilian part of Guiana are nowhere evident.

CONCLUSIONS

The herpetofauna of Guiana, as it is known at present, is a composite fauna with a complex history. A number of endemic species belong to old genera (endemic or with disjunct, relict distributions) that apparently inhabited certain parts of the area since the Cretaceous. Other endemics probably originated in the region during periods of isolation in forest or savanna refuges, which are assumed to have existed during arid and wet phases in the Pleistocene–Holocene, respectively. The most important forest refuge was the Guiana Refuge on the northern slopes of the Tumuc-Humac and Acarai mountains. A less important role was played by the Imerí Refuge in the region of Serra Imerí and Serra da Neblina. The species restricted to higher altitudes survived the arid phases in disjunct forests on the higher slopes of the tepuis, collectively known as Tepui Refuges. During arid phases of the Pleistocene and Holocene, the species isolated in the refuges underwent differentiation and, depending on the time of their arrival in the area and also on their rates of evolution, they differentiated into endemic genera, species, or subspecies.

Although some species show relationships to Andean species, these are not direct and only indicate that both Andean and Guianan species evolved from the same or related lowland species. The Guianan species of *Atractus* (colubrid snakes), *Eleutherodactylus* (leptodactylid frogs) and *Centrolenella* (glass frogs) are in this category. The presence of two species of the Andean teiid lizard genus *Euspondylus* in the Guiana Highlands is the only evidence for a direct link with the Andes. As these species are poorly known from only a few individuals each, their taxonomic position remains uncertain. Therefore, it would be premature to conclude on the basis of this meager evidence that there would have been any invasions of Guiana from the Andes.

A number of species invaded Guiana from the south via a wide belt of cerradolike vegetation, connecting central and northeastern Brasil with southeastern Venezuela, during the last arid phase. When the climate became more humid and the forests expanded, these species were left stranded on the isolated savannas of Guiana, most of them in the east. During this same period a number of savanna-inhabitants from northwestern South America invaded the western part of Guiana, where they exist today as representatives of the llanos fauna. Within Guiana there are differences between the western part, where sandstone tepuis are present, and the eastern part, which generally has a much lower elevation. A number of species (most of them endemic) are restricted to the sandstone region; others (mostly invaders from southern and central Brasil or from the Amazon Valley) occur only in the east. Apparently Guiana has been, and still is being, invaded from the northwest and from the southeast. Within Guiana the Essequibo-Rio Branco Depression seems to have acted as a barrier to the eastern dispersal of western elements and to a lesser extent for the dispersal of eastern elements to the west. The notable exceptions are some of the species from central and southeastern Brasil. Also this depression (and the low coastal area of Amapá) served as corridors into northern Guiana for a number of Amazonian species.

Endemism in the entire region is high in amphibians (52%) but much lower in reptiles (27%). At elevations above 1000 m, only frogs, lizards and snakes occur; endemism for frogs there is 33 percent, for reptiles 24 percent. Endemism for amphibians below 1000 m is 47 percent (frogs only 40%, caecilians only 69%), for reptiles 24 percent. From these data it is clear that although frogs have a high degree of endemism at higher elevations, the amount of endemism in the lowlands is even higher. However, part of this probably results from our still scanty knowledge of this group; of the 83 endemic frogs, 29 (35%) have yet to be named.

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RESUMEN

Limitado por el Orinoco, Brazo Cassiquiare, Rio Negro, el Amazonas y el Atlántico, la Guayana es geológicamente uno de los territorios más antiguos de América del Sur. Su mayor parte viene formado por el escudo guayaní precámbrico, cuya arenisca de Roraima cubre partes del sur de Venezuela y de la Guyana occidental, con restos aislados en la Guyana oriental y en el Surinam central. La altura media no pasa de los 1000 m, pero los restos areniscos pueden alcanzar hasta 3000 m. Debido a su posición aislada y a su elevación relativamente considerable, estas montañas (tepuyes) representan ser como islas subtropicales en un mar o llanura tropical. La exploración biológica de esta altiplanicie guayaní se emprendió a mediados del siglo pasado y se prosigue aún hoy, sin haber explorado más que una pequeña parte

de los tepuyes y de una manera suficiente tan sólo su aspecto herpetológico. Dado este estado de cosas, por fuerza hemos de limitarnos a interpretar los datos obtenidos de la herpetofauna de la altiplanicie de la Guayana.

Actualmente se conocen en la Guayana 178 especies de anfibios y 230 reptiles, totalizando así las 408 especies herpetológicas. No se conoce las salamandras. En dicho número se comprenden: cinco tortugas marinas, un chacón (Gekkonidae) cosmopolita, cinco especies importadas de las Antillas y tres cuya presencia en la Guayana es de origen dudoso. El residuo puede clasificarse en cinco grandes grupos—endémicos (38%), amazónicos (37%), de vasta extensión (12%), llegando el límite oriental de su extensión hasta el escudo guayaní (7%) y a la Guayana del Brasil central y sudeste (5%). Si se consideran estos datos aisladamente, referidos a los reptiles y a los anfibios por separado, constatamos diferencias importantes. De los anfibios, el 52 porciento son endémicos, el 30 porciento son amazonicos y el 7 porciento de vasta extensión; mientras que para los reptiles tenemos los siguientes porcentajes—27, 42 y 16, respectivamente. Estas diferencias se explican por el hecho de que los anfibios necesitan para su reproducción agua y esta dependencia los hace más limitados que los reptiles en su capacidad de dispersión.

