Mem. Inst. Butantan
46:219-254, 1982

SNAKES OF THE GUIANAN REGION

Marinus S. HOOGMOED *

ABSTRACT: The study of snaks from the Guianan region got an early start in 1705 when several species were pictured by Merian. As relatively large proportion of the snakes described by Linnaeus originated from Surinam. Interest for and knowledge of this group of animals steadily increased in the 18th and 19th century (80 species known at the turn of the century), but only in the second part of the 20 th century detailed studies of snake faunas from (part of) the Guianan region appeared. No such study for the entire area has been published till now. At present a total of 134 species of snakes, belonging to 159 taxa, is known. Only 19.4% is endemic, the majority (43.4%) belong to species with an Amazonian distribution. Seventeen species (12.7%) are venemous, ten belonging to the Elapidae, seven to the Crotalidae. Several taxonomic problems are discussed, *Cercophis auratus* (Schlegel) is restored as a valid taxon and redescribed. Analysis of available distribution data shows that forest snakes are fairly evenly distributed throughout Amazonia and Guiana. Snakes restricted to open formations are spread evenly throughout Guiana, but most of them are absent in western Amazonia. When taking together ubiquists and snakes restricted to open formations there is a fair resemblance between the faunas of Guiana and Iquitos, but only a moderate one between Santa Cecilia and Guiana, possibly reflecting the influence of species belonging to the Andes foothill fauna (Napo refuge). Within Guiana apparently there are no unsurmountable barriers to snakes, the differences that are observed between the western and eastern/Brazilian part can be explained by the presence of species barely raching these areas. Probably these species are still in the process of expanding their range.

INTRODUCTION

The area to be dealt with in this paper and called Guiana is the region bordered by the Rio Orinoco, the Cassiquiare Canal, the Rio Negro, the Rio Amazonas and the Atlantic Ocean (Fig. 1). This area comprises three political units in their entirety, namely Guyana (formely British Guiana), 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

* Rijksmuseum van Matuurlijke Historie, Leiden, The Netherlands.

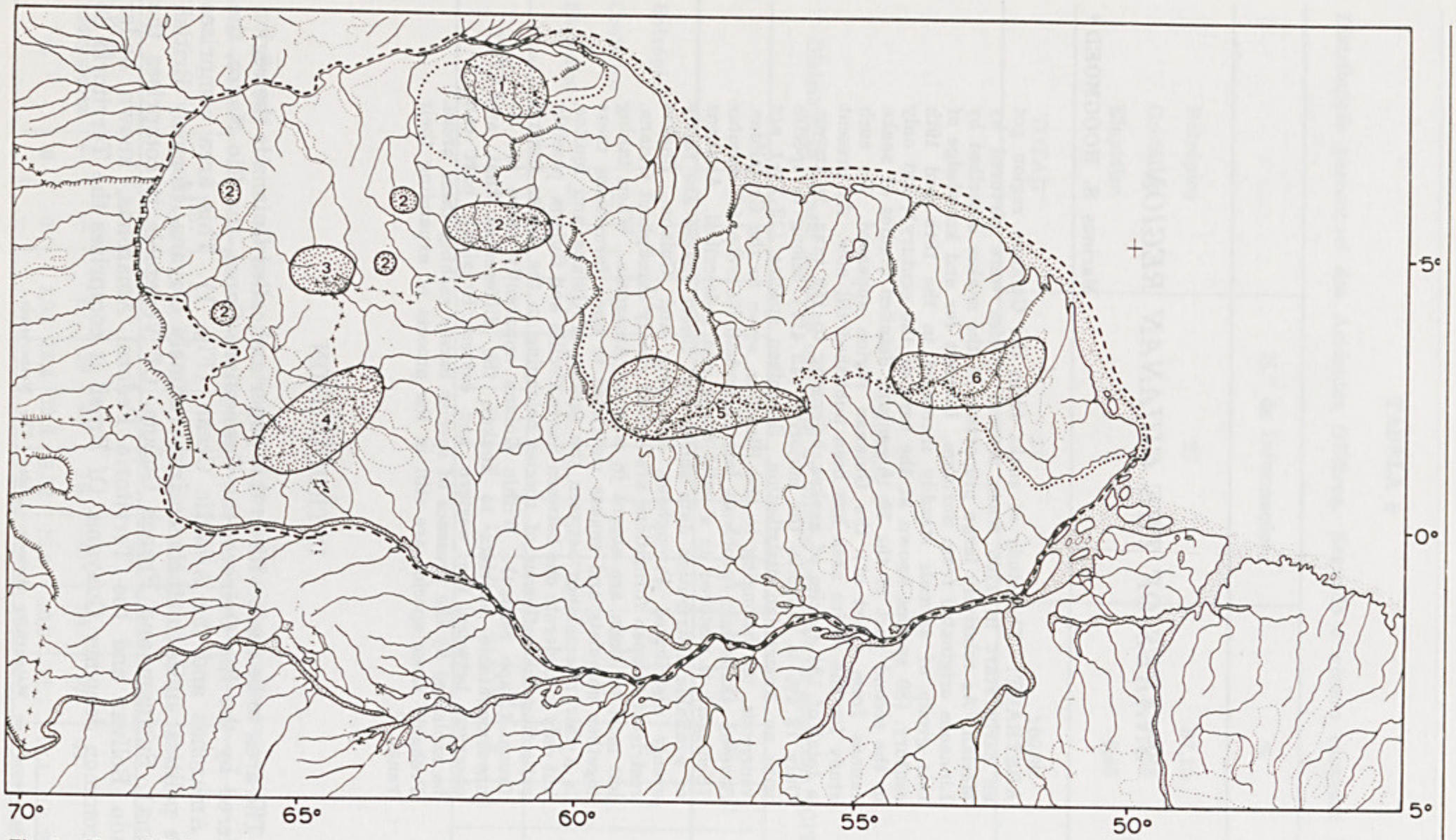

Fig. 1. Map of Guiana, showing the borders of the area as here defined (heavy broken line and as defined by Descamps et al. (1978) and by Lescure (1977) (heavy dotted line). Presumed forest refugia are gray and indicated by numbers: 1 = Imataca refuge, 2 = Roraima refuge (and associated tepui refuges), 3 = Ventuari refuge, 4 = Imerí refuge, 6 = Oyapock refuge. The line of fine dots (also in fig. 4) represents the 200 m contour line.

Amapá, the Territorio de Roraima and those parts of the states of Pará and Amazonas that are situated north of the Rio Amazonas and the Rio Negro (Hoogmoed, 1979:242). French investigators (Lescure, 1977; Descamps *et al.*, 1978) tend to delimit Guiana as the area bordered by the Rio Barama (Venezuela) in the west and by the Rio Araguari (Brasil) in the southeast, the southern border being the watershed between rivers emptying directly into the Atlantic Ocean and those belonging to the Amazonian drainage. In my opinion this definition of Guiana is rather artificial and not in accordance with the biogeographical, geological and geographic data. More elaborate reasons for this rejection of the French definition are given in my 1979 paper on the herpetofauna of the Guianan region. In the same paper an extensive description of the physical features of the Guianan region is also provided (Hoogmoed, 1979:242-249).

HISTORY OF THE STUDY OF GUIANAN SNAKES

The coast of the Guianas was discovered in 1499 by Alonso de Ojeda and Amerigo Vespucci and was afterwards known as the "Spanish Main", "Wild Coast" or the "Côte Ferme". Because of tales about fabulous richness in the interior of the area many expeditions explored the region, particularly during the 16th century, in their search for El Dorado. Some of these expeditions, notably those of Sir Walter Raleigh penetrated fairly deep into the interior via large rivers like the Orinoco, but most hardly ventured inland and merely explored river mouths. It soon became evident that El Dorado either was difficult to locate, or did not exist at all, although the last possibility was only admitted reluctantly. Hence the character of the expeditions gradually changed and their main aim became the establishment of trading posts at the mouths of rivers. This process started in the second quarter of the 17th century, one of the main factors being the founding in 1621 of the "Westindische Compagnie" (West Indian Company) in the Netherlands, a trading society with interest primarily in obtaining overseas trading facilities. During part of the 17th century (1624-1654) this company even conquered a large area in northeast Brazil. The height of this conquest was during the government of Prince Johan Maurits of Nassau, who had a keen interest in science and, among his companions had scientists like Piso and Marcgraf and artists like Eckhout and Post. Their efforts must have stimulated in the Netherlands a lively interest in objects for natural history from overseas countries which led to the establishment of cabinets of natural history. Although the natural history objects collected during the Brazilian conquest were at least partly transported to the Netherlands, their present whereabouts are not known and they probably got lost. Shortly after the Brazilian episode came to an end, the Dutch settled in the coastal area of present day Surinam and Guyana. This colonisation led to an increase in traffic between Europe (mainly the Netherlands and England) and Guiana and, as a consequence, to the publication of several travelstories. Among these were the books by Warren (1667, 1669), who also paid attention to the natural history of the areas he visited. He mentioned snakes that were nearly thirty foot long. No doubt he is referring to

the anaconda, *Eunectes murinus*. The same author mentions snakes which "are knotty, with Horns in their Tails, and Tusks two Inches long upon the upper Chap". In my opinion there is little doubt he is referring to the rattlesnake of the coastal area of Surinam, *Crotalus durissus dryinus* L. Van Berkel (1695) also refers to the rattlesnake when he describes the "Colony of Berbice" in Guyana, and to the anaconda when he is describing Surinam. However, large parts of this book have been copied from those by Warren. The first reliable pictures of snakes, which can be identified, were provided by Merian (1705a, b) in her monumental treatise on the insects of Surinam, and were painted on the spot in Surinam when she stayed there during the period 1699-1701. The species she depicted were the gardenboa *Corallus enydris* L.) (twice) and the burrowing snake *Anilius scytale* (L.). Apparently settlers and sailors provided cabinets of natural history with a steady flow of material from tropical conustries. For the Netherlands this mainly involved present day Indonesia, South- and West-Africa and Surinam. The richness of these cabinets is well illustrated by Seba's monumental Thesaurus (4 volumes), in the first two volumes of which (1734/5) many snakes were illustrated. Among these snakes are at least 40 species of American provenance, even though their origin may be stated as being Cape of Good Hope or the East Indies. For several of these, Surinam is indicated as the place of origin. As the plates published by Seba were used by many subsequent writers, notably Linnaeus, for the description of species, Seba's work is of paramount importance to taxonomy. Unfortunatelly, of the 14 species stated by Seba to originate from either Berbice or Surinam, only seven are referable to six nominal taxa (*Boa c. constrictor* L., *Dipsas v. variegata* (D., B. & D.), *Helicops angulatus* (L.), *Leimadophis typhlus*(1) (L.), *Philodryas v. viridissimus* (L.) and *Oxybelis fulgidus* (Daudin). Other Guianan snakes possibly depicted by him were *Liophis cobella* (L.) and *Drymoluber dichrous* (Peters). The remainder either is unidentifiable on the basis of the drawing and the description, or could be interpreted in several ways. Many of the other figured South American snakes also occur in Surinam and probably originate from that country as well. Seba's first collection was sold to Czar Peter the Great and subsequently got lost for the greater part. His second collection was auctioned 16 years after his death in 1752 and part of it now is in the Zoological Museum in Leningrad (Juriev, 1981). Unfortunately I could not yet examine that material and solve some of the remaining problems.

Another important contribution to our knowledge of Guianan snakes was made by Scheuchzer (1735a, b, 1738) in his Physica Sacra. In this work he depicted a number of snakes from the collection of J. H. Linck, a pharmacist with a famous cabinet in Leipzig. The drawings were well done and most of them can be identified relatively easily. The snakes were generally drawn life size and apparently in the position they were

(1) Throughout this paper I have adopted the generic names *Leimadophis*, *Liophis* and *Lygophis* as used by Peters & Orejas-Miranda (1970), although I am fully aware of the studies that have been going on recently in this group of related genera. The most recent paper dealing with this subject is that by Dixon (1980), who classified all species belonging to these genera as *Liophis*. Although I sympathise with his views and accept his arguments I did not adopt his classification here, because this would have included too many alterations in the manuscript of this paper. I did, however, use some of his as yet unpublished results, which are acknowledged as "personal communication".

preserved in. Thus, in many cases it is possible to reconstruct the glass jars they were stored in by taking a ruler and a pair of compasses and drawing a few tangent lines. This to illustrate the exactness with which the drawings were executed, much more accurately depicting the actual specimens than those in the famous work of Seba. The largest part of the snakes depicted and rather superficially, described (47 of 64) aparently originated from South America and of these 47, ten were stated to come from Surinam. For two of these (*Cylindrophis rufus* (Laur.) and *C. maculatus*, (L.) both from Southeast Asia), the locality obviously is in error, the other eight do occur in Surinam. Ammong the species reported by Scheuchzer for the fist time from the Guianan region are *Erythrolamprus a. aesculapii* (L.), *Leptophis a. ahaetulla*, (L.) *Lygophis l. lineatus* (L.), *Oxybelis argenteus* (Daudin), *Oxyrhopus p. petola* (L.) and *Rhinobothryum lentiginosum* (Scopoli). Scheuchzer's work also was frequently referred to by subsequent writers, like for instance Gronovius (1756), and its importance for herpetology may be illustrated by the history of the name *Coluber jaculatrix* Linnaeus, 1766, still cited by Peters & Orejas-Miranda (1970) with a questionmark in the synonymy of *Lygophis l. lineatus* (L.). This was based only on the inclusion of the references to it in Lacépède and Latreille in the synonymy of this species as presented by Hoge (1952). However, the matter is relatively simple: Linnaeus (1766) referred to species n.o 26 of Gronovius (1756), who in turn referred to Scheuchzer (1735b), plate 715 fig. 2 and provided a fairly good description. Combining these data it is evident that *Coluber jaculatrix* Linnaeus, 1766 is a synonym of *Lygophis lineatus* (Linnaeus, 1758). Therefore the importance of Scheuchzer's work for herpetology should not be neglected. Unfortunately the present whereabouts of the material from Lincke's cabinet is not known. Apparently it is not in one of the museums in the DDR (Peters, Obst, personal comunications).

Sundius (1749), contributing to Linnaeu's (1749) Amoenitates Academicae, described ten species of snakes from Surinam, all but one of which can be identified. He added *Thamnodynastes pallidus* (L.) and *Micrurus lemniscatus* (L.) to the list of snakes known from the Guianan region. Gronovius (1756), in describing his own collection, mentioned 18 species of snakes from Surinam, of which four actually come from Southeast Asia one from Europe, three are unidentifiable and ten could be identified as Guianan snakes, of which *Leptodeira a. annulata* (L.) *Philodryas olfersii herbeus* (Wied) and *Thamnodynastes strigilis* (Thunberg) constitute new faunal records. Linnaeus (1758) based himself on material present in Swedish collections of which a large proportion either had been obtained by purchase from the Netherlands (among others part of the Seba collection was acquired for the king of Sweden), or had been collected by Rolander, one of Linnaeus pupils, in Surinam, or apparently had come from Surinam through the Netherlands along other channels. In the 10th edition of his Systema Natura Linnaeus only mentioned three species as coming from Surinam, but in his synonymies he included many references to Surinam species described by Sundius, Gronovius and Seba. In Houttuyn's so-called Dutch edition of Linnaeus's Systema Natura (1764), which was only partly a translation and primarily an elaboration based on material in his own collection and that

of e.g., Gronovius, a total of 12 snakes was stated to have come from Surinam. Two of these are of Southeast Asian provenance, the other ten indeed are from Surinam. Houttuyn added two more species to the known snake fauna of the Guianas, viz. *Typhlops reticulatus* (L.) and *Corallus caninus* (L.). It sems useful to indicated here that the description of *Typhlops reticulatus* by Linnaeus was based on two descriptions and a plate in older literature and that he himself apparently did not have any material of this species available. His synonymy included a reference to Scheuchzer's (1735b) plate 747 fig. 4 and to Gronovius's description of his seventh species, the *Anguis* with 177 ventrals and 37 subcaudals. The first reference is correct (Dixon & Hendricks, 1979), the second, however, is not. After long deliberations both Dixon and I came independently to the conclusion that Gronovius did not describe *Typhlops reticulatus* but in fact was referring to *Amphisbaena fuliginosa* L., a wormlizard. By selecting RMNH 7660 as the neotype, Dixon & Hendrick (1979) stabilised the nomenclature of *Typhlops reticulatus*.

Barrère (1741) in his popular account of the natural history of French Guiana mentioned several species of snakes from that country, of which only one, *Crotalus durissus* L., is identifiable.

Fermin (1765) and Hartsinck (1770) gave popular accounts of the natural history of Surinam, but most of the snakes they mentioned are difficult to identify. Linnaeus (1766), Laurenti (1768), Linck (1783) and Gmelin (1789) did not add any new species to the list of known Guianan snakes. Until the end of the 18th century nearly all material of Guianan snakes came from Surinam, which in this context should be widely interpreted as comprising also eastern Guyana (Berbice and Demerara). In 1802 Latreille (1802a, b) reported several snakes from French Guiana, comprising the most common species like *Boa constrictor*, anaconda and rattlesnake. Daudin (1803a-d) in his "Histoire naturelle.....des reptiles" presented a nearly complete compilation of the snakes at that moment known from the Guianan region, most still only recorded from Surinam, but also some species that had become known from French Guiana or Cayenne (as the colony sometimes also was called, in reference to its capital). Only three species formerly known from the area under consideration were not included in Daudin's compilation. On the other hand he reported five species new for the region, of which *Sibon nebulata* (L.) and *Pseudoeryx plicatilis* (L.) were already known to science, the other three (*Clelia c. clelia* (Daudin), *Tripanurgos compressus* (Daudin) and *Micrurus psyches* (Daudin)) were described here for the first time. Fitzinger (1826), basing himself on the literature, added three species which had been described recently (*Leimadophis poecilogyrus amazonicus* Amaral, *Xenodon severus* (L.) (including *X. aeneus* Boie from Surinam in its synonymy) and *Micrurus s. surinamensis* (Cuvier)).

Our knowledge of Guianan snakes spectacularly increased by the publication of Schlegel's (1837) "Essaie sur la physionomie des serpens". This book was mainly based on the rich collections of the Rijksmuseum van Natuurlijke Historie in Leiden, Netherlands which in the eighteen twenties and thirties had in Surinam a very active collector, the pharmacist H. H. Dieperink, who regularly sent large consignments of pre-

served material to Leiden (Holthuis, 1959). Moreover, Schlegel had good contacts with the Paris herpetologists Duméril and Bibron and also used part of the collections of the Paris museum. From this time on snakes from other areas within Guiana became known in growing numbers. Through Schlegel's efforts in 1837 a total of 54 snakes was known from Guiana. It might become boring to mention all the 21 species added to the Guianan snake-fauna by Schlegel, but I wish to record here four which Schlegel described for the first time. They include *Dipsas pavonina* Schlegel and *Dendrophidion dendrophis* (Schlegel), both based on specimens from French Guiana, and *Pseustes sulphureus dieperinkii* (Schlegel) and *Cercophis auratus* (Schlegel), both described from Surinam and both with a confused history. The allocation of *Dipsas Dieperinkii* Schlegel, 1837 was cleared by Brongersma (1937), who considered it a synonym of *Pseustes s. sulphureus* as used by Amaral (1930), and by Hoge & Romano (1969) who considered it a distinct subspecies of *Pseustes sulphureus* (Wagler). *Dendrophis aurata* Schlegel, 1837 never has been allocated properly until now, possibly because it was confused with Schlegel's *Dryiophis auratus*, a synonym of *Oxybelis aeneus* (Wagler). The species was described on the basis of a single specimen from Surinam, collected there by Mr. Dieperink. The species served Fitzinger (1843) as type of his genus *Cercophis*. Duméril, Bibron and Duméril (1854) did not know where to place it and did not pursue the matter. As far as I am aware, the species was only cited by Schlegel (1858), it was not mentioned by Günther (1858) or by Boulenger (1893, 1894, 1896) in their Catalogues of Snakes in the British Museum, nor by Amaral (1930) or Peters & Orejas-Miranda (1970) in their respective checklists of South-American snakes. Romer (1956:580) considered *Cercophis* a junior synonym of *Oxybelis*. Keiser (1974), acting in accordance with my advice, did not include *Dendrophis aurata* Schlegel, 1837 in the synonymy of *Oxybelis aeneus* (Wagler). I did investigate the type-specimen (RMNH 813), which unfortunately is in a rather poor condition (e.g. the epidermis has largely disappeared) but still good enough to allow taxonomic conclusions. In my opinion this species, described y Schlegel (1837) and made the type of a new genus by Fitzinger (1843), is completely different from any other known South American snake and therefore properly should be called *Cercophis auratus* (Schlegel, 1837). It can be recognised by a combination of the following characters: scales on the back smooth, without pits, arranged in 15-15-11 longitudinal rows, of which the vertebral one is enlarged, ventrals (140) fewer than the subcaudals (163), which are paired, anal divided, a very long slender body and tapering tail, with the thickest part of the body just anteriorly to the cloaca, head small, distinctly wider than the neck, mandibular teeth subequal, maxillary teeth 20 followed by two enlarged, solid teeth, separated by a diastema from the preceeding teeth. Scalation of the head (Fig. 2) : one pre- and two postoculars, a small, rectangular loreal, temporals 1+2, eight supralabials, fourth and fifth bordering the eye, ten infralabials, five of which are in contact with the anterior pair of chinshields. This does not seem the place to speculate on the proper position of this species within the Colubrids, that would ask for more and preferably recently collected material to provide us with much needed additional information on the osteology. However, most likely this is a member of the Xenodontinae.

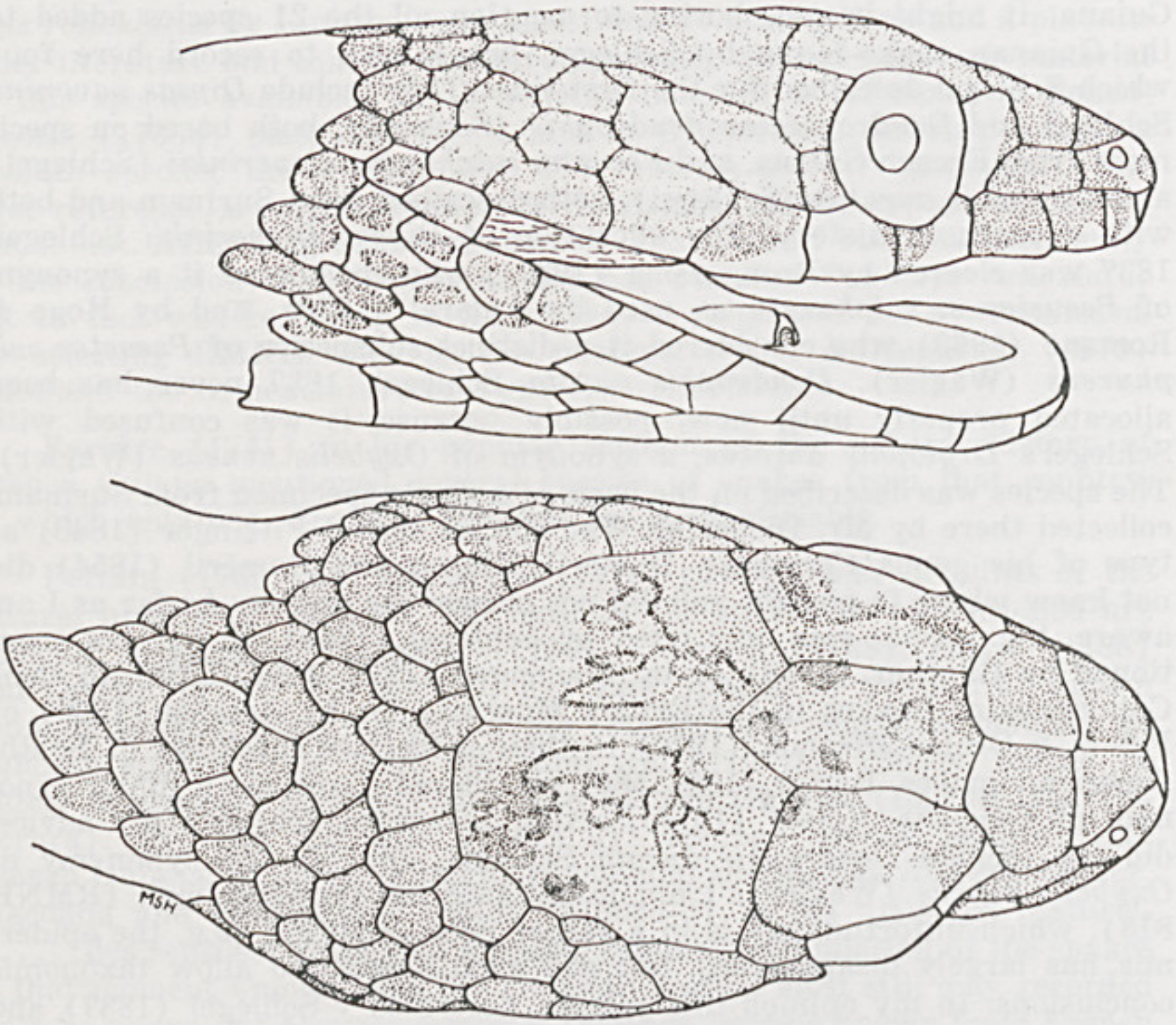

Fig. 2. *Cercophis auratus* (Schlegel), lateral and dorsal view of head of holotype, RMNH 813.

The first paper dealing with the reptiles and amphibians of British Guiana (Troschel, 1848) increased our knowledge of Guianan snakes by adding five more taxa to the list. Among these were *Phimophis guianensis* (Troschel), new to science, and the first mention of *Crotalus durissus ruruima* Hoge. This rattlesnake was considered as one species throughout British Guiana, but specimens from the coastal savannas (*C. d. dryinus* (L.)) and from the surroundings of Mount Roraima on the border of Guyana, Venezuela and Brazil (*C. d. ruruima* Hoge) were separately mentioned. Although the monumental work of Duméril, Bibron & Duméril (1844, 1854) was a land-mark in the history of herpetology, it did not substantially contribute to our knowledge of Guianan snakes, because this work only added six more taxa to the list. Two taxa (*Dipsas v. variegata* (D., B. & D.) and *Atractus torquatus* (D., B. & D.)) which were (validly) described here for the first time, had previously been reported from

the region by respectively Seba (1735) and by Schlegel (1837) (in the synonymy of this composite *Atractus badius*). Another one (*Ablabes purpurans*) falls into the synonymy of *Liophis miliaris* (L.) (Dixon (1978)), personal communication). Of the six taxa reported for the first time from Guiana none were new to science. One of these species (*Typhlophis squamosus* (Schlegel) had been reported from Cayenne in the original description, but had not yet been included in general works used to compile the present survey. Minor additions to the list of Guianan snakes were made by Günther (1858) (with whose data I combined Gray's (1849)), Jan & Sordelli (1860-1881), Kappler (1885), Boulenger (1893, 1894, 1896) and Van Lidth de Jeude (1898, 1904, 1917). Amaral's (1930) checklist, based upon a survey of the literature added another ten taxa, bringing the total up to 91. Roze (1966) compiled the data on Venezuelan snakes and enlarged the total to 116 by adding to the list 25 new taxa, which were mainly based on the extension of known ranges into the Guianas, on the splitting of formerly monotypic taxa, and to a large proportion (about 1/3) on the description of several new taxa by Roze. The checklist by Peters & Orejas-Miranda (1970) compiled most known data on South American snakes and listed a total of 135 from the Guianas. Hoogmoed (1979) gave a summary of the available information, combining literature data with those from his own research and from fieldnotes, mainly on Surinam snakes. At approximately the same time, Lancini's (1979) book on Venezuelan snakes appeared and together they increased the known number of snake taxa in Guiana to 157. Gasc & Rodriguez (1980b) dealt with the snakes of French Guiana mainly on the basis of recently collected material and listed for this country a total of 77 taxa (one of which was mentioned only in the general discussion). Unfortunately they did not sufficiently take into account the old literature and their list is far from complete. They (1979) described as new *Atractus zidoki*, which had also been reported by Hoogmoed (1979) as *Atractus* sp. A, and in another paper (1908a) *Geophis alasukai*, which is a junior synonym of *Atractus flammigerus* (F. Boie).

Summarizing, we can say that since the end of the last century the number of snake-taxa known for the region doubled. Thus, in the past 85 years an equal number of taxa became known as in the previous 229 years.

The gradual increase and present state of our knowledge about Guianan snakes is reflected in the graph (Fig. 3) and in the appendix 1 which include 159 nominal taxa.

Differences with the list provided by Hoogmoed (1979) are the result of diverse causes:

1. Oversight of previous literature records.
2. Descriptions of new taxa and new locality data.
3. Identifications of hitherto questionable taxa and re-identifications.
4. Revisions of genera.
5. Hoogmoed (1979) only listed full species, subspecies were not taken into account.

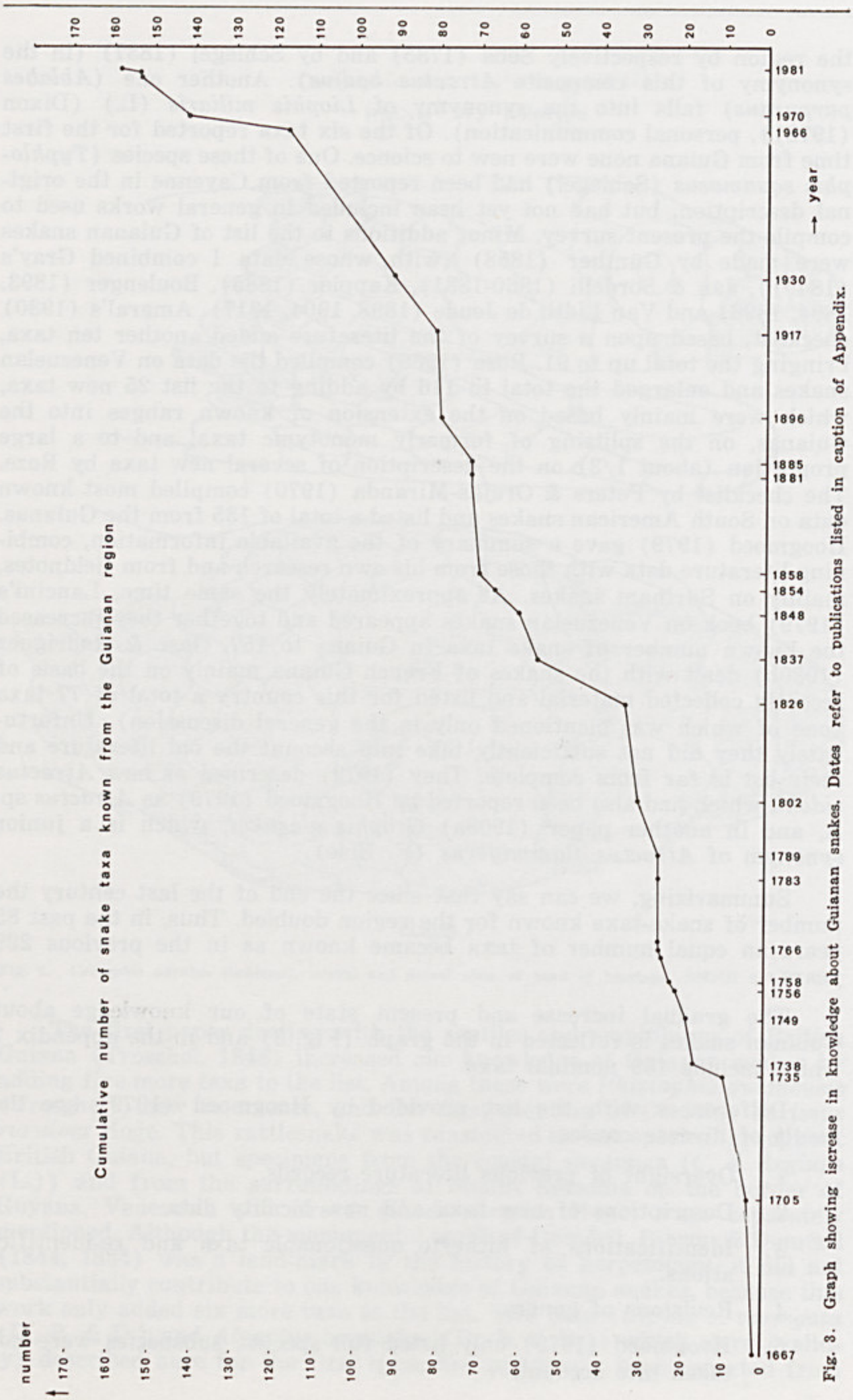

Fig. 3. Graph showing iscrease in knowledge about Guianan snakes. Dates refer to publications listed in caption of Appendix.