Noventa y dos especies de anfibios y 59 de reptiles son endémicos de la Guayana, con una pequeña porción fuera de los límites de la región que estamos describiendo. Las especies de los otros grupos pueden formar subespecies endémicas en este territorio (39 subespecies pertenecen a 29 especies). La mayor parte de las especies endémicas se concentran en la parte occidental de la Guayana y pueden clasificarse en endémicos de llanura y de altura, según se hallen por debajo o por encima de los 1000 m de altitud. Aproximadamente el 19 porciento de los anfibios endémicos y el 15 porciento de los reptiles endémicos son de altura, ateniéndonos sólo a la parte occidental. Géneros endémicos tales como *Otophryne* y *Oreophrynella* parecen representar reliquias del joven Terciario, *Stefania* parece representar una radiación reciente y la posición de *Riolama* no queda muy clara. Los géneros endémicos residuales (*Allophryne*, *Rhinatrema*, *Peltocephalus*, *Amapasaurus*, *Mesobaena*) son endémicos de llanura y su historial está probablemente asociado con el de los refugios de Guayana y de Imerí. Una especie endémica de *Euparkerella* apunta tener alguna relación con las montañas del sudeste brasileño. La *"Hylodes" duidensis* que hasta hace poco se creía estaba emparentada con formas del sudeste brasileño, resulta ser bastante diferente y más bien representa una derivación de los eleutherodactylini de llanura. La mayor parte de los endémicos de altura son derivaciones subtropicales de parientes de la llanura tropical. Los endémicos de altura tienen una extensión limitada a uno o varios tepuyes. El orígen de la mayor parte de los endemicos de llanura se explica probablemente por la formación en el pasado de refugios forestales a través de los cambios climáticos del período cuaternario. De esos supuestos refugios en la región es el de la Guayana el más importante, siendo de menor importancia el de Imerí. Estos refugios, separados por la sabana, han procurado en su día una especificación alopátrica en todo un territorio donde hasta hace poco se creía sin barreras ecológicas de importancia.

Las especies amazónicas las tratan otros autores en otros artículos. En todo caso se dividen en cuatro subgrupos. Algunas de estas especies llegan hasta la parte septentrional de la Guayana por la depresión del Essequibo-Rio Branco, o siguiendo las formaciones abiertas del Amapá costero y de la Guayana francesa septentrional.

La mayor parte de las especies de vasta extensión son de orígen sudaméricano, y una especie de orígen centroaméricano refuerza la hipótesis de los refugios forestales. Las especies que llegan al límite oriental del escudo guayaní son de orígen mixto y vienen tratadas en otros capítulos.

Las especies del Brasil central y sudeste que llegan a la Guayana están por lo general presente en la parte oriental y muchas de ellas asociadas a las vegetaciones abiertas. Su extensión es probablemente correlativa a la extensión de las vegetaciones abiertas del último período árido, como lo prueba su existencia en las sabanas actualmente aisladas de la Amazonía.

No parece que haya en la Guayana barreras geográficas de importancia, aunque la depresión del Essequibo-Rio Branco ha debido de hacer de barrera a la extensión de ciertas especies de llanura y a no pocas formas de derivación de las de altura. La extensión característica en formas de llanura se debe probablemente, en la mayoría de los casos a la competición ecológia u a otras condiciones particulares del medio ambiente.

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APPENDIX

APPENDIX 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana. Habitats: A = aquatic, D = dry forest, E = forest-edge situations, M = marine, Mf = montane forest, P = perianthropic, R = rainforest, S = savanna and other open vegetation like swamps, Sa = saxicolous, X = unknown. Type of distribution: Ab = Amazon basin, Ad = Disjunct amazonian, Ae = Highland endemics, Am = Amazonian, Ap = Periferal amazonian, Car = Caribbean, Cos = Cosmopolitan, Ea = Eastern limit, Le = Lowland endemics, Sb = Southern Brasil, Unc = Uncertain, W = Widespread. Species noted by * are endemic.

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
Anurans											
*Pipa aspera**	0–860	AR	AR	–	–	–	–	–	–	–	Le
Pipa pipa	0–90	ARS	ARS	AR	–	A	A	A	A	A	Am
*Colostethus beebei**	0–490	R	R	–	–	–	–	–	–	–	Le
Colostethus brunneus	0–1524	R	R	R	–	–	–	R	–	–	Am
*Colostethus degranvillei**	80–680	R	–	–	–	–	–	–	–	–	Le
Colostethus shrevei	457–1828	–	Mf	–	–	X	X	X	–	–	Ap
Colostethus sp. "A"*	701–2133	–	Mf	–	–	–	–	–	–	–	Le
Colostethus sp. "B"*	1700	–	X	–	–	–	–	–	–	–	Ae
*Dendrobates azureus**	315–430	R	–	–	–	–	–	–	–	–	Le
*Dendrobates leucomelas**	50–800	–	DMf	–	–	X	–	–	–	–	Le
Dendrobates quinquevittatus	14–200	R	–	R	–	R	R	R	R	–	Ab
*Dendrobates steyermarki**	600–1200	–	R	–	–	–	–	–	–	–	Le
*Dendrobates tinctorius**	0–610	R	–	–	–	–	–	–	–	–	Le
Phyllobates femoralis	14–610	R	R	R	–	R	R	R	R	–	Am
Phyllobates pictus	6–250	R	R	–	–	R	R	R	R	R	Am
*Phyllobates pulchripectus**	120–310	–	–	R	–	–	–	–	–	–	Le
Phyllobates trivittatus	20–680	R	R	–	–	R	–	R	R	–	Am
Rana palmipes	0–457	R	R	R	R	R	R	R	R	–	W
Adenomera andreae	0–1234	R	R	R	–	R	R	R	R	R	Am
Adenomera hylaedactylus	0–500	R	R	R	–	–	R	R	R	R	Am
*Adenomera lutzi**	± 450	–	X	–	–	–	–	–	–	–	Le
Ceratophrys calcarata	90	–	S	–	–	X	X	–	–	–	Ea
Ceratophrys cornuta	50–700	R	–	R	–	R	–	R	R	–	Am
*Eleutherodactylus chiastonotus**	0–700	R	–	R	–	–	–	–	–	–	Le
*Eleutherodactylus gutturalis**	30–310	R	–	R	–	–	–	–	–	–	Le
*Eleutherodactylus inguinalis**	180–700	R	–	–	–	–	–	–	–	–	Le
Eleutherodactylus lacrimosus	0–310	R	–	R	–	R	R	R	–	–	Ad
*Eleutherodactylus marmoratus**	30–1463	R	RMf	R	–	–	–	–	–	–	Le
*Eleutherodactylus pulvinatus**	1400	–	E	–	–	–	–	–	–	–	Ae
Eleutherodactylus urichi	0	–	E	–	E	–	–	–	–	–	Car
Eleutherodactylus vilarsi	1234	–	Mf	–	–	R	–	R	–	–	Ea
Eleutherodactylus zeuctotylus	0–700	R	R	–	–	–	–	R	–	–	Ap
Eleutherodactylus sp. "A"*	90–1463	R	R	–	–	–	–	–	–	–	Le
Euparkerella sp. "A"*	914	–	Mf	–	–	–	–	–	–	–	Le

APPENDIX 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana (continued).