1. Among the first group are *Cercophis auratus* (Schlegel), *Waglerophis merremii* (Wagler) and *Leptomicrurus schmidti* Hoge & Romano, for which definite Guianan localities are known (Schlegel, 1837; Boulenger, 1894 and Gasc & Rodrigues, 1980b; Hoge & Romano, 1966). *Pliocercus euryzonus euryzonus* Cope has been reported from Amazonian Brazil, but it is not clear whether it really does occur in the Guianan region or just comes close to it. For completeness sake it has been included here.

2. The second group comprises among others *Typhlops minuisquamus*, recently described by Dixon & Hendricks (1979), and *Atractus zidoki*, described by Gasc & Rodriguez (1979), previously reported as *Atractus* sp. A by Hoogmoed (1979). In this group also should be included *Eunectes deschauenseei* Dunn & Conant, formerly known from Isla Marajó only, but recently reported from eastern French Guiana, from swamps near the river Approuage, by Matz & Matz (1981), who substantiated their report with colour-photographs of living specimens. Hereby the known range of this species is considerably extended to the northwest and follows a pattern of distribution well known for several other reptiles and amphibians inhabiting marshy areas in the lower Amazonian region (*Crocodilurus lacertinus* (Daudin), *Peltocephalus tracaxa* (Spix), *Melanosuchus niger* (Spix) and *Hydrolaetare schmidti* (Cochran & Goin). *Masticophis mentovarius suborbitalis* (Peters) recently was reported from the northwestern part of the Guianan region by Lancini (1979), whereas Wiest (1978) reported *Chironius m. multiventris* Schmidt & Walker from the extreme southern edge. Harris & Simmons (1978) described the new subspecies *Crotalus durissus trigonicus* from the Rupununi savanna in southern Guyana.

Bothrops eneydae Sandner Montilla is only hesitantly included in the list of Guianan snakes on the basis of the fact that Hoge & Romano Hoge (1981) included it in their checklist of poisonous snakes of the world. However, I did not yet have the opportunity to examine the original description, or the holotype, which apparently already got lost (Sandner Montilla, 1981, personal communication). Personnally I have my strong doubts about the validity of this species, but until further information becomes available it is retained on the list.

3. A number of hitherto questionable identifications could be corrected, either in generic revisions or because additional material became available for study. Thus, the following synonymies for names in Hoogmoed (1979) can be listed:

Leptotyphlops sp. A = *Leptotyphlops amazonicus* Orejas-Miranda

Chironius sp. A = *Chironius exoletus* (L.)

Chironius bicarinatus = *Chironius exoletus* (L.)

Chironius cinnamomeus = *Chironius scurrulus* (Wagler)

Oxyrhopus sp. A = *Oxyrhopus formosus* (Wied)

Liotyphlops incertus Amaral = *Liotyphlops ternetzii* (Boulenger)

Aporophis crucifer Ahl = *Leimadophis melanotus* (Shaw)

Liophis purpurans (D., B. & D.) = *Liophis miliaris* (L.)

These synonymies need some explanation. *Leptotyphlops* sp. A was identified as *L. amazonicus* on the basis of material seen in Venezuelan museums and collected during field-work in Venezuela in 1978. *Chironius* sp. A was identified as *C. exoletus* and *C. cinnamomeus* as *C. scurrulus* on the basis of the revision of the genus *Chironius* by Wiest (1978). *C. bicarinatus* from Guiana (Hoogmoed, 1979:275) was based on a number of specimens seen by me in 1975 in collections in French Guiana (SEPANGUY, Institut Pasteur) and Surinam (Surinaams Museum), without access to literature and insufficient material for comparisons. The specimens compared well with specimens of *C. bicarinatus* (Wied) from Brazil present in these collections, and were tentatively identified as such. However, upon consulting Wiest (1978) it soon became evident that in reality they belong to *C. exoletus*. Thus, the record in Hoogmoed (1979) of. *C. bicarinatus* occurring in Guiana is based on a misidentification. *Oxyrhopus* sp. A was identified as *O. formosus* on the basis of recently collected additional material while taking into account the remarks made by Gasc & Rodrigues (1980). According to Mr. C. P. Kofron (1979, personal communication), *Liotyphlops incertus* identical with *L. ternetzii*, a species formerly known from southern Brazil, Paraguay and northern Argentina, but recently reported from the area around Belém by Da Cunha & Do Nascimento (1975). I investigated the holotype of *Aporophis crucifer* in the Berlin museum and came to the conclusion that it is identical with *Leimadophis melanotus*. According to Dixon (1978, personal communication) *Liophis purpurans* is a synonym of *L. miliaris*.

4. *Typhlops unilineatus* has been omitted from the list, because according to Dixon & Hendricks (1979) this probably is an oriental species.

A partial revision of the genus *Atractus* (Hoogmoed, 1980) led me to consider *A. micheli* Mocquard and *A. subbicinctum* (Jan) (the latter name not mentioned by Hoogmoed, 1979) as synonyms of *A. badius* (F. Boie). Also it turned out that two names considered synonyms of *A. badius* since 1837 were good species (*A. flammigerus* (F. Boie), *A. schach* (F. Boie)), well differentiated from *A. badius* in scale characters, hemipenial morphology and colour pattern. Consequently these names were restored to species level. Gasc & Rodrigues (1979), at approximately the same time, described a new species, *A. zidoki*, from French Guiana, which also had been discovered in Surinam. *Geophis alasukai* from French Guiana was described by Gasc & Rodrigues (1980a), who paid much attention to this unexpected find and devoted quite a discussion to the supposed relationships of this taxon with species of the group *omiltemanus* in Mexico. The very strange distribution indeed was explained away as being the result of an ancient wide distribution having been interrupted due to vegetational changes as a result of climatic fluctuations. Examination of the types of *Geophis alasukai* convinced me that it actually is identical with *Atractus flammigerus*. However, I must add that the genus *Atractus* is in a state of confusion as becomes evident rapidly when studying species belonging to this genus. Lack of material of many species is one of the main factors frustrating thorough taxonomic work on this group. From the papers by Hoogmoed (1980) and Gasc & Rodrigues (1979, 1980a) it is evident that a revision of the genus is highly

desirable and that it should pay much attention to hemipenial morphology, scale structure, body proportions and osteology. Until such a revision is made hypotheses about relationships within this group and about its zoogeographic affinities remain highly speculative.

5. Whereas Hoogmoed (1979) only listed species, in the present paper subspecies have been taken into account as well, stablishing the total number of taxa. It would lead us too far afield to consider these differences in detail here.

Some of the identifications leading to my present estimate of 159 snake-taxa for the Guianan region are not beyond doubt as has already been suggested above in the case of taxa either just or not reaching Guiana. However, there are some other problems as well. For instance, *Chironius scurrulus*, as used by me, may be a composite of two taxa, either species or subspecies. In this connection I may refer to the description and pictures of this species in Lancini (1979), which closely agree with those in Wagler (1824), while all describe the species as being reddish brown with dark spots, having a lighter belly with darker spots. Specimens (juveniles, halfgrowns, adults) I have investigated from Surinam, Peru and Bolivia agree in all scale characters with the description of *C. scurrulus*. However, they differ in colour by being immaculately grey-green. The taxonomic consequences of this observation are not yet clear, but investigation of the holotype showed that *Dendrophis viridis* D., B. & D., 1854 constitutes a synonym of the green form and is not a synonym of *Chironius fuscus* (L.) as Peters & Orejas-Miranda (1970) thought. Boulenger (1894) treated the green form as a separate variety B. of his *C. fuscus*. Both Duellman (1978) and Dixon & Soini (1977) reported the juveniles of *C scurrulus* to be leaf-green with a gradual change to a mottled brown pattern in adults. Wiest (1978:249) synonymised *D. viridis* with *C. scurrulus* and attributed the colour differences to ontogenetic changes, juveniles being green, adults having various colours, ranging from yellow to black. He also pointed out that the name *C. cinnamomeus* was used by recent authors (Hoge, 1964; Peters & Orejas-Miranda, 1970 (and also Hoogmoed, 1979) for reddish brown or cinnamon coloured specimens of *C. scurrulus* and that *Natrix cinnamomea* Wagler possibly is a synonym of *Pseustes poecilonotus polylepis* (Peters). During a recent study of Spix and Wagler type specimens in the Zoologische Staatssammlung München (Hoogmoed & Gruber, in preparation), one of the syntypes of *Natrix scurrula* Wagler (ZSMH 2628/0) was located, so contrary to what Wiest (1978:249), who actually examined the specimen, and Hoge & Do Maranhão Nina (1964:74) were led to believe, apparently not all type material of this species was destroyed in World War II.

Another problem is posed by the species of *Thamnodynastes*. In Guiana two species occur: *T. pallidus* (L.) with an entire anal, smooth dorsal scales without apical pits, arranged in 17-17-13 rows, 137-160 ventrals, 82-90 paired subcaudals, an entire nasal and a relatively large, orange eye, and another species with divided or undivided anal, smooth dorsal scales which have only one indistinct apical pit, arranged in 19-19-15 rows, 137-150 ventrals, 62-75 paired subcaudals, a semidivided nasal and a relatively small, brown eye, whose identification is somewhat more complicated. Using the key provided by Peters & Orejas-Miranda

(1970) this species keys out as *T. strigatus* (Günther), a species from southern Brazil. However, in males of the Guiana-form there are no supra-anal tubercles as in *T. strigatus*, moreover they do agree fairly well with the description of *T. strigilis* (Thunberg), known from the area with keeled dorsal scales (see e.g. Lancini, 1979, fig. 60), and I tentatively identified them as *T. strigilis*. So either *T. strigilis* has smooth scales in certain populations (already indicated by Boulenger (1885) when he described *Thamnodynastes Nattereri* var. *laevis*), or *T strigatus* reaches the Guianan region as well, or the taxon here tentatively called *T. strigilis* is a new species. Dr. Bailey is actively working on these problems, so I may refer to his paper in this volume.

ZOOGEOGRAPHY

At present 159 snake-taxa belonging to 135 species are known to occur in the Gianan region. Of these, 29 taxa, belonging to 17 species are venomous snakes of the families Elapidae and Crotalidae. The remainder belong to the families Anomalepidae, Leptotyphlopidae, Thyphlopidae, Aniliidae, Boidae and Colubridae (table 1).

TABLE 1

Families of Guianan snakes

	taxa	species
Anomalepidae	2	2
Leptotyphlopidae	7	7
Typhlopidae	4	4
Aniliidae	2	1
Boidae	9	6
Colubridae	106	98
Elapidae	18	10
Crotalidae	11	7
	159	135

When trying to make a zoogeographic analysis of the Guianan region we should realise that there are widely diverse ecological conditions within the confines of Giana. The altitude of the region varies from sea-level to nearly 3000 m, and consequently there are differences in vegetation related to the altitude. Vegetationtypes to be encountered range from tropical lowland rainforest and savanna forest to montane forest, cloud forest and mangrove forest, from lowland savanna to altitudinal savanna and also include lowland swamp and riverine forest. Especially the savannas play an important role in the distribution of certain organisms in South America, by either acting as barriers or as dispersal

routes, depending on the ecological preferences of the organism involved. They are mainly situated in the western part of Guiana, where they connect with the llanos of Central Venezuela; in the northern, coastal area of the Guianas and Amapá, and in the interior, in the area forming a diagonal band from northwest to southeast, coinciding with a zone of lower annual precipitation (figs. 4, 5). During the past decade or so, the hypothesis has been postulated (Haffer, 1969, 1979; Van der Hammen, 1974) that under the influence of climatic fluctuations in the Pleistocene and Holocene the vegetation responded by exhibiting more or less simultaneous contractions and expansions. During dry climatic phases the sevannas would expand, and the forest would retract to refuge-areas in climatically favoured (= relatively wet) areas, thus offering good opportunities for the extension of savanna-inhabiting species. During wet climatic phases the opposite would occur, the forest would expand again and the savannas would retract to relatively dry areas with unfavourable edaphic factors. Since its propagation this hypothesis has been used do explain quite satisfactorily distribution patterns of several groups of animals and plants in South America. For the rattlesnake *Crotalus durissus*, a savanna-inhabitant, and also for the rainforest-inhabitant *Lachesis muta*, the bushmaster (fig. 6), the hypothesis offers a good explanation for the facts as we observe them today. During dry climatic phases the original stock of *Crotalus durissus* was able to spread through lowland South America from Central America. During wet phases different populations became isolated and presently can be recognised as different subspecies e.g. in Guiana there are four subspecies known: *C. d. cumanensis* Humboldt in the northwestern part of the area, *C. d. dryinus* L. in the coastal savannas, *C. d. ruruima* Hoge in the border area between Brazil and Venezuela and *C. d. trigonicus* Harris & Siimmons on the Rupununi-savanna in Guyana.

Forty five species of Guianan snakes are known to occur on savannas or in comparable habitats like open, grassy swamps (table 2). Twenty four of these are restricted to this habitat, the others may be found in rainforest or in edge-situations as well. The remaining species are inhabitants of rainforest, montane forest or cloud forest. However, our knowledge about the ecological requirements of snakes within the forest or the savanna is very limited. Nevertheless, the main patterns are evident and we can use that knowledge in the zoogeographical analysis.

According to their distribution the snakes of the Guianan region can be grouped into several assemblages. Hoogmoed (1979) discerned eight main distribution patterns, which were partly subdivided, to yield 12 patterns, for the entire herpetofauna. Gasc & Rodrigues (1980b) distinguished five for snakes in French Guiana and Duellman (1978) recognised eight in the herpetofauna of Santa Cecilia in Ecuador, of which five involve Guianan species as well. The establishment of distribution patterns is important to answer questions about the origin of the present fauna and it may also serve to solve the question of how the fauna reached the region. As stated above, a factor limiting the possibilities of interpretation is our scant knowledge of the ecological requirements of snakes, many of which are only known from one or a few specimens.