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
Hydrolaetare schmidti	0–80	A	--	A	--	A	--	A	--	--	Ab
*"Hylodes" duidensis**	1402	--	R	--	--	--	--	--	--	--	Ae
Leptodactylus bolivianus	0–650	RES	RES	RES	RES	RES	RE	RE	RE	RE	W
Leptodactylus fuscus	0–1215	S	S	S	S	--	--	S	--	S	Sb
Leptodactylus longirostris	0–1340	S	S	S	--	?	--	S	?	?	Am
Leptodactylus macrosternum	240–305	S	S	S	S	S	--	S	--	S	Am
Leptodactylus mystaceus	0–700	R	R	R	--	R	R	R	R	R	Am
Leptodactylus pentadactylus	0–500	RE	RE	R	E	R	X	R	X	X	W
Leptodactylus rhodomystax	0–650	R	R	R	--	R	R	R	R	--	Ap
*Leptodactylus rugosus**	90–1368	--	Sa	Sa	--	Sa	--	--	--	--	Le
Leptodactylus stenodema	180–700	RSa	--	RSa	--	RSa	RSa	--	--	--	Am
Leptodactylus wagneri	0–1250	R	R	R	R	R	R	R	R	R	Am
Leptodactylus sp. "A"*	100	Sa	--	--	--	--	--	--	--	--	Le
Leptodactylus sp. "B"	0–620	R	?	?	--	?	?	?	?	?	Am
Leptodactylus sp. "C"*	90	--	D	--	--	--	--	--	--	--	Le
Lithodytes lineatus	0–240	R	R	R	--	R	R	R	--	--	Am
Physalaemus enesefae	75–300	--	SE	--	S	--	--	--	--	--	Ea
Physalaemus ephippifer	30–240	R	--	R	--	--	--	--	--	--	Am
Physalaemus petersi	0–206	R	--	R	--	--	R	R	R	--	Ab
Physalaemus pustulosus	0–305	--	S	--	S	--	--	--	--	--	Ea
Pleurodema brachyops	0–305	--	S	--	S	--	--	--	--	--	Ea
Pseudopaludicola pusilla	50–240	S	S	--	S	--	--	--	--	--	Ea
*Atelopus flavescens**	10–70	R	--	--	--	--	--	--	--	--	Le
*Atelopus franciscus**	5	R	--	--	--	--	--	--	--	--	Le
Atelopus pulcher	80–600	R	R	R	--	--	R	R	R	--	Ap
Atelopus sp. "A"*	0–206	R	--	--	--	--	--	--	--	--	Le
Bufo ceratophrys	?–1234	--	R	--	--	X	X	--	--	--	Ap
Bufo granulosus	0–1290	S	S	S	S	S	--	S	S	S	W
Bufo guttatus	30–900	RSa	RE	R	--	--	R	R	--	--	Ap
Bufo marinus	0–1290	SE	SE	SE	SE	SE	SE	SE	SE	SE	W
*Bufo nasicus**	500–1350	--	R	--	--	--	--	--	--	--	Le
Bufo typhonius	0–1219	R	R	R	R	R	R	R	R	R	W
Bufo sp. "A"*	0–206	R	--	R	--	--	--	--	--	--	Le
Bufo sp. "B"	0–300	R	R	R	--	R	--	R	R	--	Am
Dendrophryniscus minutus	170	R	R	R	--	?	R	R	?	--	Am
Melanophryniscus moreirae	20	--	--	S	--	--	--	--	--	--	Sb
*Oreophrynella macconnelli**	1067	--	Mf	--	--	--	--	--	--	--	Ae
*Oreophrynella quelchii**	2590	--	S	--	--	--	--	--	--	--	Ae
Oreophrynella sp. "A"*	2400	--	S	--	--	--	--	--	--	--	Ae
*Allophryne ruthveni**	10–200	R	R	--	--	--	--	--	--	--	Le

APPENDIX 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana (continued).