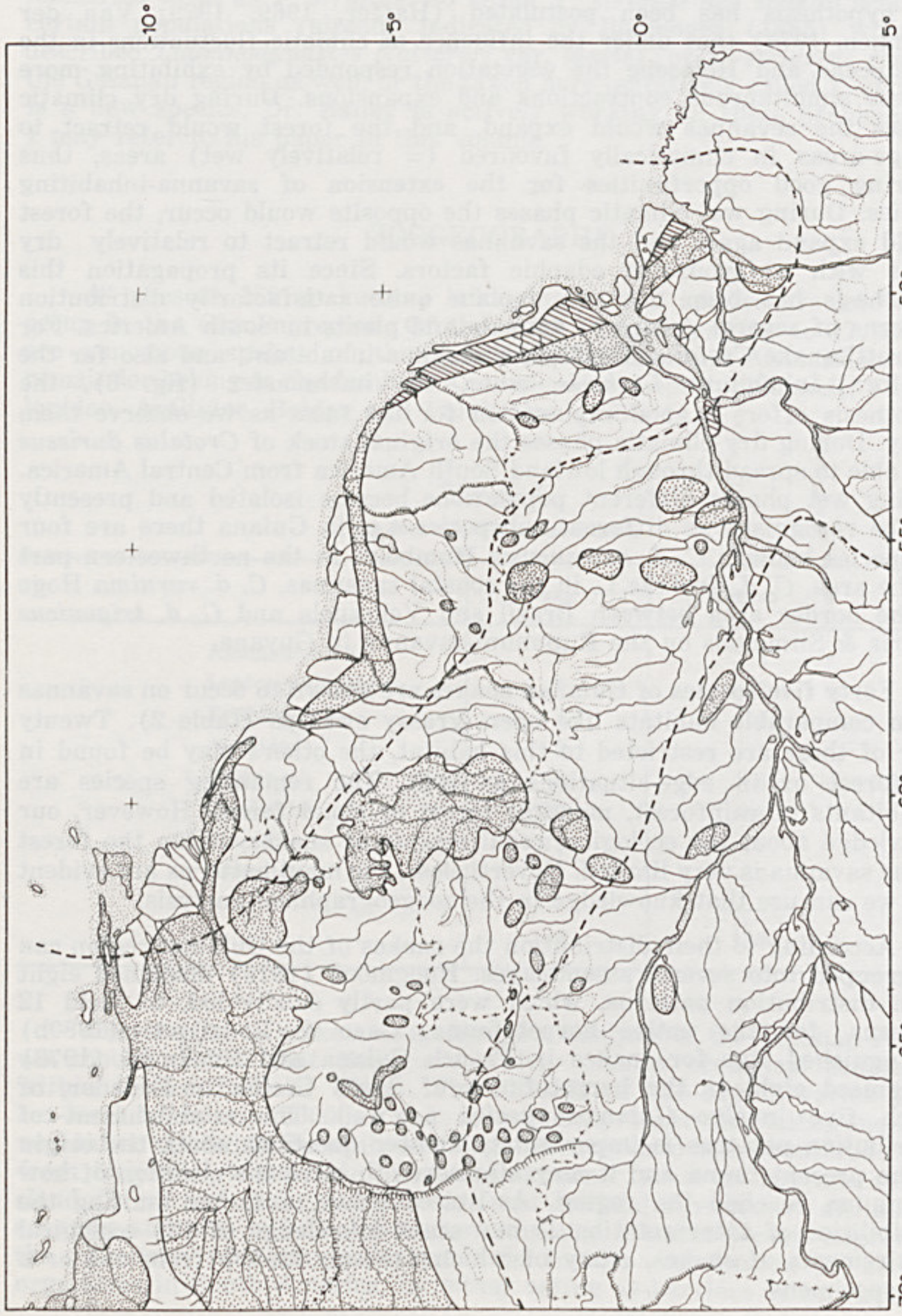

Fig. 4. Map of Guiana showing the distribution of forest and savannas. Forested areas white, inundated savannas hatched, savannas stippled. The zone with lower rainfall (cf. fig. 5) has been indicated with heavy broken lines (after Hoogmoed, 1979).

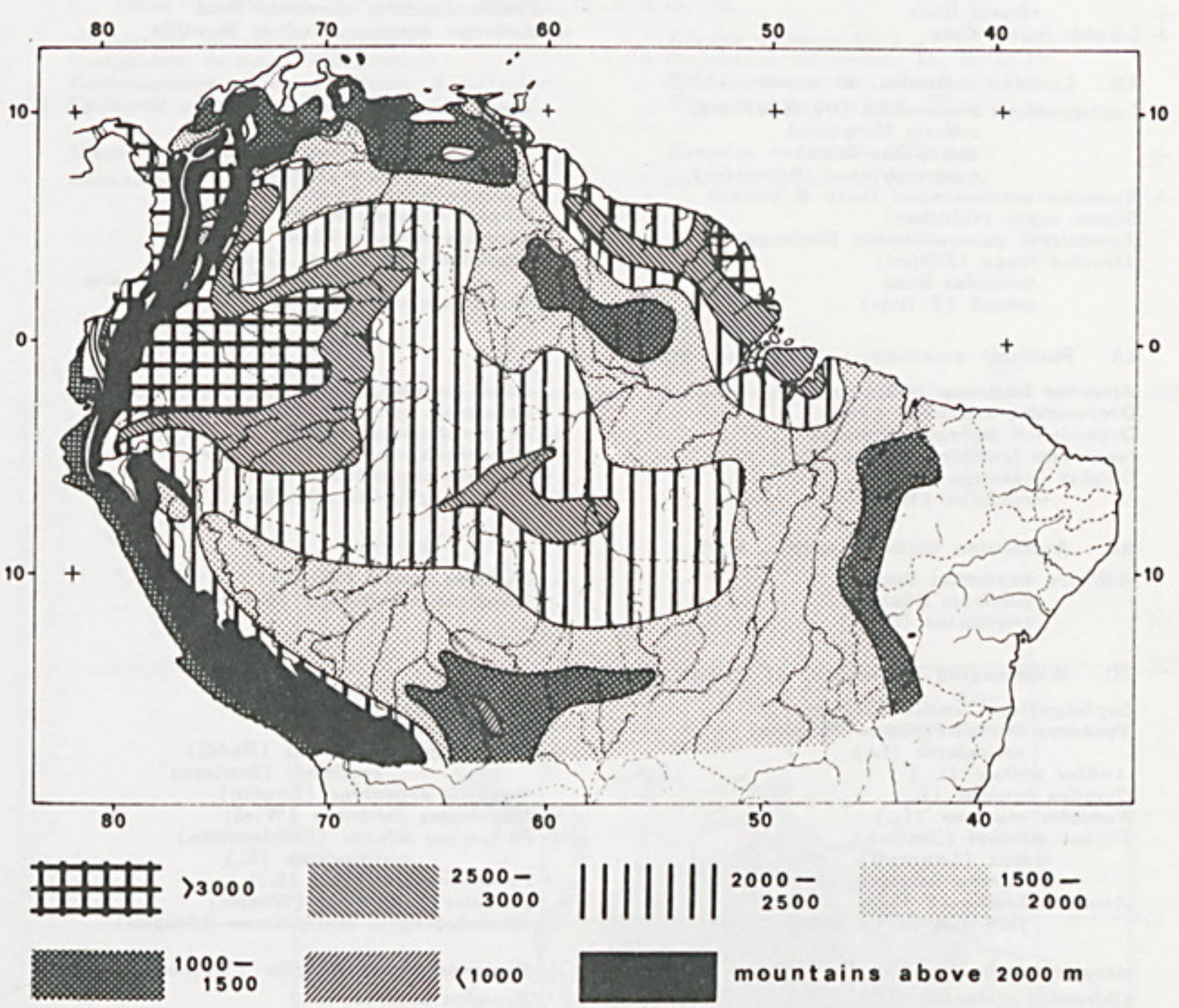

Fig. 5. Rainfall (mm) distribution in northern South America (after Hoogmoed, 1979).

Of the groups discerned by Hoogmoed (1979), the ones comprising wide-ranging cosmopolitan species, species with uncertain distributions and species with disjunct populations in Upper Amazonia and near the mouth of the Rio Amazonas, do not include any snakes. Twenty five species from regions as far apart as Europe, South Africa, Indonesia and the Antilles have been reported from Guiana, all demonstrably based on wrongly labelled material and consequently not considered in the present compilation (appendix). Only one species of snake (*Typhlops lumbricallis* (L.) has aparrently succesfully been introduced into Guyana from the Antilles. The remaining 134 species can be grouped as follows (table 2, figs. 7, 8, 9) :

HOOGMOED, M. S. Snakes of the guianan region. *Mem. Inst. Butantan*, *46*:219-254,1982.

TABLE 2

Guianan snakes arranged according to their distribution (see text for further explanation). Species restricted to open formations (mostly savannas) are indicated with a +, species occurring in open formations, in forest and in edge-situations (ubiquists) are indicated with a °. Species without a mark are considered as strictly forest species, which may however occur in forest-edges.

1A. Altitudinal endemics: 6 species, 4.5%.

Atractus duidensis Roze
\+ *riveroi* Roze
\+ *Liophis ingeri* Roze
Liophis trebbaui Roze
\+ *Thamnodynastes chimanta* Roze
\+ *Bothrops eneydae Sandner* Montilla

1B. Lowland endemics: 20 species, 14,9%.

\+ *Leptotyphlops amazonicus* Orejas-Miranda
collaris Hoogmoed
\+ *dimidiatus* (Jan)
septemstriatus (Schneider)
\+ *Eunectes deschauenseei* Dunn & Conant
Dipsas copei (Günther)
Apostolepis quinquelineata Boulenger
Atractus favae (Filippi)
insipidus Roze
schach (F.Boie)
Atractus steyermarki Roze
trilineatus Wagler
zidoki Gasc & Rodrigues
Cercophis auratus (Schlegel)
Helicops hogei Lancini
Liophis canaima Roze
Xenodon werneri Eiselt
Leptomicrurus collaris (Schlegel)
schmidti Hoge & Romano
Micrurus averyi Schmidt

2A. Periferal amazonian: 12 species, 9%.

Atractus latifrons (Günther)
Drepanoides anomalus (Jan)
Drymoluber dichrous (Peters)
Imantodes lentiferus (Cope)
Liophis breviceps Cope
undulatus (Wied)
Ninia hudsoni Parker
Pseudoboa coronata Schneider
\+ *Thamnodynastes pallidus* (L.)
Xenopholis scalaris (Wucherer)
° *Micrurus lemniscatus* (L.)
psyches (Daudin)

2B. Amazonian basin: 5 species, 3.8%.

Helicops hagmanni Roux
polylepis Günther
trivittatus (Gray)
Hydrops martii (Wagler)
Rhadinea brevirostris (Peters)

2C. Wideranging amazonian: 41 species, 30.6%.

Leptotyphlops tenella Klauber
Typhlops brongersmianus Vanzolini
reticulatus (L.)
Anilius scytale (L.)
Corallus caninus (L.)
° *Eunectes murinus* (L.)
Dipsas catesbyi (Sentzen)
indica (Laurenti)
pavonina Schlegel
Atractus badius (F.Boie)
flammigerus (F.Boie)
Atractus torquatus (D., B. & D.)
Chironius carinatus (L.)
° *fuscus* (L.)
multiventris Schmidt & Walker
° *scurrulus* (Wagler)
Erythrolamprus aesculapii (L.)
Helicops angulatus (L.)
\+ *leopardinus* (Schlegel)
\+ *Hydrodynastes bicinctus* (Herrmann)
° *Hydrops triangularis* (Wagler)
Leimadophis typhlus (L.)
° *Liophis cobella* (L.)
\+ *Mastigodryas bifossatus* (Raddi)
° *boddaerti* (Sentzen)
Oxybelis argenteus (Daudin)
Oxyrhopus formosus (Wied)
\+ *Philodryas olfersii* (Lichtenstein)
viridissimus (L.)
° *Pseudoeryx plicatilis* (L.)
Pseustes sulphureus (Wagler)
Rhinobothryum lentiginosun (Scopoli)
\+ *Thamnodynastes strigilis* (Thunberg)
° *Xenodon severus* (L.)
Micrurus hemprichii (Jan)
spixii Wagler
° *surinamensis* (Cuvier)
° *Bothrops atrox* (L.)
bilineatus (Wied)
brazili Hoge
° *castelnaudi* D., B. & D.

3 Widespread: 24 species, 17.9%.

° *Boa constrictor* (L.)
° *Corallus enydris* (L.)
° *Epicrates cenchria* (L.)
Dipsas variegata (D., B. & D.)
Chironius exoletus (L.)
° *Clelia clelia* (Daudin)
Dendrophidion dendrophis (Schlegel)
Drymarchon corais (H.Boie)
Imantodes cenchoa (L.)
° *Leimadophis reginae* (L.)
° *Leptodeira annulata* (L.)
° *Leptophis ahaetulla* (L.)
\+ *Lygophis lineatus* (L.)
° *Oxybelis aeneus* (L.)
fulgidus (Daudin)
Oxyrhopus petola (L.)
Pseustes poecilonotus (Günther)
Siphlophis cervinus (Laurenti)
Spilotes pullatus (L.)
° *Tantilla melanocephala* (L.)
Tripanurgos compressus (Daudin)
Xenodon rabdocephalus (Wied)
\+ *Crotalus durissus* (L.)
Lachesis muta (L.)

TABLE 2 (Continued 1)

4. Reaching eastern limit: 14 species, 10.4%.

Leptotyphlops macrolepis (Peters)
Typhlops minuisquamis Dixon & Hendricks
Sibon nebulata (L.)
Atractus elaps (Günther)
major Boulenger
Drymobius rhombifer (Günther)
Erythrolamprus bauperthuisii D., B. & D.
+ *Leimadophis melanotus* (Shaw)
+ *Masticophis mentavarius* D., B. & D.
+ *Mastigodryas pleei* (D., B. & D.)
+ *Phimophis guianensis* (Troschel)
Pliocercus euryzonus Cope
+ *Pseudoboa neuwiedii* (D., B. & D.)
Micrurus isozonus (Cope)

5. From Central or Northeastern Brazil: 12 species, 9%.

Typhlophis squamosus (Schlegel)
Liotyphlops ternetzii (Boulenger)
Leptotyphlops cupinensis Bailey & Carvalho
+ *Cyclagras gigas* (D., B. & D.)
Elapomorphus quinquelineatus (Raddi)
Leimadophis poecilogyrus (Wied)
Liophis miliaris (L.)
+ *Oxyrhopus trigeminus* D., B. & D.
+ *Phimophis guerini* (D., B. & D.)
Waglerophis merremii (Wagler)
Xenodon neuwiedii (Günther)
+ *Micrurus ibiboboca* (Merrem)

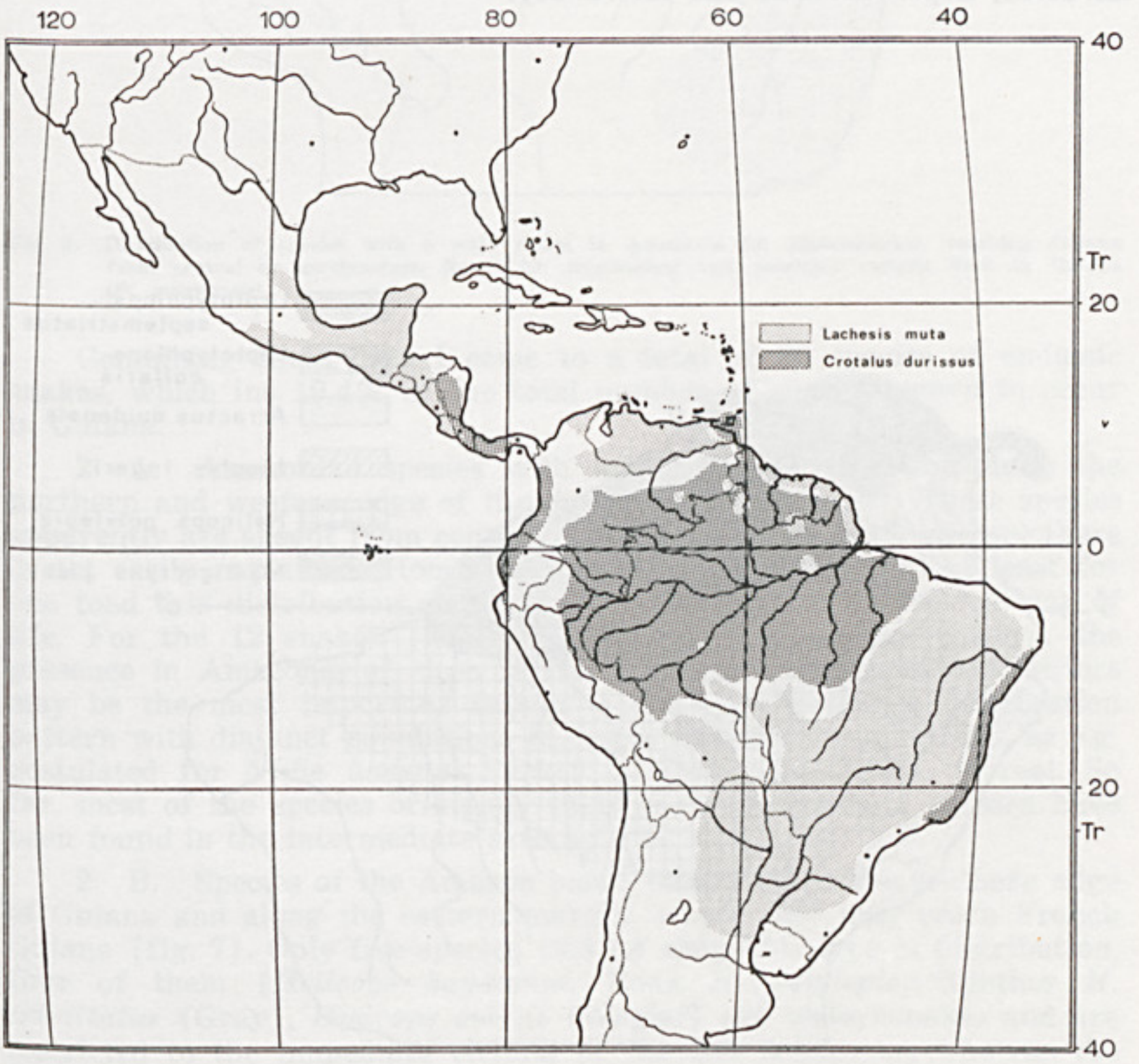

Fig. 6. Distribution of *Crotalus durissus* and *Lachesis muta* after Hoge (1965), Hoge & Hoge-Romano (1981) and Müller (1969).