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
Aparasphenodon venezolanus	90	—	X	—	—	—	—	—	—	—	Le
Hyla baumgardneri	0–609	—	SD	S	—	—	—	—	—	—	Am
*Hyla benitezi**	800–1700	—	SaMf	—	—	—	—	—	—	—	Le
Hyla boans	0–1216	R	R	R	R	R	R	R	R	R	W
*Hyla boesemani**	0–650	S	S	S	—	—	—	—	—	—	Le
Hyla brevifrons	0–90	R	—	R	—	R	R	—	R	—	Ad
Hyla calcarata	0–200	R	—	—	—	R	R	R	R	—	Am
Hyla crepitans	0–1420	S	S	S	S	S	—	X	X	X	W
Hyla egleri	0–240	SE	E	E	—	—	—	—	—	—	Am
Hyla fasciata	80–200	R	—	—	—	—	R	R	R	R	Am
*Hyla fuentei**	20	S	—	—	—	—	—	—	—	—	Le
Hyla garbei	90–100	S	—	—	—	S	S	S	S	—	Ea
Hyla geographica	0–305	E	E	E	E	E	E	E	E	E	Am
*Hyla ginesi**	610–1113	—	Mf	—	—	—	—	—	—	—	Le
*Hyla grandisonae**	low	—	X	—	—	—	—	—	—	—	Le
Hyla granosa	0–200	RE	RE	RE	—	RE	RE	RE	RE	—	Am
*Hyla helenae**	10	R	—	—	—	—	—	—	—	—	Le
*Hyla kanaima**	700–1463	—	RMf	—	—	—	—	—	—	—	Le
*Hyla lemai**	929–1400	—	Mf	—	—	—	—	—	—	—	Le
Hyla leucophyllata	20–650	RE	RE	RE	—	RE	RE	RE	RE	RE	Am
Hyla marmorata	0–600	E	E	E	—	E	E	E	E	—	Ap
Hyla microcephala	0–305	—	S	—	S	S	—	—	—	—	W
*Hyla minuscula**	0–305	S	S	—	S	—	—	—	—	—	Le
Hyla minuta	0–1700	S	S	S	S	X	—	X	X	X	Am
*Hyla multifasciata**	0–1290	SE	SE	SE	—	—	—	—	—	—	Le
Hyla nana	0–20	S	—	S	—	—	—	—	—	S	Sb
*Hyla ornatissima**	90–180	R	R	R	—	—	—	—	—	—	Le
*Hyla proboscidea**	200–600	R	—	—	—	—	—	—	—	—	Le
Hyla punctata	0–20	S	S	S	—	—	—	S	S	S	Am
Hyla raniceps	0–10	S	—	—	—	—	—	—	—	—	Sb
*Hyla rodriguezi**	1210–1400	—	SMf	—	—	—	—	—	—	—	Ae
Hyla rostrata	0–20	S	S	—	S	S	—	—	—	—	Ea
Hyla rubra	0–140	S	S	S	S	S	—	—	R	—	W
Hyla senicula	30	R	—	—	—	—	—	—	—	—	Sb
*Hyla sibleszi**	900–1706	—	Mf	—	—	—	—	—	—	—	Le
*Hyla surinamensis**?	?	X	—	—	—	—	—	—	—	—	Le
Hyla x-signata	0–305	S	S	S	S	—	—	—	—	—	Sb
Hyla sp. "A"*	1402–1463	—	Mf	—	—	—	—	—	—	—	Ae
Hyla sp. "B"*	1463	—	Mf	—	—	—	—	—	—	—	Ae
Hyla sp. "C"*	130	R	—	—	—	—	—	—	—	—	Le
Hyla sp. "D"*	0–240	S	—	—	—	—	—	—	—	—	Le

APPENDIX 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana (continued).

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
Hyla sp. "E"*	130	R	--	--	--	--	--	--	--	--	Le
Hyla sp. "F"*	0	S	--	--	--	--	--	--	--	--	Le
Hyla sp. "G"*	100–650	R	--	--	--	--	--	--	--	--	Le
Hyla sp. "H"*	1210	S	--	--	--	--	--	--	--	--	Ae
Hyla sp. "I"*	1700	--	S	--	--	--	--	--	--	--	Ae
Hyla sp. "J"*	?	--	X	--	--	--	--	--	--	--	Le
Hyla sp. "K"*	240–305	S	S	--	--	--	--	--	--	--	Le
Hyla sp. "L"*	0–240	E	--	--	--	--	--	--	--	--	Le
Hyla sp. "M"*	140	E	--	--	--	--	--	--	--	--	Le
Hyla sp. "N"*	140–240	SE	--	--	--	--	--	--	--	--	Le
Hyla sp. "O"*	1250–1290	--	SE	--	--	--	--	--	--	--	Ae
Osteocephalus buckleyi	20–1402	R	R	R	--	R	R	R	R	R	Am
Osteocephalus leprieuri	0–2400	R	R	--	--	R	R	R	R	--	Ap
Osteocephalus taurinus	10–1250	RE	R	R	--	R	R	R	R	R	Am
Osteocephalus sp. "A"*	200	R	--	--	--	--	--	--	--	--	Le
Phrynohyas coriacea	0	X	--	--	--	--	R	--	R	--	Ap
*Phrynohyas resinifictrix**	10–90	R	--	R	--	--	--	--	--	--	Le
Phrynohyas venulosa	0–1231	SE	SE	SE	SE	SE	SE	SE	SE	SE	W
Phyllomedusa bicolor	10–650	RES	RES	RES	--	RES	RES	RES	RES	--	Ap
Phyllomedusa hypocondrialis	0–650	ES	ES	ES	--	ES	ES	ES	ES	ES	Am
Phyllomedusa tomopterna	20–650	R	--	--	--	--	R	R	R	--	Am
Phyllomedusa trinitatis	0–200	--	RE	--	--	--	--	--	--	--	Ea
Phyllomedusa vaillanti	0–650	R	R	R	--	R	R	R	R	R	Am
Sphaenorhynchus eurhostus	0–305	S	S	S	--	S	--	S	--	--	Am
*Stefania evansi**	10–1402	--	RMf	--	--	--	--	--	--	--	Le
Stefania ginesi *	2225	--	SSa	--	--	--	--	--	--	--	Ae
*Stefania goini**	1402	--	X	--	--	--	--	--	--	--	Ae
*Stefania marahuaquensis**	600–1200	--	Mf	--	--	--	--	--	--	--	Le
*Stefania scalae**	970–1200	--	Mf	--	--	--	--	--	--	--	Le
*Stefania woodleyi**	700	--	RMf	--	--	--	--	--	--	--	Le
Stefania sp. "A"*	1402	--	Mf	--	--	--	--	--	--	--	Ae
Stefania sp. "B"*	1700	--	S	--	--	--	--	--	--	--	Ae
Stefania sp. "C"*	2400	--	SSa	--	--	--	--	--	--	--	Ae
Lysapsus limellus	90–890	--	S	S	--	--	--	--	--	S	Sb
Pseudis paradoxus	0–550	S	S	S	--	--	--	--	--	S	Sb
Centrolenella fleischmanni	200	R	--	--	R	R	R	--	--	--	Ea
*Centrolenella geijskesi**	200	R	--	--	--	--	--	--	--	--	Le
*Centrolenella oyampiensis**	90	R	--	--	--	--	--	--	--	--	Le
*Centrolenella pulidoi**	610	--	Mf	--	--	--	--	--	--	--	Le
*Centrolenella taylori**	200–1320	R	RMf	--	--	--	--	--	--	--	Le

APPENDIX 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana (continued).

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
Centrolenella sp. "A"*	1234	–	X	–	–	–	–	–	–	–	Ae
Centrolenella sp. "B"*	120–200	R	–	–	–	–	–	–	–	–	Le
*Chiasmocleis hudsoni**	200–240	R	–	–	–	–	–	R	–	–	Le
*Chiasmocleis shudikarensis**	0–300	R	–	–	–	–	–	–	–	–	Le
Ctenophryne geayi	0–140	R	R	–	–	R	–	R	R	–	Am
Elachistocleis ovalis	0–1066	S	S	S	S	S	?	S	S	S	Am
Hamptophryne boliviana	0–240	R	R	–	–	–	–	R	R	R	Am
*Otophryne robusta**	200–1981	SaR	SaMf	SaR	–	X	–	–	–	–	Le
Relictivomer pearsei	20–1210	S	S	–	–	S	–	–	–	–	Ea
*Synapturanus mirandaribeiroi**	120–240	R	R	R	–	–	–	R	–	–	Le
Caecilians											
*Epicrionops nigrus**	660	–	R	–	–	–	–	–	–	–	Le
*Rhinatrema bivittatum**	20–300	R	R	R	–	–	–	–	–	–	Le
Potomotyphlus kaupii	0–50	–	A	–	–	A	A	A	A	–	Am
*Typhlonectes compressicauda**	0–40	A	A	A	–	–	–	–	–	–	Le
*Brasilotyphlus braziliensis**	40	–	–	X	–	–	–	–	–	–	Le
Caecilia gracilis	0–106	R	R	R	–	–	–	–	X	–	Am
*Caecilia pressula**	250	–	X	–	–	–	–	–	–	–	Le
Caecilia tentaculata	0–250	R	R	–	R	R	R	R	R	R	W
*Microcaecilia rabei**	100–400	R	R	–	–	–	–	–	–	–	Le
*Microcaecilia unicolor**	0–690	R	R	–	–	–	–	–	–	–	Le
Microcaecilia sp. "A"*	250	R	–	–	–	–	–	–	–	–	Le
*Oscaecilia zweifeli**	50	–	A	–	–	–	–	–	–	–	Le
Siphonops annulatus	0–?	X	X	X	X	X	X	X	X	X	Am
Chelonians											
Caretta caretta	0	M	M	–	–	–	–	–	–	–	Cos
Chelonia mydas	0	M	M	–	–	–	–	–	–	–	Cos
Eretmochelys imbricata	0	M	M	–	–	–	–	–	–	–	Cos
Lepidochelys olivacea	0	M	M	–	–	–	–	–	–	–	Cos
Dermochelys coriacea	0	M	M	–	–	–	–	–	–	–	Cos
Kinosternon scorpioides	0–690	A	A	A	A	A	A	A	A	A	W
Testudo carbonaria	0–300	SR	SR	S	S	–	–	S	–	S	Am
Testudo denticulata	0–650	R	R	R	R	R	–	R	R	R	Am
Rhinoclemys punctularia	0–240	SAR	SAR	SAR	SAR	SAR	SAR	–	–	–	Ea
Peltocephalus tracaxus	0–100	SA	SA	SA	–	–	–	?	–	–	Ab
Podocnemis dumeriliana	0–100	A	A	?	–	–	–	–	A	–	Am
Podocnemis expansa	0–100	A	A	A	–	A	–	A	A	–	Am
Podocnemis erythrocephala	20–100	–	A	A	–	–	–	–	–	–	Am
Chelus fimbriatus	0–100	A	A	A	–	A	?	A	A	?	Ab
Phrynops geoffroanus	0–305	–	A	A	–	A	–	–	–	A	Sb
Phrynops gibbus	0–229	RA	A	A	–	SAR	A	–	RA	–	Ap

APPENDIX 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana (continued).

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
Phrynops nasutus	10–80	A	A	A	–	A	A	A	A	A	Ap
Platemys platycephala	0–650	RA	RA	RA	–	A	A	A	A	?	Am
Crocodilians											
*Crocodylus intermedius**	0–100	–	A	–	A	–	–	–	–	–	Le
Caiman crocodilus	0–650	RAS	A	A	A	A	A	A	A	A	W
Paleosuchus palpebrosus	0–240	RAE	A	A	–	RA	A	A	A	–	Am
Paleosuchus trigonatus	100–300	RAE	A	A	–	RA	–	A	A	A	Am
Melanosuchus niger	0–200	A	A	A	–	A	A	A	A	–	Ab
Snakes											
*Liotyphlops incertus**	?	X	–	–	–	–	–	–	–	–	Le
Typhlophis squamosus	?	X	X	X	X	–	–	–	–	–	Am
*Leptotyphlops amazonicus**	90–460	–	S	–	–	–	–	–	–	–	Le
*Leptotyphlops collaris**	0–475	R	–	–	–	–	–	–	–	–	Le
Leptotyphlops cupinensis	650	R	–	R	–	–	–	–	–	–	Sb
*Leptotyphlops dimidiatus**	20	S	S	S	–	–	–	–	–	–	Le
Leptotyphlops macrolepis	0–200	R	X	X	X	X	–	–	X	–	Ea
*Leptotyphlops septemstriatus**	20–850	R	R	R	–	–	–	–	–	–	Le
Leptotyphlops tenella	0–496	R	R	R	–	–	?	R	?	–	Am
Leptotyphlops sp. "A"	?	–	X	X	–	–	–	?	–	–	Am
Typhlops brongersmianus	0–500	R	R	R	R	R	R	R	R	R	Am
Typhlops lumbricalis	0	–	X	–	–	–	–	–	–	–	Car
Typhlops reticulatus	0–100	R	R	R	–	?	?	R	?	?	Am
*Typhlops unilineatus**	0	X	–	–	–	–	–	–	–	–	Le
Anilius scytale	0–2100	R	R	R	–	R	R	R	R	R	Am
Boa constrictor	0–240	RES	RES	RES	RES	RES	RES	RES	RES	RES	W
Corallus caninus	0–100	R	R	R	–	R	R	R	R	R	Am
Corallus enydris	0–200	RES	RES	RES	RES	RES	RES	RES	RES	RES	W
Epicrates cenchria	0–1000	RES	RES	RES	–	RES	RES	RES	RES	RES	W
Eunectes murinus	0–240	RAS	RAS	RAS	RAS	RAS	RAS	RAS	RAS	RAS	Am
Dipsas catesbyi	0–200	R	R	R	–	R	R	R	R	R	Am
*Dipsas copei**	0–200	X	X	–	–	–	–	–	–	–	Le
Dipsas indica	0–150	R	R	R	–	R	R	R	R	R	Am
Dipsas pavonina	0–200	R	R	–	–	–	R	R	X	X	Am
Dipsas variegata	0–100	X	R	–	X	–	X	–	X	–	W
Sibon nebulata	0–890	RE	RE	RE	X	X	X	–	–	–	Ea
Aporophis crucifer	0	?	–	–	–	–	–	–	–	–	Unc
*Apostolepis quinquelineata**	140–500	R	R	–	–	–	–	–	–	–	Le
Atractus badius	0–240	R	R	–	X	X	X	X	E	X	Am
*Atractus duidensis**	2050–2133	–	X	–	–	–	–	–	–	–	Ae
Atractus elaps	200	–	X	–	–	X	X	X	R	–	Ea