1 A. Altitudinal endemic are those species with a distribution restricted to altitudes above 1000 m, usually inhabiting the summit or talus slopes of one or a few adjacent tepuis (sandstone tablemountains) (fig. 7). These snakes usually are only known from a few specimens and the distributions as plotted only reflect our scant knowledge of these creatures. As was recently demonstrated for *Bothrops lichenosus* Roze, which according to Da Cunha & Do Nascimento (1975) is a synonym of *B. castelnaudi* D., B. & D., they may turn out to be identical with widely distributed lowland species. At the moment we know of six species (4.5%) of snakes showing this distribution, all in southeastern Venezuela.

1 B. Lowland endemics are those species which occur below 1000 m and whose ranges do not (or only slightly) extend beyond the Guianan region (fig. 7). They may or may not occur to altitudes over 1000 m. Eventually part of the species considered to belong to this group may prove to have a much larger distribution. Among the 20 species (14.9%) this group, not less than 14 are burrowing snakes, which generally are difficult to collect (genera *Leptotyphlops*, *Apostolepis*, *Atractus*, *Leptomicrurus* and *Micrurus*).

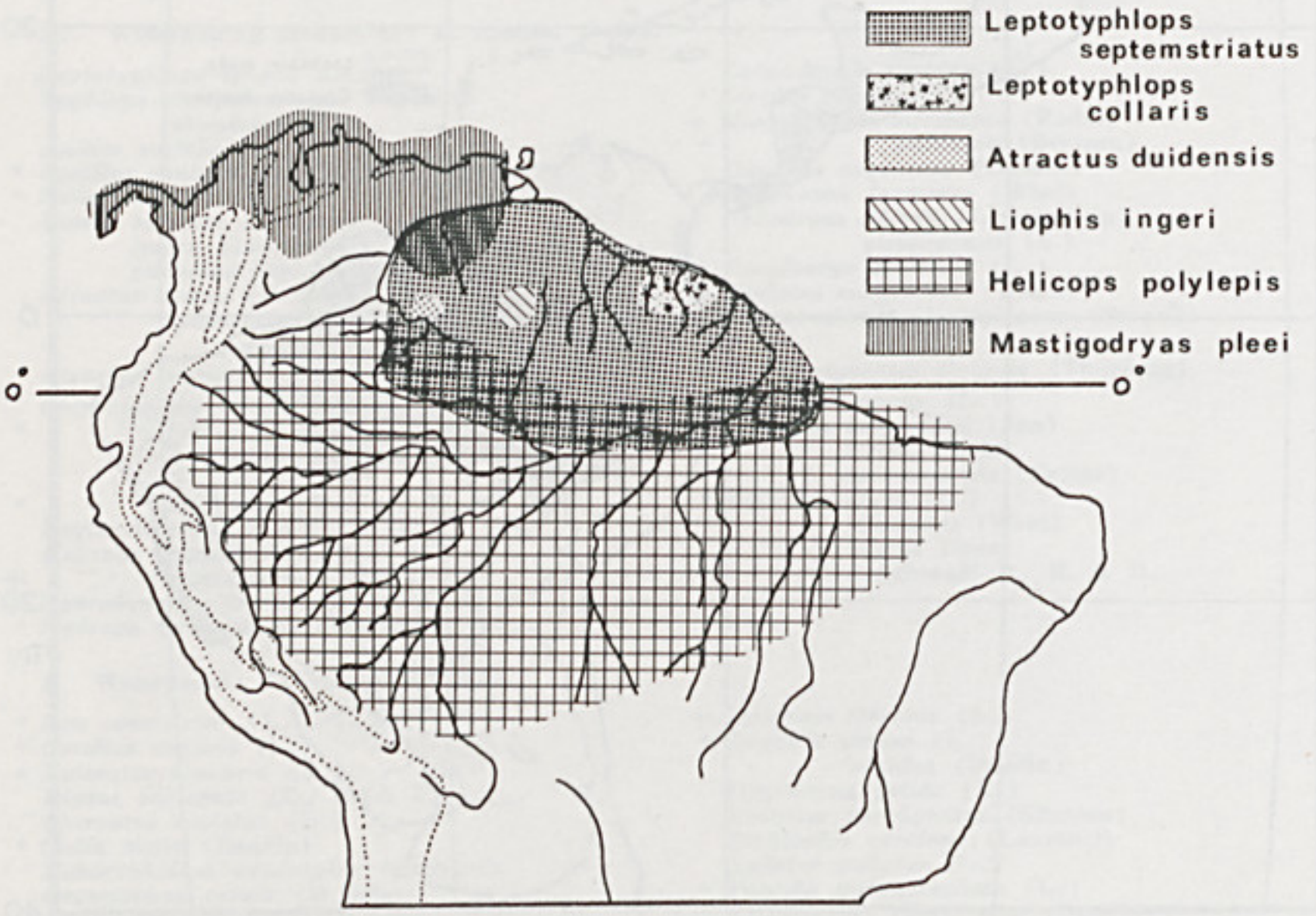

Fig. 7. Distribution of endemic species, of a species reaching Guiana from the northwest (*M. pleei*) and of a species with an Amazonian basin distribution (*H. polylepis*).

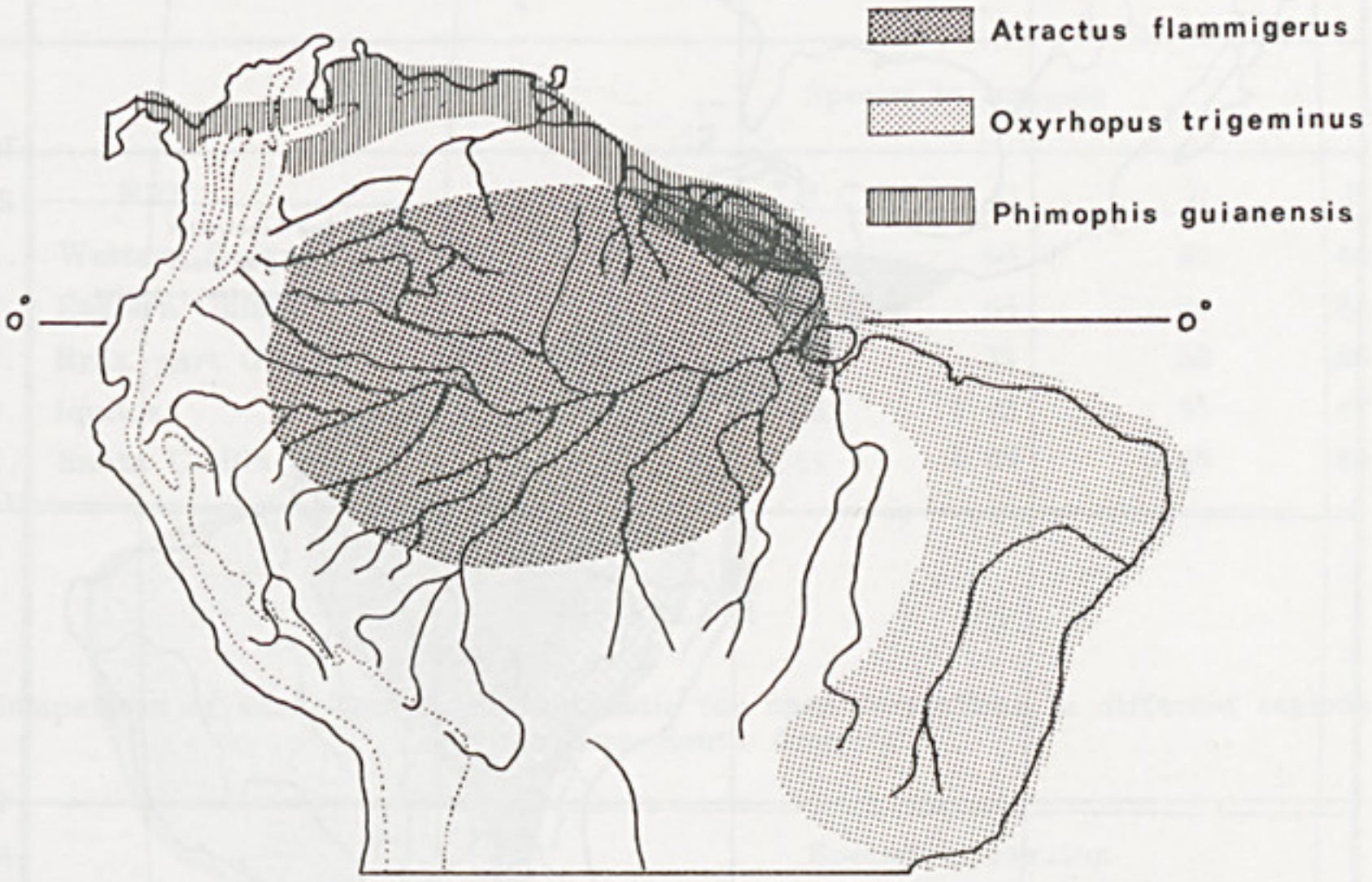

Fig. 8. Distribution of species with a wide range in Amazonia (*A. flammigerus*), reaching Guiana from central or northeastern Brazil (*O. trigeminus*) and reaching eastern limit in Guiana (*P. guianensis*).

Combining these data I come to a total of 26 species of endemic snakes, which ins 19.4% of the total number of snakes known to occur in Guiana.

2 A. Amazonian species with a periferal distribution along the northern and western edge of the Amazon basin (fig. 9). These species apparently are absent from central Amazonia, though their absence there is not easily explained. Hoogmoed (1979) pointed out that at least for one toad this distribution seems to be a result of its saxicolous way of life. For the 12 snakes (9%) showing this distribution pattern, the presence in Amazonia of close relatives or other ecological competitors may be the most important reason. I don't think that a distribution pattern with disjunct populations in upper Amazonia and Guiana, as e.g. postulated for *Ninia hudsoni* Parker by Duellman (1978), is real. So far, most of the species originally thought to show such a pattern have been found in the intermediate area as well.

2 B. Species of the Amazon basin, occurring on the southern edge of Guiana and along the eastern margin, where they may reach French Guiana (fig. 7). Only five species (3.8%) show this type of distribution, four of them (*Helicops hagmanni,* Roux *H. polylepis,* Günther *H. trivittatus* (Gray), *Hydrops martii* (Wagler) are waternsnakes and are restricted to the immediate vicinity of the Rio Amazonas, whereas the fifth (*Rhadinea brevirostris* (Peters), not a watersnake) enters French Guiana and Surinam apparently from the east.

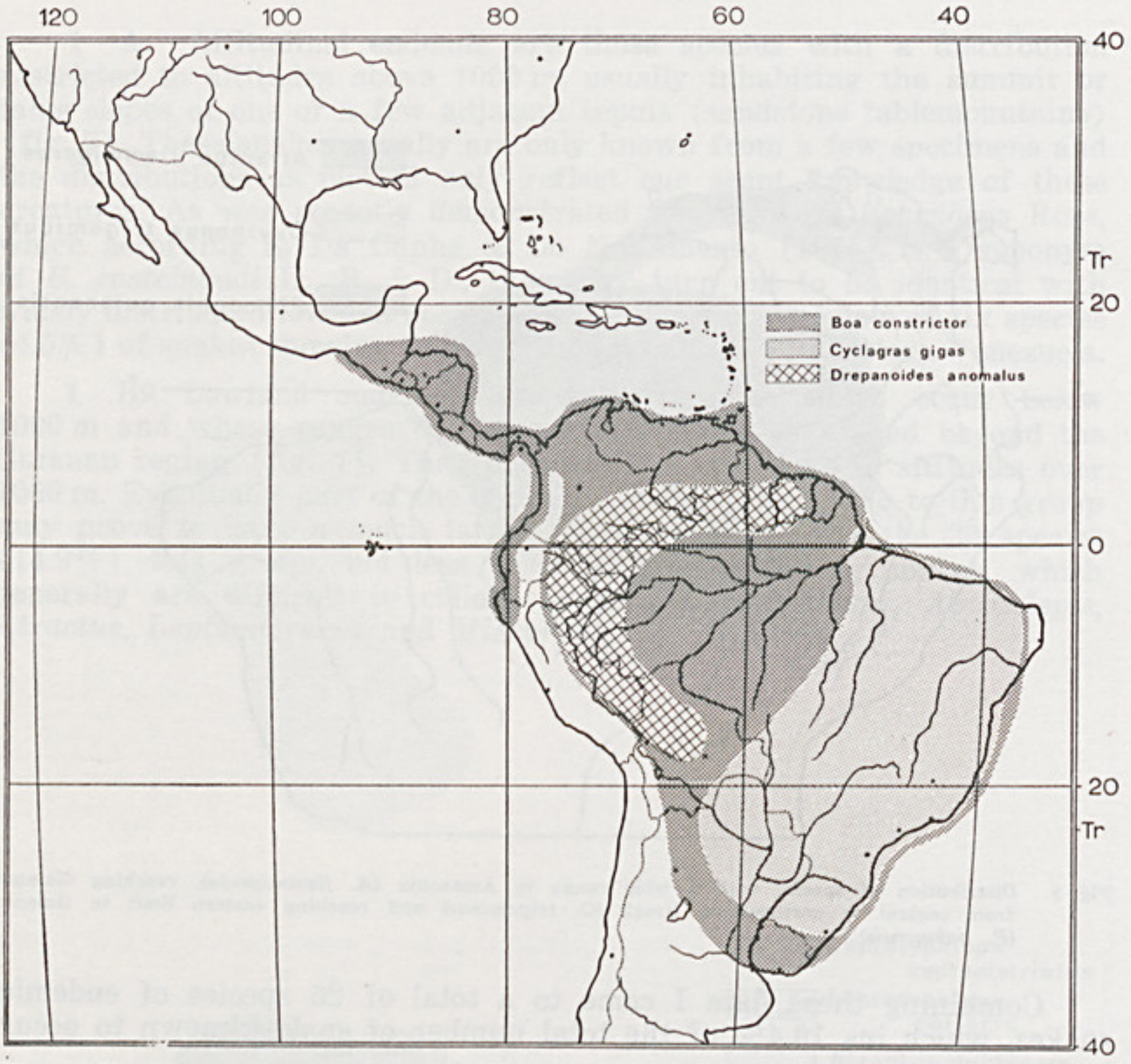

Fig. 9. Distribution of widespread species (*B. constrictor*), of peripheral Amazonian species (*D. anomalus*) and reaching Guiana from central Brazil (*C. gigas*).

2 C. Species widespread through Amazonia (fig. 8), often (22 out of 41) differentiated into several subspecies, make up the largest group, consisting of 41 species (30.6%). Generally these are forest--dwellers, a number of them are generalists which may also be found in edge and open situations and only five (*Helicops leopardinus* (Schlegel), *Hydrodynastes bicinctus* (Hermann), *Mastigodryas bifossatus* (Raddi), *Philodryas olfersii* (Lichtenstein), *Thamnodynastes strigilis* (Thunberg)) are restricted to open formations like savannas (two, *P. olfersii* and *M. bifossatus*) and swamps (the remaining three).