APPENDIX 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana (continued).

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
*Atractus favae**	0–20	X	–	–	–	–	–	–	–	–	Le
*Atractus insipidus**	400	–	X	–	–	–	–	–	–	–	Le
Atractus latifrons	140	R	–	–	–	X	X	X	R	–	Ap
Atractus major	200	–	X	–	–	X	X	X	E	–	Ea
*Atractus micheli**	0	X	–	–	–	–	–	–	–	–	Le
*Atractus riveroi**	1000–2000	–	S	–	–	–	–	–	–	–	Ae
*Atractus steyermarki**	200–2160	–	X	–	–	–	–	–	–	–	Le
Atractus torquatus	0–240	R	R	X	–	X	X	X	?	X	Am
*Atractus trilineatus**	0	–	R	–	X	–	–	–	–	–	Le
Atractus sp. "A"*	150–500	R	–	–	–	–	–	–	–	–	Le
Chironius bicarinatus	?	X	–	–	–	–	–	–	–	–	Sb
Chironius carinatus	0–1050	RE	RE	RE	RE	RE	RE	RE	RE	RE	W
*Chironius cinnamomeus**	20	S	–	?	–	–	–	–	–	–	Le
*Chironius cochranae**	0–240	R	R	R	–	–	–	–	–	–	Le
Chironius fuscus	0–2250	RES	RES	RES	RES	RES	RES	RES	RES	RES	W
Chironius scurrulus	40	–	–	R	–	–	–	R	R	–	Ab
Chironius sp. "A"*	20–200	RS	–	–	–	–	–	–	–	–	Le
Clelia clelia	0–500	RES	RES	RES	X	X	X	X	ES	X	W
Cyclagras gigas	0	–	–	S	–	–	–	–	–	S	Sb
Dendrophidion dendrophis	0–490	R	R	R	R	R	R	R	R	–	W
Drepanoides anomalus	0–230	RE	RE	–	–	RE	RE	RE	RE	RE	Ap
Drymarchon corais	0–240	RE	RE	RE	RES	RE	RE	RE	RE	RE	W
Drymobius rhombifer	0–240	R	R	R	R	R	R	R	R	–	Ea
Drymoluber dichrous	0–500	R	R	R	–	R	R	R	R	–	Ap
Elapomorphus quinquelineatus	0	X	–	–	–	–	–	–	–	–	Sb
Erythrolamprus aesculapii	0–240	R	R	R	–	R	R	R	R	R	Am
Erythrolamprus bauperthuisii	50	–	R	–	R	–	–	–	–	–	Ea
Helicops angulatus	0–100	A	A	A	A	A	A	A	A	A	Am
Helicops hagmanni	40	–	–	A	–	A	–	A	–	–	Ab
*Helicops hogei**	?	–	A	–	–	–	–	–	–	–	Le
Helicops leopardinus	0	AS	A	A	–	A	?	A	RA	A	Am
Helicops polylepis	?	–	–	A	–	A	–	A	RA	A	Ab
Helicops trivittatus	?	–	–	A	–	–	–	A	–	–	Ab
Hydrodynastes bicinctus	0–240	AS	A	AS	–	A	–	A	–	–	Am
Hydrops martii	0–40	–	–	A	–	A	–	A	A	–	Ab
Hydrops triangularis	0–240	RA	A	A	A	A	–	A	RA	A	Am
Imantodes cenchoa	0–1050	R	R	R	R	R	R	R	R	R	W
Imantodes lentiferus	100	R	–	–	–	R	R	R	R	–	Ap
Leimadophis melanotus	0–890	–	ES	–	ES	ES	–	–	–	–	Ea
Leimadophis poecilogyrus	?	X	–	E	–	–	E	E	–	E	Sb

APPENDIX 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana (continued).

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
Leimadophis reginae	0–650	RES	MfRES	RES	RES	RES	RES	RES	RES	RES	W
Leimadophis typhlus	0–240	RE	RE	RE	RE	RE	RE	RE	RE	RE	Am
Leptodeira annulata	0–1250	RES	RES	RES	RES	RES	RES	RES	RES	RES	W
Leptophis ahaetulla	0–240	RES	RES	RES	RES	RES	RES	RES	RES	RES	W
Liophis breviceps	0–500	R	--	--	--	R	R	R	R	--	Ap
*Liophis canaima**	500	--	X	--	--	--	--	--	--	--	Le
Liophis cobella	0–40	AES	AES	AES	--	AES	AES	AES	AES	AES	Am
*Liophis ingeri**	1900	--	S	--	--	--	--	--	--	--	Ae
Liophis miliaris	30–1210	RAE	RAE	RAE	--	--	--	--	--	X	Sb
*Liophis purpurans**	0–20	X	X	--	--	--	--	--	--	--	Le
*Liophis trebbaui**	1020	--	X	--	--	--	--	--	--	--	Ae
Liophis undulatus	0–20	X	--	--	--	--	X	X	--	--	Ap
Lygophis lineatus	0–1250	S	S	S	S	S	S	S	S	S	W
Mastigodryas bifossatus	50–305	S	S	S	S	S	--	S	S	S	Am
Mastigodryas boddaerti	0–1800	RES	RES	RES	RES	RES	RES	RES	RES	RES	Am
Mastigodryas pleei	90–500	--	S	--	S	S	--	--	--	--	Ea
Ninia hudsoni	230	R	--	--	--	--	R	--	--	--	Ap
Oxybelis aeneus	0–500	RES	RES	RES	RES	RES	RES	RES	RES	RES	W
Oxybelis argenteus	0–500	R	R	R	--	R	R	R	R	R	Am
Oxybelis fulgidus	0–200	RE	R	R	--	X	X	X	E	X	W
Oxyrhopus petola	0–240	RE	RE	RE	RE	X	X	X	R	X	W
Oxyrhopus trigeminus	20	S	--	X	--	--	--	--	--	--	Sb
Oxyrhopus sp. "A"*	200	R	--	--	--	--	--	--	--	--	Le
Philodryas olfersii	0–240	S	S	S	--	S	--	S	DS	DS	Am
Philodryas viridissimus	0–200	R	R	R	--	R	R	R	RE	R	Am
Phimophis guerini	20	S	--	--	--	--	--	--	--	--	Sb
Phimophis guianensis	0–20	S	S	--	S	--	--	--	--	--	Ea
Pseudoboa coronata	0–100	R	R	--	--	R	R	R	RE	R	Ap
Pseudoboa neuwiedii	0–500	S	S	S	S	S	--	S	--	--	Ea
Pseudoeryx plicatilis	0	AS	A	A	--	--	--	A	RA	A	Am
Pseustes poecilonotus	30–490	RE	RE	RE	RE	RE	RE	RE	RE	RE	W
Pseustes sulphureus	0–240	RE	RE	RE	--	RE	RE	RE	RE	RE	Am
Rhadinea brevirostris	30–240	R	R	R	--	R	R	R	R	R	Ab
Rhinobotryum lentiginosum	10–490	R	--	--	--	--	--	R	R	R	Am
Siphlophis cervinus	0–200	R	R	R	--	R	R	R	R	R	W
Spilotes pullatus	0–90	RE	RE	RE	RE	RE	RE	RE	RE	RE	W
Tantilla melanocephala	0–1200	RE	RES	RE	RE	RE	RE	RE	RE	RE	W
*Thamnodynastes chimanta**	2200	--	S	--	--	--	--	--	--	--	Ae
Thamnodynastes pallidus	0–20	S	S	--	--	--	--	X	RE	--	Ap
Thamnodynastes strigilis	0–40	S	S	--	S	S	--	X	--	--	Am
Tripanurgos compressus	90	R	R	R	--	R	R	R	R	R	W

APPENDIX 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana (continued).

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
Xenodon neuwiedii	?	X	—	—	—	—	—	—	—	—	Sb
Xenodon rabdocephalus	0–250	R	R	—	—	R	R	R	R	R	W
Xenodon severus	0–500	RES	RES	RES	RES	RES	RES	RES	RES	RES	Am
*Xenodon werneri**	80–200	R	—	—	—	—	—	—	—	—	Le
Xenopholis scalaris	230	R	R	—	—	R	R	R	R	R	Ap
*Leptomicrurus collaris**	150–850	R	R	—	—	—	—	—	—	—	Le
*Micrurus averyi**	609	R	—	—	—	—	—	—	—	—	Le
Micrurus hemprichii	500	—	R	—	—	R	R	R	R	R	Am
Micrurus ibiboboca	30	S	—	—	—	—	—	—	—	—	Sb
Micrurus isozonus	50	—	X	—	X	X	—	—	—	—	Ea
Micrurus lemniscatus	20–400	R	R	R	—	R	R	R	RS	R	Ap
Micrurus psyches	20–240	R	R	—	—	R	—	—	—	—	Ap
Micrurus spixii	80	—	R	—	—	R	R	R	R	R	Am
Micrurus surinamensis	30–90	SA	X	X	—	X	X	X	A	X	Am
Bothrops atrox	0–1066	RES	RES	RES	RES	RES	RES	RES	RES	RES	Am
Bothrops bilineatus	200–475	R	R	R	—	R	R	R	R	—	Am
Bothrops brazili	20–822	R	R	R	—	R	—	R	R	R	Am
Bothrops castelnaudi	2000	—	S	—	—	R	R	R	R	—	Am
Crotalus durissus	0–2194	S	S	S	S	—	—	—	—	—	W
Lachesis muta	30–200	R	R	R	—	R	R	R	R	R	W
Lizards											
Coleodactylus amazonicus	0–690	R	R	R	—	—	—	R	—	—	Am
Coleodactylus meridionalis	200–800	—	R	—	—	—	—	—	—	—	Sb
*Gonatodes annularis**	100–929	R	R	R	—	—	—	—	—	—	Le
Gonatodes humeralis	0–700	RE	RED	RE	—	RE	RE	RE	RE	RE	Am
*Gonatodes varius**	?	X	—	—	—	—	—	—	—	—	Le
Gonatodes vittatus	0–305	—	ES	—	ES	—	—	—	—	—	Ea
Hemidactylus mabouia	0–30	EP	EP	EP	—	EP	EP	EP	EP	—	Cos
*Hemidactylus palaichthus**	50–550	X	SSa	—	S	—	—	—	—	—	Le
Lepidoblepharis festae	0–200	—	—	R	—	R	R	R	R	—	Ad
*Phyllodactylus dixoni**	90	—	SSa	—	—	—	—	—	—	—	Le
Pseudogonatodes guianensis	50–240	R	RD	—	—	—	R	R	R	—	Ap
Sphaerodactylus molei	0	—	E	—	E	—	—	—	—	—	Ea
Thecadactylus rapicauda	0–490	RE	RE	RE	RES	RE	RE	RE	RE	RE	W
Anolis aeneus	0	—	P	—	—	—	—	—	—	—	Car
Anolis auratus	0–1700	S	S	S	S	S	S	—	—	—	W
Anolis chrysolepis	0–2100	R	RMf	R	—	R	R	R	R	—	Am
Anolis fuscoauratus	0–1066	RE	RE	RE	RE	RE	RE	RE	RE	RE	Ap
Anolis gibbiceps	?	—	X	—	X	—	—	—	—	—	Ea
Anolis marmoratus	0–20	P	—	—	—	—	—	—	—	—	Car

APPENDIX 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana (continued).