3. Widespread species ranging from Mexico or lower Central America over entire cis-Andean tropical South America (fig. 9). Usually (18 out of 24) these are differentiated into subspecies along various patterns. Only two *Lygophis lineatus* (L.) and *Crotalus durissus* (L.) out of 24 species are restricted to savanna habitat, the remainder are forest-dwellers or generalists. This group constitutes 17.9% of the total. It comprises both species with a Central American origin like the rattlesnake *C. durissus*, and species of South American provenance ranging into lower Central America, like *Corallus enydris* (L.).

TABLE 3

Comparison of rainforest snake-faunas in different regions in northern South America

FRF		Species in common				
		A	B	C	D	E
A.	Western Guiana	85	70	60	60	44
B.	Eastern Guiana	0.80	91	64	60	44
C.	Bras. part Guiana	0.77	0.79	71	53	36
D.	Iquitos	0.71	0.68	0.68	85	47
E.	Santa Cecilia	0.64	0.61	0.58	0.68	53

TABLE 4

Comparison of snake-faunas characteristic for open formations in different regions in northern South America

FRF		Species in common				
		A	B	C	D	E
A.	Western Guiana	20	13	10	2	0
B.	Eastern Guiana	0.72	16	11	2	0
C.	Bras. part Guiana	0.63	0.79	12	2	0
D.	Iquitos	0.18	0.22	0.29	2	0
E.	Santa Cecilia	0	0	0	0	0

TABLE 5

Comparison of open formation snake-faunas (including species restricted to this habitat and ubiquists) in different regions in northern South America

FRF		Species in common				
		A	B	C	D	E
A.	Western Guiana	41	34	31	21	15
B.	Eastern Guiana	0.87	37	32	21	15
C.	Bras. part Guiana	0.84	0.91	33	21	15
D.	Iquitos	0.65	0.69	0.74	24	17
E.	Santa Cecilia	0.52	0.56	0.60	0.81	18

4. Species reaching their eastern distribution limit in Guiana may belong to different assemblages (fig. 7, 8). They may belong to species occurring in the upper Amazon basin (three), to species of northwestern South America (eight) or to species occuring in Central and northern South America (three). There is a relatively large proportion of savanna inhabitants (5 out of 14) and a low number polytypic species (three out of 14) in this group. Three of the savanna snakes (*Leimadophis melanotus* (Shaw), *Masticophis mentovarius* (D., B. & D.), *Mastigodryas pleei* (D., B. & D.)) just reach Guiana in its northwestern part, entering the savannas in the north of Estado Bolívar in Venezuela, which are connected with the extensive llanos of Central Venezuela and eastern Colombia; the other two (*Phimophis guianensis* (Troschel) and *Pseudoboa neuwiedii* (D., B. & D.)) occur further east in the coastal savannas of the three Guianas. This group of 14 species constitutes 10.4% of the total.

5. The last group consists of species apparently reaching Guiana from northeastern, central or even southeastern Brazil (fig. 9). Among the 12 species (9%) of this group there is again a relatively large proportion of inhabitants of open formations. *Cyclagras gigas* (D., B. & D.) inhabits swampy areas, *Oxyrhopus trigeminus* D., B. & D., *Phimophis guerini* (D., B. & D.) and *Micrurus ibiboboca* (Merrem) inhabit dry, sandy savannas and may be considered as part of the cerrado-caatinga fauna of central and northeastern Brazil. Of several of the remaining species it is not clear to me which are their habitat preferences, but several more may turn out to be open formation snakes.

The wording employed in the description of several of the groups mentioned already indicates in which areas the species originated. For the endemics this is fairly uncomplicated, they apparently evolved within the confines of Guiana, either in a small isolated area, formed by a tepui, as is the case in the altitudinal endemics, or they evolved in lowland refugia in the Guianan region. As among the lowland endemics there are both forest and savanna species, two types of refugia are important here: savanna refugia and forest refugia. These refugia are thought to have been formed under the influence of changing climate in the Pleistocene and Holocene. Under wet climatic conditions savanna inhabitants were pushed back to relatively small, isolated patches of savanna, probably in the Roraima region on the border of Venezuela, Brazil and Guyana, and in the Paroe/Sipaliwini region on the border of Surinam and Brazil, whereas the forest inhabitants could spread widely through the area together with the expanding forests. During dry climatic conditions, the opposite happened: savanna inhabitants roamed far and lowland forest inhabitants were restricted to isolated patches of forest, probably the Guiana refuge on the northern versant of the Tumuc Humac Mountains in southern Surinam and French Guiana, and the Imerí and Imataca refuges in southeastern Venezuela (Haffer, 1979:140). These refuges are situated in areas where rainfall is high, compared with surrounding regions (figs. 1, 5). In the expanding phase of certain vegetations, after periods of isolation, when populations of one original species came in contact, they could either merge completely, with no reproductive barriers, behaving like one species; they could have differentiated enough to show ecological incompatibility, only merging in

the zone of contact and for the greater part being allopatric, behaving like subspecies; or they could show complete reproductive isolation and behave like species, occurring sympatrically without any mixing of gene-pools. It will be evident that this process was not restricted to Guiana, but supposedly took place in all of South America, also influencing the evolution and distribution patterns of the other groups discerned here. In Amazonia several areas are recognised which could have served as refugia for vegetation and fauna with corresponding requirements and whence the entire Amazon basin could have been repopulated under favourable climatic conditions. However, distribution within this large area is not uniform and often different subspecies occur allopatrically. In the case of species with an Amazonian Arc distribution several closely allied species or ecologically similar species may be involved.

Sufficient distribution data and at least an indication of ecological requirements were available to permit comparison of snakefaunas from within Guiana with areas in the Amazon basin, viz., Iquitos (Dixon & Soini, 1977) and Santa Cecilia (Duellman, 1978). To this end the Guianan region was divided into three parts, e.g.: Western Guiana, the area west of the Essequibo River and Rio Branco; Eastern Guiana, Guyana east of the Essequibo River, Surinam, French Guiana and Amapa north of the Rio Araguari; and Brazilian Guiana, the area between Tumuc Humac Mountains and the Rio Amazonas. To get an impression of the amount of faunal relationship between these more or less natural subdivisions of Guiana mutually and with the outside localities mentioned, the Faunal Resemblance Factor (FRF) was computed for each combination of regions, using the formula: $FRF \frac{2C}{N_1+N_2}$ (Duellman, 1965, 1966) where N_1 and N_2 are the numbers of species occurring in any two regions and C is the number of species common to the two regions compared. In tables 3-5 the total number of species in each locality is on the diagonal (bold face lettering) 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. Comparison of the FRF's for the three Guianan region shows that there is a great resemblance between those regions, without indication of a break somewhere. For forestsnakes there is a fairly good resemblance with both Iquitos and Santa Cecilia, but in all cases this resemblance is slightly greater for Iquitos than for Santa Cecilia, which is farther removed from the Guianan region. The data suggest a gradual transition along an east-west gradient, both within Guiana and from Santa Cecilia to Iquitos to Guiana. However, sufficient data from the area between Iquitos and Guiana are lacking and also, considering the list of snakes recorded for Santa Cecilia I get the impression that it is less complete than that of Iquitos. This impression is reinforced by the FRF between Iquitos and Santa Cecilia for rainforest snakes, 0.68, which is much less than might be expected for areas not separated by barriers. Nevertheless, it seems to make sense to postulate that the rainforest snakes are fairly evenly distributed throughout Amazonia and Guiana, differences being caused by species with relatively small distribution

areas in respectively upper Amazonia and lowland Guiana. For snakes restricted to open formations there also is good resemblance between the several areas within Guiana, but there is only a slight resemblance with the Iquitos region and none at all with Santa Cecilia where no open formations and species associated with them, occur (Duellman, 1978). When considering all snakes which may be found in open situations, the picture is different. There is a fair resemblance between Iquitos and the Guianan regions, and only a moderate one between Santa Cecilia and the Guianan regions.

From the FRF's no distinct break between the compared rainforest snakefaunas is evident and it is only possible to conclude that for these snakes there are no unsurmountable barriers between the Andes and the mouth of the Rio Amazonas. Within Guiana rainforest snakes are evenly distributed. The Essequibo River does not constitute a barrier for them as it does e.g. for frogs (Hoognoed, 1979). For savanna snakes the picture is slightly different. Here we find a high resemblance between the Brazilian part of Guiana and eastern Guiana, whereas the resemblance of each of these parts with western Guiana is distinctly lower. Upon closer examination it appears that this difference within Guiana is not due to the presence of any barrier, but can be explained on the one hand by the presence in western Guiana of a few snakes which just cross the Orinoco and enter Guiana from the llanos, and on the other hand by the presence in eastern Guiana and the Brazilian part of Guiana of species reaching those areas from central or northeastern Brazil and not (yet) penetrating beyond Surinam.

CONCLUSIONS

The snakefauna of the Guianan region as we know it today is a composite of species of different origins. The largest fraction consists of Amazonian species, of which the ones with a wide range in Amazonia form the majority. These probably originated in the Napo lowland rainforest refuge at the eastern base of the Andes in Ecuador/Peru, whence they dispersed eastward after the onset of wetter climatic conditions. The group with an Amazonian basin distribution probably evolved in galleryforests along the Rio Amazonas, whereas the distribution of snakes having a periferal distribution might be explained by their having differentiated in submontane forest refuges along the eastern flank of the Andes. Species with a distribution encompassing both Central and South America may have originated either in Central or in South America, from where they expanded into the adjacent region. The majority is of South American provenance, only five (*Imantodes cenchoa* (L.), *Leptodeira annulata* (L.), *Leptophis ahaetulla* (L.), *Tantilla melanocephala* (L.) and *Crotalus durissus* (L.)) invaded South America from Central America. These species either evolved in savanna refugia (*C. durissus* (L.), *Lygophis lineatus* (L.)), or they evolved in forest refugia. The majority of the forest species has a wide range in South America and evolved into subspecies which may be indicative for the refuges in which the species survived (well demonstrated by for instance

the distribution of *Lachesis muta* (L.)) (fig. 6). Species which only occur in western Guiana mostly are invaders from the west (NW South America, Central America) or from the southwest (Upper Amazonian basin), but *Pseudoboa neuwiedii* (D., B. & D.) may be a former endemic of Guiana that extended its range to the northwest, to reach Panama. Species occurring in eastern Guiana, not reaching further west than Surinam, apparently are invaders from the southeast. The savanna inhabiting species in this group evolved in savanna refugia in northeastern and central Brazil. They probably reached Guiana via a wide belt of cerrado-like vegetation, connecting northeastern Brazil with southeastern Venezuela, during the last arid period (figs. 4, 5). When the climate became more humid and the forests expanded again, these species were left stranded on the isolated savannas of Guiana, most of them in the east. The rainforest species in this group probably evolved in a rainforest refuge south of Belém.

The lowland endemics mainly are forestsnakes and for them possible refuges in Guiana are important: Guiana —, Imataca — and Imerí refuges. Of the altitudinal endemics at least four are savanna species and they may have evolved in the open formations covering the tops of certain Venezuelan tepuis. For the other two altitudinal endemics (*Atractus duidensis* Roze, *Liophis trebbaui* Roze) habitat data are not available.

Endemism in Guianan snakes is not particularly high (19.4%) compared to that in amphibians (52%) or reptiles in general (27%), but still is considerable. Part of this level of endemicity undoubtedly is due to our poor understanding of many South American snake genera, notably *Atractus, Oxyrhopus, Leptotyphlops,* and the scarcity of certain species in collections. Future research should continue assembling distribution data, which are still badly needed for many species from many areas, and one of the main objectives should be to gather basic ecological data, to establish niche preferences, food consumed, reproductive strategy, etc. When this information becomes available, zoogeographic analysis of South American snakes can be more fruitful and more firmly based than hitherto.

ACKNOWLEDGEMENTS

Fieldwork in Venezuela in 1978 was made possible through grants from the Melchior Treub Foundation of the Royal Dutch Academy of Sciences and from the Treub Society. Fieldwork in Surinam (1968, 1974/75, 1979/81) was supported by grants W 956-2, W 87-78, W 87-127 and W 84-191 from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), which also supported visits to Venezuelan and Brazilian museums in 1976 (WR 87-1313). Tranks are due to Mr. J. J. A. M. Wessendorp and Miss I. M. van Noortwijk (both from the Rijksmuseum van Natuurlijke Historie, Leiden), who respectively executed figs. 3, 5, 6, 9 and figs. 7, 8.

BIBLIOGRAPHIC REFERENCES

AMARAL, A. Estudos sobre ophidios neotropicos. XVIII — Lista remissiva dos ophidios da região neotropica. *Mem. Inst. Butantan, 4*:I-VIII, 129-271, 1930.

BARRÈRE, P. *Essai sur l'Histoire naturelle de la France Equinoxiale ou Dénombrement Des Plantes, des Animaux, & des Minèraux, qui se trouvent dans l'isle de Cayenne, les isles de Remire, sur les Côtes de la Mer, & dans le Continent de la Guyane avec leurs noms differens, Latin, François & Indiens, & quelques Observations sur leur usage dans la Médecine & dans les Arts*: 1-215. Paris, 1741.

BERKEL, A. VAN. *Amerikaansche Voyagien, Behelzende een Reis na Rio de Berbice, Gelegen op het vaste Land van Guiana, aande Wilde-Kust van America, Mitsgaders een andere na de Colonie van Suriname, Gelegen in het Noorder Deel van het gemelde Landschap Guiana. Ondermengd met alle de bijzonderheden noopende de Zeden, Gewooten en Levenswijs der Inboorlingen, Boom en Aardgewassen, Waaren en Koopmanschappen, en andere aanmerkelijke zaaken:* 4 pp., Eerste Deel: Reis na Rio de Berbice: 1-104, 2 pls. Tweede Deel: Reis na Suriname: 105-139. Amsterdam, 1965.

BOULENGER, G.A. A list of Reptiles and Batrachians from the Province Rio Grande do Sul, Brazil, sent to the Natural-History Museum by Dr. H. von Ihering. *Ann. Mag. Nat. Hist. 15*:(5)191-196, 1885.

———— *Catalogue of the snakes in the British Museum* (Natural History). Vol. I., containing the families Typhlopidae, Glauconiidae, Boidae, Ilysiidae, Uropeltidae, Xenopeltidae, and Colybridae aglyphae, part.: I-XIII, 1-447, pls. I-XXVIII. London, 1893.

———— *Catalogue of the snakes in the British Museum* (Natural History). Vol. II., containing the conclusion of the Colubridae aglyphae: I-XI, 1-382, pls. I-XX. London, 1894.

———— *Catalogue of the snakes in the British Museum* (Natural History). Vol. III., containing the Colubridae (Opisthoglyphae and Proteroglyphae), Amblycephalidae, and Viperidae: I-XIV, 1-727, pls. I-XXV. London, 1896.

BRONGERSMA, L.D. Herpetological notes XIV-XVI. XV. The type of Dipsas dieperinkii Schlegel, 1837, and the genus Pseustes Fitzinger, 1843. *Zool. Med., 20*(1): 5-6, fig. 1, 1937.

CUNHA, C.R. & NASCIMENTO, F.P. Ofídios da Amazônia. V. Bothrops lichenosus Roze, 1958, sinônimo de Bothrops castelnaudi Duméril, Bibron e Duméril, 1854, com nova descrição e comentários. *Bol. Mus. Par. Goeldi, Nov. Ser. Zool., 80*:1-14, tabs. 1-2, 1975.

———— Ofídios da Amazônia. VI. Liotyphlops ternetzii (Boulenger, 1896), ofídio raro e de hábitos subterrâneos, na região leste do Pará (Ophidia, Anomalepididae). *Bol. Mus. Par. Goeldi,* Nov. Ser. Zool., *82*:1-8, fig. 1, 1975.

DAUDIN, F.M. *Histoire naturelle, génerale et particulière des reptiles.* Tome V: 1-361, pls. LIX-LXX. Paris, 1803a.

———— *Histoire naturelle, génerale et particulière des reptiles.* Tome VI: 1-447, pls. LXXI-LXXX. Paris, 1803b.

———— *Histoire naturelle, génerale et particulière des reptiles.* Tome VII: 1-436, pls. LXXXI-XCII. Paris, 1803c.

———— *Histoire naturelle, génerale et particulière des reptiles.* Tome VIII: 1-439, pls. XCIII-C. Paris, 1803d.