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
Anolis ortonii	0–929	RE	RMfE	RE	--	RE	RE	RE	RE	RE	Am
Anolis punctatus	0–700	RE	RE	RE	--	RE	RE	RE	RE	--	Am
Anolis roquet	0	--	P	--	P	--	--	--	--	--	Car
Iguana iguana	0–305	REAS	REAS	REAS	REAS	REAS	REAS	REAS	REAS	REAS	W
Plica plica	0–970	R(Sa)	RE(Sa)	R	--	R	R	R	RE	R	Am
Plica umbra	0–690	RE	R	R	--	R	R	R	R	R	Am
Polychrus marmoratus	0–1050	E	E	E	E	E	E	E	E	E	Am
*Tropidurus bogerti**	1600–2400	--	SSa	--	--	--	--	--	--	--	Ae
Tropidurus torquatus	20–1020	SSa	SSa	S	S	--	--	--	--	S	Sb
*Uracentron azureum**	0–500	R	R	R	--	--	--	--	--	--	Le
Uracentron werneri	?	--	X	--	--	X	--	--	--	--	Ea
*Uranoscodon superciliosa**	0–250	RE	RE	RE	--	--	--	--	--	--	Le
Mabuya mabouya	0–490	RES	RES	RES	RES	RES	RES	RES	RES	RES	W
Alopoglossus angulatus	30–600	R	R	R	--	--	R	R	RE	--	Am
*Amapasaurus tetradactylus**	200	--	--	R	--	--	--	--	--	--	Le
Ameiva ameiva	0–1150	RES	RES	RES	RES	RES	RES	RES	RES	RES	W
Ameiva bifrontata	50–305	--	S	--	S	S	--	--	S	--	Ea
Arthrosaura kockii	0–690	R	R	R	--	--	--	--	R	--	Am
Arthrosaura reticulata	40–2164	R	R	R	--	--	R	R	R	--	Ap
*Bachia cophias**	0–1100	R	R	R	--	--	--	--	--	--	Le
*Bachia flavescens**	0–1100	R	R	--	--	--	--	--	--	--	Le
*Bachia guianensis**	90–300	--	RD	--	--	--	--	--	--	--	Le
Bachia parkeri	609	--	S	--	--	X	--	--	--	--	Ap
Cercosaura ocellata	0–305	RE	S	RE	--	--	--	R	R	R	Am
Cnemidophorus lemniscatus	0–1130	S	S	S	S	S	--	--	--	--	W
Crocodilurus lacertinus	0–90	RA	RA	RA	--	--	--	RA	--	--	Ab
Dracaena guianensis	0–40	--	--	RAE	--	--	--	RAE	RAE	--	Ab
*Euspondylus phelpsi**	1700–1917	--	X	--	--	--	--	--	--	--	Ae
Euspondylus sp. "A"*	1450	--	X	--	--	--	--	--	--	--	Ae
*Gymnophthalmus underwoodi**	0–800	RES	RES	RES	--	--	--	--	--	--	Le
Iphisa elegans	0–650	R	R	R	--	R	R	R	R	R	Am
*Kentropyx borckianus**	0	S	S	--	--	--	--	--	--	--	Le
Kentropyx calcaratus	0–1067	RE	RE	RE	--	RE	RE	RE	E	RE	Am
*Kentropyx striatus**	0–1420	S	S	S	S	S	--	--	--	--	Le
*Kentropyx williamsoni**	40	--	--	X	--	--	--	--	--	--	Le
*Leposoma guianense**	0–823	R	R	R	--	--	--	--	--	--	Le
*Leposoma percarinatum**	0–450	RA	R	R	--	--	--	--	--	--	Le
Neusticurus bicarinatus	0–1000	RA	RA	RA	--	--	--	RA	--	--	Am
*Neusticurus racenisi**	100–1215	--	X	X	--	--	--	--	--	--	Le
*Neusticurus rudis**	0–1800	RA	RA	--	--	--	--	--	--	--	Le
*Neusticurus tatei**	400–1400	--	X	--	--	--	--	--	--	--	Le

Appendix 10:1.—Altitudinal and geographical distribution of amphibians and reptiles in Guiana (continued).

Species	Elevation (m)	Eastern Guiana	Western Guiana	Brasilian part of Guiana	Western and Central Venezuela	Amazonian Colombia	Amazonian Ecuador	Upper Amazonian Brasil	Amazonian Perú	Amazonian Bolivia	Type of distribution
Prionodactylus argulus	10–300	R	R	R	--	R	R	R	RE	R	Am
Ptychoglossus brevifrontalis	200	R	--	--	--	--	R	--	R	--	Ap
*Riolama leucosticta**	2621	--	S	--	--	--	--	--	--	--	Ae
Tretioscincus agilis	0–700	R	RD	S	--	--	R	--	--	--	Am
Tupinambis nigropunctatus	0–540	RES	RES	RES	RES	RES	--	RES	RES	--	Am
Amphisbaenians											
Amphisbaena alba	0–305	RES	RES	RE	RES	RE	RE	RE	RE	RE	W
Amphisbaena fuliginosa	0–490	RES	RES	RES	RES	RES	RES	RES	ES	RES	W
*Amphisbaena gracilis**	0	--	X	--	--	--	--	--	--	--	Le
Amphisbaena mitcheli	0	--	--	?	--	--	--	--	--	--	Unc
*Amphisbaena rozei**	500–750	--	X	--	--	--	--	--	--	--	Le
*Amphisbaena slevini**	40	--	--	R	--	--	--	--	--	--	Le
*Amphisbaena stejnegeri**	0	R	--	--	--	--	--	--	--	--	Le
*Amphisbaena vanzolinii**	140–250	R	--	--	--	--	--	--	--	--	Le
Bronia brasiliana	?	--	--	?	--	--	--	--	--	--	Unc
*Mesobaena huebneri**	100	--	X	--	--	--	--	--	--	--	Le
Total Amphibians (178)		121	125	70							
Total Reptiles (230)		172	186	135							
Total Species (408)		293	311	205							