DESCAMPS, M.; GASC, J.P.; LESCURE, J. & SASTRE, C. Étude des écosystemes guyanais. II. Données biogéographiques sur la partie orientale des Guyanes. *C.R. Soc. Biogéogr., 467*:55-82, figs. 1-15, 1978.

DIXON, J.R. The Neotropical Colubrid Snake Genus Liophis. The Generic Concept. *Contr. Biol. Geol. Milw. Publ. Mus., 31*:1-40, figs. 1-2, tables 1-3, 1980.

DIXON, J.R. & HENDRICKS, F.S. The wormsnakes (family Typhlopidae) of the Neotropics, exclusive of the Antilles. *Zool. Verh., 173*:1-39, figs. 1-10, 1979.

DIXON, J.R. & SOINI, P. The reptiles of the upper Amazon basin, Iquitos region, Peru. II. Crocodilians, turtles and snakes. *Contr. Biol. Geol. Milw. Publ. Mus., 12*:1-91, 1977.

DUELLMAN, W.E. A biogeographic account of the herpetofauna of Michoacan, Mexico. *Univ. Kansas Publ. Mus. Nat. Hist., 15*(14): 627-709, figs. 1-5, tables 1-14, 1965.

———— The Central American herpetofauna: An ecological perspective. *Copeia* 1966(4): 700-719, figs. 1-8, tables 1-5, 1966.

———— The Biology of an Equatorial Herpetofauna in Amazonian Ecuador. *Univ. Kansas Mus. Nat. Hist. Misc. Publ., 65*:1-352, figs. 1-198, tables 1-34, pls. I-IV, 1978.

DUMÉRIL, A.M.C. & BIBRON, G. *Erpétologie générale ou histoire naturelle complète des reptiles*, t.6: I-XII, 1-609, 1 p., 1844.

DUMÉRIL, A.M.C.; BIBRON, G. & DUMÉRIL A. *Erpétologie générale ou histoire naturelle complète des reptiles*, 7(1): I-VII, 4pp., I-XVI, 1-780; 7(2): I-XII, 781-1536. Paris, 1854.

FERMIN, P. *Histoire naturelle de la Hollande équinoxiale: ou description des animaux, plantes, fruits et autres curiosités naturelles, qui se trouvent dans la colonie de Surinam; avec Leurs Noms différents, tant François, que Latin, Hollandois, Indiens & Négre-Anglois:* 1-XII, 1-240, 1 pl. Amsterdam, 1765.

FITZINGER, L.I. *Neue Classification der Reptilien nach ihren natürlichen Verwandschaften. Nebst einer Verwandschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des K.K. Zoologischen Museum's zu Wien*, 1826. 8pp., 1-66, 1 table.

———— *Systema Reptilium.* Fasciculus primus: Amblyglossae, 1-106, 1-VI.

GASC, J.P. & RODRIGUES, M.T. Une nouvelle espèce du genre Atractus (Colubridae, Serpentes) de la Guyane française. *Bull. Mus. natn. Hist. nat. Paris*, 4e ser., *1*, A(2): 547-557, figs. 1-6, 1979.

———— Sur la présence du genre Geophis (Colubridae, Serpentes) dans la région guyanaise. Description d'une nouvelle espèce de Guyane française. *Bull. Mus. natn. Hist. nat.*, Paris, 4e ser., 1, A(4): 1121-1130, figs. 1-4, pl. 1., 1980a.

———— Liste préliminaire des Serpents de la Guyane française. *Bull. Mus. natn. Hist. nat.*, Paris, 4e ser., *2*, A(2): 559-598, figs. 1-12, 1980b.

GMELIN, J.F. *Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species; cum Caracteribus, Differentiis, Synonymis, Locis.* Tome I, Pars III, 1033-1056. Lyon, 1789.

GRAY, J.E. *Catalogue of the specimens of snakes in the collection of the British Museum:* I-XV, 1-125. London, 1849.

GRONOVIUS, L.T. *Amphibiorum Animalium Historia Zoologica exhibens Amphibiorum, qui in Museo Laurentii Theodori Gronovii, J.U.D. adservantur, descriptiones ordine systematico. In: Musei Ichtologici. Tomus secundus sistens piscium indigenorum & nonnullorum exoticorum, quorum maxima pars in Museo Laurentii Theodori Gronovii, J.U.D. adservator, nec non quorandam in aliis Museis observatorum descriptiones. Accedunt nonnullorum exoticorum Piscium icones aeri incisae, et Amphibiorum animalium.* Historia Zoologica: 47-88. Leiden, 1756.

GÜNTHER, A. *Catalogue of Colubrine snakes in the collection of the British Museum*, London: I-XVI, 1-281. London, 1858.

HAFFER, J. Speciation in Amazonian Forest Birds. *Science, 165*:131-137, figs. 1-6, 1969.

———— Quaternary Biogeography of Tropical Lowland South America. In: W.E. Duellman (ed.): The South American Herpetofauna: Its origin, evolution, and dispersal. *Univ. Kansas Mus. Nat. Hist. Monogr. 7*:107-140, figs. 5.1-5.11, app. 5.1., 1979.

HAMMEN, T. van der. The Pleistocene changes of vegetation and climate in tropical South America. *J. Biogeogr., 1*(1): 3-26, figs. 1-22, 1974.

HARRIS, H.S. & SIMMONS, R.S. A new subspecies of Crotalus durissus (Serpentes: Crotalidae) from the Rupununisavanna of Southwestern Guyana. *Mem. Inst. Butantan, 40/41*: 305-311, figs. 1-2, 1978.

HARTSINCK, J.J. *Beschryving van Guiana, of de Wilde Kust, in Zuid-America, Betreffende de Aardrykskunde en Historie des Lands, de Zeeden en Gewoontes der Inwooners, de Dieren, Vogels, Visschen, Boomen en Gewassen, als mede de eerste Ontdekking dier Kust, de Bezittingen der Spanjaarden, Franschen en Potugeezen en voornaamelijk de Volkplantingen der Nederlanderen, als Essequebo, Demarary, Berbice, Suriname, En derzelver Rivieren, met de noodige Kaarten en Afbeelingen der Forten, waarby komt eene verhandeling over den Aart en de Gewoontes der Neger-Slaaven. Alles uit echte stukken opgesteld.* Vol. 1: I-XII, 4pp., 1-520, 9 pls. Vol. 2: 521-962, 15 pp. Asterdam, 1770.

HOGE, A.R. Notes on Lygophis Fitzinger. Revalidation of two sub-species. *Mem. Inst. Butantan, 24*(2): 245-268, figs. 1-5, 1 map. pl. 1, tables, 1952.

———— Serpentes da Fundação "Surinaam Museum". *Mem. Int. Butantan, 30*(1960-62): 51-64, 1 map, 1964.

———— Preliminary account of neotropical Crotalinae (Serpentes Viperidae). *Mem. Inst. Butantan, 32*:109-184, maps 1-10, pls. 1-20, 1965.

———— & MARANHÃO NINA, A.C. Serpentes coletadas pelo Instituto Nacional de Pesquisas da Amazônia. *Mem. Inst. Butantan, 30* (1960-62): 71-96, maps 1-3, pls. 1-11, 1964.

———— & ROMANO, S.A.R.W.D.L. Leptomicrurus in Brasil (Serpentes-Elapidae). *Mem. Inst. Butantan, 32*:1-8, figs. 1-3, 1966.

————. & ROMANO, S.A. Notes on Pseustes dieperinckii (Schlegel) Serpentes. *Mem. Inst. Butantan, 34*:89-92, 2 figs., 1969.

———— & ROMANO-HOGE, S.A.R.W.L. Poisonous snakes of the world. Part 1.. Checklist of the pit vipers. Viperoidea, Viperidae, Crotalinae. *Mem. Inst. Butantan, 42/43* (1978/79): 179-310, figs. 1-66, 1981.

HOLTHUIS, L.B. The Crustacea Decapoda of Suriname (Dutch Guiana). *Zool. Verh., 44*: 1-296, figs. 1-68, pls. I-XVI, maps 1-2, 1959.

HOOGMOED, M.S. The Herpetofauna of the Guianan Region. In: W.E. Duellman (ed.): The South American Herpetofauna: Its origin, evolution, and dispersal. *Univ. Kansas Mus. Nat. Hist. Monogr., 7*: 241-279, figs. 10.1-10.13, tables 10.1-10.8, app. 10.1, 1979.

———— Revision of the genus Atractus in Surinam, with the resurrection of two species (Colubridae, Reptilia). Notes on the herpetofauna of Surinam VII. *Zool. Verh., 175*: 1-47, figs. 1-17, pls. 1-6, table 1, 1980.

HOUTTUYN, M. *Natuurlyke Historie of uitvoerige beschryving der dieren, planten en mineralen, volgens het samenstel van den heer Linnaeus.* 1764. vol. I(6): 8 pp., 1-562, pls. 50-56.

JAN, G. & SARDELLI, F. *Iconographie générale des Ophidiens.* 1860-66. Tome I, livr. 1-17: 1-11.

———— *Iconographie générale des Ophidiens.* 1866-70. Tome II, livr. 18-34: 1-9.

———— *Iconographie générale des Ophidiens.* 1870-81. Tome III, livr. 35-50: 1-11.

JURIEV, K.B. Albert Seba and his contribution to the development of herpetology. In: Ananjeva, N.B., and L.J. Borkin. The fauna and ecology of Amphibians and Reptiles of the Palaearctic Asia. Acad. Sc. USSR. *Proc. Zool. Inst., 101*: 109-120, figs. 1-2, 1981.

KAPPLER, A. Die Tierwelt im Hollandischen Guiana. *Das Ausland Wochenschrift für Länder und Volkerkunde* 58, no. 27, 6 July 1885 pp. 537-539, no. 40, 5 October 1885, pp. 798-800, no. 41, 12 October 1885, pp. 815-818, no. 42, 19 October 1885, pp. 838-840, no. 43, 26 October 1885, pp. 857-859.

KEISER, E.D. A systematic study of the neotropical vine snake Oxybelis aeneus (Wagler). *Bull. Tex. Mem. Mus.*, *22*: 1-51, figs. 1-3, tables 1-14, 1974.

LANCINI, V.A.R. *Serpientes de Venezuela*, p. 1-262, figs. 1-119. Caracas, 1979.

LATREILLE, P.A. In: C.S. Sonnini & P.A. Latreille: *Histoire naturelle des reptiles, avec figures dessinées d'après nature.* Vol. III: 1-335, 6 pls., 1 table. Paris, 1802a.

———— In: C.S. Sonnini & P.A. Latreille: *Histoire naturelle des reptiles, avec figures dessinées d'après nature.* Vol. IV: 1-410, 13 pls. Paris, 1802b.

LAURENTI, J.N. *Synopsin reptilium*, p. 1-214, pls. I-V. Vienna, 1768.

LESCURE, J. Diversité des origines biogéographiques chez les Amphibiens de la region guyanaise. In: H. Descimon (ed.): *Biogéographie et evolution en Amerique tropicale. Publ. Lab. Zool. E.N.S.*, *9*: 53-65, map 1, 1 map., 1977.

LIDTH DE JEUDE, J.T. van. Catalogue ostéologique des poissons, reptiles et amphibiens. *Mus. Hist. Nat. Pays-Bas* X(2): *Reptiles*, 2 pp., 1-52. Leiden, 1898.

———— Reptiles and batrachians from Surinam. *Notes Leyden Museus.* 1904. 25: 83-94, pl. 7.

———— Articles on snakes. In: H.D. Benjamins & J.F. Snelleman. *Encyclopaedie van Nederlandsch West-Indië*, I-X, 2 pp., 1-782. 's Gravenhage/Leiden, 1914/1917.

LINCK, J.H. *Index Musaei Linckiani, oder kurzes systematisches Verzeichniss der vornehmsten Stücke der Linckischen Naturaliensammlung in Leipzig.* Erster Theil: I-XXXVI, 1-297. Leipzig, 1783.

LINNAEUS, C. *Amoenitates Academicae, seu dissertationes variae Physicae, Medicae, Botanicae.* Vol. I: 6 pp., 1-610 + 9 pp., 15 pls., 1749.

———— *Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, Locis.* Ed. 10. Tomus I: 1-823. Stockholm, 1758.

———— *Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species cum characteribus, differentiis, synonymis, Locis.* Ed. 12. Tomus I: 1-532. Stockholm, 1766.

MATZ, G., & MATZ, J. Les Boidés ou Serpents Constricteurs. 7. Eunectes Wagler. *Aquarama, 15*(61):37-39, 3 figs., 1981.

MERIAN, M.S. *Metamorphosis insectorum Surinamensium. In qua Erucae ac Vermes Surinamenses, cum omnibus suis Transformationibus, ad vivum delineantur & describuntur, singulis eorumin Plantas, Flores & Fructus collocatis, in quibus reperta sunt; Tum etiam Generatio Ranarum, Bufonum rariorum, Lacertarum, Serpentum, Araneorum & Formicarum exhibetur; Omnia in America ad vivum naturali magnitudine picta atque descripta*, 1705a., 4 pp., 1-60, pls. 1-60.

- ———— *Metamorphosis Insectorum Surinamensium. Ofte Verandering der Surinaamsche Insecten. Waar in de Surinaamsche Rupsen en Wormen met alle des zelfs Veranderingen na het leven afgebeeld en beschreeven worden, zynde elk geplaast op die Gewassen, Bloemen en Vruchten, daar sy op gevonden zyn; waar in ook de generatie der Kikvorschen, wonderbaare Padden, Hagedissen, Slangen, Spinnen en Mieren werden vertoond en beschreeven, alles in America na het leven en levensgroote geschildert en beschreeven*, 1705b. 4 pp., 1-60, pls. 1-60.

MÜLLER, P. Vertebratenfaunen brasilianischer Inseln als Indikatoren für glaziale und postglaziale Vegetationsfluktuationen. *Zool. Anz. Suppl.*, *33*:97-107, figs. 1-12, 1969.

PETERS, J.A. & OREJAS-MIRANDA, B. Catalogue of the Neotropical Squamata: Part I. Snakes. *Bull. U.S.N.M.*, *297*:I-VIII, 1-347, 1970.

ROMER, A.S. *Osteology of the Reptiles.* I-XXI, 1-772, figs. 1-248. Chicago, 1956.

ROZE, J. *La taxonomia y zoogeografia de los ofidios en Venezuela.* Ed. Bibl. 28. Col. Cienc. Biol. III: 1-362, figs. 1-79, maps 1-80. Caracas, 1966.

SANDNER MONTILLA, F. Nueva especie del Gen. Bothrops (Crotalidae) de la Gran Sabana, Edo. Bolívar. Bothrops eneydae nsp. *Mem. Cien. Ofidiología*, *I*:1-4, 1976.

SCHEUCHZER, J.J. *Geestelyke Natuurkunde* (Physica Sacra), 13. Amsterdam, 1735a.

———— *Geestelyke Natuurkunde*, 15. Amsterdam, 1735b.

———— *Geestelyke Natuurkunde*, 14. Amsterdam, 1738.

SCHLEGEL, H. *Essai sur la physionomie des serpens.* Partie générale: I-XXVIII, 1-251. Partie descriptive: 1-606, I-XV, 1 p. La Haye, 1837.

———— Handleiding tot de beoefining der dierkunde. Vol. II: I-XX, 1-628, 2 pp. Breda, 1858.

SEBA, A. *Locupletissimi rerum naturalium thesauri accurata descriptio, et iconobus artificiossissimis expressio, per universam physices historiam*, 1734. Vol. I: 34 pp., 1-178, 2 pls., pls. 1-111.

———— *Locupletissimi rerum naturalium thesauri accurata descriptio, et iconobus artificiosissimis expressio, per universam physices historiam.* 1735. Vol. 2: 34 pp., 1-154, 1 pl., pls. 1-114.

SUNDIUS, P. Surinamensia Grilliana. In: C. Linnaeus. *Amoenitates Academicae.* 1749. 483-508, pl. 17.

TROSCHEL, F.H. Amphibien. In: R. Schomburgk: *Reisen in British Guiana, in den Jahren 1840-1844.* Im Auftrag Sr. Mäjestät des Königs von Preussen ausgeführt von Richard Schomburgk. 1848. Vol. 3. Versuch einer Fauna und Flora von Britisch-Guiana: 645-661.

WAGLER, J. *Serpentum Brasiliensium species novae ou Histoire Naturelle des espèces nouvelles de serpens, recueillies et observées pendant le voyage dans l'intérieur de Brésil dans les années 1817, 1818, 1819, 1820 exécuté par de Sa Majesté le Roi de Bavière, publiée par Jean de Spix.* 1824. 1-75, pls. 1-26.

WARREN, G. *An Impartial Description of Surinam upon The Continent of Guiana in America. With a History of several strange Beasts, Birds, Fishes, Serpents, Insects, and Customs of that Colony*, & c. 4 pp., 1-28. London, 1667.

———— *Een onpartydige Beschrijvinge van Surinam, Gelegen op het vaste Landt van Guiana in America.* Mistgaders een Verhael van alle vreemde Beesten, Vogels, Visschen, Slangen, ende Wormen: Gelijck mede van de Gewoonheden ende Manieren van deze Colonie: 1p., 1-20. Amsterdam, 1669.

WIEST, J.A. *Revision of the neotropical snake genus Chironius Fitzinger (Serpentes, Colubridae).* Unpublished thesis Texas A & M University, 1978.

APPENDIX 1

Species reported from Guiana	authors																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Liotyphlops ternetzii (Boulenger)																							S		S	G			
Typhlophis squamosus (Schlegel)																	C		G		GBr		GBr		G	G		C	
Leptotyphlops amazonicus Orejas-Miranda																								V	V	G	V		
collaris Hoogmoed																										G		C	
cupinensis Bailey & Carvalho																									Br	G			
dimidiatus (Jan)																									G	G	V		
macrolepis (Peters)																						S			G	G		C	
septemstriatus (Schneider)																								V	G	G	V	C	
tenella Klauber																					C	S	A	V	G	G	V	C	
Typhlops brongersmianus Vanzolini																										G			
lumbricalis (L.)																					(B)	(S)			(G)	(G)			
minusquamus Dixon & Hendricks																													X
reticulatus (L.)								S		S			S				G			S	B	S	G	V	A	G	V	C	
Anilius s. scytale (L.)		S		S	S					S			S	S	S		SC	BC		S	G	S	G	V	G			C	
phelpsorum Roze																								V	V	G	V		
Boa c. constrictor L.			S		S										S	B	G	BrC		S	CBr	S		V	A	G	V	C	
Corallus caninus (L.)									S				S		S		SC		C	S	G	S	G	V	G	G	V	C	
c. enydris (L.)		S		S									S	S	S	B	G	G		S	G	S	G	V	G	G	V	C	
cookii Gray																							Br	V			V		
Epicrates c. cenchria (L.)							S	S	S			S	S	S	S	B	C	BC		S	BC	S	A	V	G	G	V	C	
maurus Gray																									G				
Eunectes deschauenseei Dunn & Conant																													X
m. murinus (L.)																									Am	G			
gigas (Latreille)	S												SC		S	B	SC	B		S	G	S	G	V	G		V	C	
Dipsas catesbyi (Sentzen)															G		SC	BSBr	C	S	BSBr	S	G		Am	G	V	C	
copei (Günter)																					S			V	G	G	V		
i. indica Laurenti														S							B	S	G		BBr	G		C	
pavonina Schlegel															G	B	SC	G			BBr	S	G	V	G	G	V	C	
v. variegata (D., B. & D.)		G?															S	S	S		G		G	G	G	G	V	C	
Sibon n. nebulata (L.)													S		S		S	B	S	S	B	S	G	V	A	G	V		
Apostolepis quinquelineata Boulenger																					B		BBr		B	G			
Atractus badius (Boie)															C		SC	B	S	S	SC	S	G		A	G		C	
duidensis Roze																								V	V	G	V		
elaps (Günther)																								V		G	V		
favae (Filippi)																										G			
flammigerus (Boie)															C		SC				Br							C	
insipidus Roze																								V	V	G	V		
latifrons (Günther)																										G		C	
Atractus major Boulenger																								V		G	V		
riveroi Roze																								V	V	G	V		
schach (Boie)															C							S							
steyermarki Roze																								V	V	G	V		
torquatus (D., B. & D.)															C			S		S	G		G			G			
trilineatus Wagler																		B			G		G	V	G	G	V		
zidoki Gasc & Rodrigues																										G		C	
Cercophis auratus (Schlegel)															S														
Chironius c. carinatus (L.)															SC	B	SC	BBr		S	B	S	A	V	A	G	V	C	
exoletus (L.)																									SBr	G			
f. fuscus (L.)																B	C	BBr			BC	S	G		G	G	V	C	
m. multiventris Schmidt & Walker																													X
cochranae Hoge & Romano																									S	G		C	
scurrulus (Wagler)																									Br	G	V	C	
Clelia c. clelia (Daudin)													S	S	S	B	C	SB		S	SB	S	A	A	A	G	V	C	
Cyclagras gigas (D., B. & D.)																										G			

APPENDIX 1 (continuation)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Dendrophidion dendrophis (Schlegel)															C		C	C		S	C		G		A	G		C	
Drepanoides anomalus (Jan)																										G			
Drymarchon c. corais (Boie)															S	B	SC	BBr	S		BC	S	A	V	Am	G	V	C	
Drymobius rhombifer (Günther)																										G	V		
Drymoluber dichrous (Peters)																							Br		V	G	V	C	
Elapomorphus quinquelineatus (Raddi)																	C				G		G			G			
Erythrolamprus a. aesculapii (L.)				S	S	S		S		S		S			S		SC	BBr		S	SBBr	S	G	V	Am	G	V	C	
bauperthuisii D., B. & D.																								V	V	G	V		
Helicops angulatus (L.)			S										S	S	S	B	BC			S	B	S	A	V	A	G	V	C	
hagmanni Roux																							Br		Br	G			
hogei Lancini																									V	G	V		
leopardinus (Schlegel)																	C	C			G		G		G	G		C	
polylepis Günther																									Br	G			
trivittatus (Gray)																					Br		Br		Br	G			
Hydrodynastes b. bicinctus (Herrmann)																	S	B			G		G	V	G	G	V	C	
Hydrops m. martii (Wagler)																							Br		Am	G			
t. triangularis (Wagler)																							G		Br				
fasciatus (Gray)															S		S	SB	S	S	SGB	S	G		GBS	G		C	
neglectus Roze																							G		G				
venezuelensis Roze																								V	V		V		
Imantodes c. cenchoa (L.)																B	G	S			S		G	V	A	G	V	C	
lentiferus (Cope)																									Am	G		C	
Leimadophis melanotus (Shaw)																								V	V	G	V		
poecilogyrus amazonicus Amaral														S											Br	G			
r. reginae (L.)															S	B	G	B		S	BBr	S	G	V	A	G	V	C	
t. typhlus (L.)	S												S	S	G		SBC	B			BC		G	V	A	G	V	C	
Leptodeira a. annulata (L.)					S		S						S		S		G	BBr		S	BBr	S	A	V	Am	G	V	C	
Leptophis a. ahaetulla (L.)		S	S	S		S			S				SC		SC	B	C	B		S	BC	S	A		G			C	
coeruleodorsus Oliver.																									V	G	V		
copei Oliver																								V	G		V		
ortonii Cope																									Br				
Liophis breviceps Cope																					S		S		SBr	G			
canaima Roze																								V	V	G	V		
cobella (L.)		S	S	S					S			S			S	B	SBC	BCBr		S	G	S	G	V	A	G	V	C	
ingeri Roze																								V	V	G	V		
miliaris (L.)																B	C	B	C		G	S	G		Br	G		C	
trebbaui Roze																								V	V	G	V		
undulatus (Wied)																							G		G	G			
Lygophis l. lineatus (L.)		S					S		S	S	S				S	B	SB	BBr		S	G	S	G	V	A	G	V		
Masticophis mentovarius suborbitalis (Peters)																									V		V		
Mastigodryas bifossatus striatus (Amaral)															S	B	SC							V	VBr	G	V	C	
b. boddaerti (Sentzen)															S		SC	BBr		S	SB	S	G	V	Am	G	V	C	
pleei (D., B. & D.)																								V	V	G	V		
Ninia hudsoni Parker																									B	G			
Oxybelis aeneus (Wagler)															S		BC	Br		S	Br	S		V	A	G	V	C	
argenteus (Daudin)		S		S					S						C		G	B	C	S	G	S	G	V	A	G	V	C	
fulgidus (Daudin)	S?						S?			S			S		C	B	S	Br	S	S	Br	S		V	A	G	V	C	
Oxyrhopus formosus (Wied)																									A	G		C	
p. petola (L.)		S	S	S									S		G		SC	B			SB	S	A	V	A	G		C	
digitalis (Reuss)																								V	Br	G	V		
t. trigeminus D., B. & D.																		B			G		G		Br	G	V		
Philodryas olfersii herbeus (Wied)				S		S							S		S		G	B						V	V	G	V	C	
v. viridissimus (L.)	S		S		S	S	S			S		S	S		S	B	SC	BC		S	G	S	G	V	G	G	V	C	

APPENDIX 1 (continuation)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Phimophis guerini (D., B. & D.)																										G			
guianensis (Troschel)																B		B			G		G	G	G	G	V	C	
Pliocercus e. euryzonus Cope																									Br				
Pseudoboa coronata Schneider															S			C		S	G	S	G	V	G	G	V	C	
neuwiedii (D., B. & D.)																					C		G	V	G	G	V	C	
Pseudoeryx plicatilis (L.)													S		S		SC	BBr	S	S	G	S	G		G	G	V	C	
Pseustes poecilonotus polylepis (Peters)																							G	V	G	G	V	C	
sulphureus dieperinkii (Schlegel)															S	B	SC	B		S	B	S	G	V	G	G	V	C	
Rhadinea brevirostris (Peters)																									G	G		C	
Rhinobothryum lentiginosum (Scopoli)					S						S				C		C		G		G		G		Br	G		C	
Siphlophis cervinus (Laurenti)																	C				G		G		A	G		C	
Spilotes p. pullatus (L.)															S	B	SC	B		S	SB	S	G	A	A	G	V	C	
Tantilla m. melanocephala (L.)															S		G	B		S	BBr	S	A	V	A	G	V	C	
Thamnodynastes chimanta Roze																								V	V	G	V		
Thamnodynastes pallidus (L.)					S								S		G	B	G		C		G		G	V	G	G	V		
strigilis (Thunberg)						S												B			B			VB	V	G	V		
Tripanurgos compressus (Daudin)													S			B		BBr		S	G			V	A	G	V	C	
Waglerophis merremii (Wagler)																					G		G		G			C	
Xenodon neuwiedii (Günther)																										G			
rabdocephalus (Wied)																	SC	BBr		S		S	Br		A	G		C	
severus (L.)														S	S	B		SBBr		S	SBBr	S	G	V	A	G	V	C C	
werneri Eiselt																										G		C	
Xenopholis scalaris (Wucherer)																										G			
Leptomicrurus collaris (Schlegel)																								V	VB	G	V		
schmidti Hoge & Romano																									Br				
Micrurus averyi Schmidt																									S	G			
h. hemprichii (Jan)																			S		G	S	G	V	G	G	V	C	
ortoni Schmidt																									Br				
ibiboboca (Merrem)																		Br			G					G			
isozonus (Cope)																								V		G	V		
l. lemniscatus (L.)					S								S		G		SC	Br			G	S	G		G	G		C	
carvalhoi Roze																									Br				
diutius Burger																										G			
helleri Schmidt & Schmidt																								V	G		V	C	
p. psyches (Daudin)													S				SC	S	C		G	S	G	V	VBr		V		
circinnalis (D., B. & D.)																					G				G	G		C	
s. spixii Wagler																		Br							Br				
martiusi Schmidt																									Br	G			
obscurus (Jan)																								V	VBr		V		
s. surinamensis (Cuvier)														S	S	B	S	S	C		G	S	G		G			C	
nattereri Schmidt																										G			
Bothrops atrox (L.)																								V	V				
b. bilineatus (Wied)															G	B	SC	B		S	BBr	S	G	V	G	G	V	C	
smaragdinus Hoge															C	B				S				V	G	G	V	C	
brazili Hoge																									V				
castelnaudi D., B. & D.																								V	G	G	V	C	
eneydae Sandner Montilla																							Br	V	Br	G	V	C	
Crotalus durissus cumanensis Humboldt																													X
dryinus L.						S	S						S		SC	E	G		G	S	B	S	G	V			V		
ruruima Hoge																									G	G		C	
triponicus. Harris & Simons																E									BrV		V		
Lachesis m. muta (L.)									S			S	G		SBC	E				S	SB	S	G	V	G	G	V	C	X
Total different taxa	2	2	6	8	10	10	2	10	4	4	5	5	25	9	49	31	55	52	20	39	71	49	73	77	130	125	88	77	5
Total according to author	—	3	14	10	10	18	3	12	5	7	7	9	33	9	47	22	63	59	25	44	79	51	75	78	142	132	88	77	159

APPENDIX 1 (continuation)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Species reported from Guiana in error																													
Cylindrophis maculatus (L.)						S		S		S		S																	
rufus (Laur.)						S				S		S																	
?Epicrates angulifer Bibron																		B											
Abastor erythrogrammus (Daudin)																			S										
Ahaetulla prasina (Boie)						S																							
Dipsas incerta (Jan)																			C		G		G		BrC				
Helicops carinicaudus (Wied)																	C	Br										C	
carinicaudus infrataeniatus (Jan)																			S										
Homalopsis buccata (L.)				S		S					S																		
Lampropeltis triangulum (Lacépède)																		Br											
Liophis cursor (Lacépède)																	C												
triscalis (L.)																					S		S	V					
Mastigodryas melanolomus alternatus (Bocourt)																												C	
Natrix natrix (L.)						S																							
Oxyrhopus petola sebae D., B. & D.																	C												
Philodryas e. elegans (Tschudi)																	G		G						S				
Sibynomorphus mikanii (Schlegel)																B													
Siphlophis pulcher (Raddi)																												C	
Aspidelaps lubricus (Laur.)										S		S																	
Micrurus ?corallinus (Merrem)																		Br											
filiformis (Günther)																					Br								
langsdorffi ornatissimus (Jan)																					Br				Br				
Vipera berus (L.)		S									S																		
"Anguis laticauda L."						S						S																	
"Platurus laurentii Daud."													S																
Typhlops unilineatus (D. & B.)																	C		C		C		C		SC	G			
Chironius bicarinatus (Wied)																										G			
Total species in error	2	—	5	1	1	—	3	2	4	1	—	—	1	5	4	5	—	5	—	3	1	4	2	—	3				

Legend of Appendix 1.

Guianan snakes, checklist and growth of knowledge about this group (also cf. fig. 3). 1 = Warren (1667), 2 = Merian (1705a,b), 3 = Seba (1734-35), 4 = Scheuchzer (1735a,b; 1738), 5 = Sundius (1749), 6 = Gronovius (1756), 7 = Linnaeus (1758), 8 = Houttuyn (1764), 9 = Linnaeus (1766), 10 = Laurenti (1768), 11 = Linck (1783), 12 = Gmelin (1789), 13 = Daudin (1803 a-d), 14 = Fitzinger (1826), 15 = Schlegel (1837), 16 = Troschel (1848), 17 = Duméril, Bibron & Duméril (1844-54), 18 = Gray (1849) + Günther (1858), 19 = Jan & Sordeli (1860-81), 20 = Kappler (1885), 21 = Boulenger (1893-96), 22 = Van Lidth de Jeude (1898, 1904, 1914/17), 23 = Amaral (1930), 24 = Roze (1966), 25 = Peters & Orejas-Miranda (1970), 26 = Hoogmoed (1979), 27 = Lancini (1979), 28 = Gasc & Rodriguez (1980b), 29 = present paper. A = Northern South America, Am = Amazonian basin, B = (British) Guyana, Br = Brasil, C = French Guiana, G = Guiana, S = Surinam, V = Venezuelan Guayana, X = taxa recorded from Guiana since 1979 or overlooked till now. Letters between brackets indicate introduced species.