

## A QUASI-HISTORICAL APPROACH TO THE NATURAL HISTORY OF THE DIFFERENTIATION OF REPTILES IN TROPICAL GEOGRAPHIC ISOLATES

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### INTRODUCTION

One of the models designed to explain observed speciation patterns in tropical areas is that first proposed by Haffer (1969) currently and inadequately called "theory of refuges". Its main premise is that, during the Holocene, world climate underwent rapid and drastic cycles, with commensurate repercussions on the distribution of plant cover. Thus, large continuous areas of rain forest would exist during the wettest part of each cycle, to be broken up during the succeeding dry episode into a number of patches, separated by open formations. These postulated isolates have been called "refuges", by analogy with the ice-free areas of glaciated Holarctica. Stenoeious species confined to refuges would differentiate during isolation.

It is clear from the premise that this is not a model of universal application; its use should be restricted to species of rigid ecological fidelity that can be shown to have undergone geographic differentiation in the near past. Within this scope it is a maximum parsimony model.

Rapid, drastic and recent climatic cycles are well documented for South America; Ab'Saber (1977a, 1979, 1979a) gives access to the relevant literature. These episodes can be dated, on a regional basis at least (Mörner, 1979) by sea level changes (Bigarella, 1964; Hurt, 1974; Fairbridge, 1976; papers in Suguio & al., eds., 1979), and it is to be expected that eventually they will be placed on a firm world-wide framework.

Partisans of the refuge model have frequently been at fault by going beyond their factual basis, by taking plausibility as equivalent to proof, or by applying the model to patterns of differentiation arrived at without the use of stringent analytic criteria — in fact, as C. W. Myers once cogently expressed in conversation, by dealing with names and not with variation. For these, and for lesser reasons, the existence of refuges has been disputed — or at least their relevance to speciation. I do not think the opponents of the model have a strong case but it is clear that re-hashing examples already presented will do little to advance knowledge. Even further detailed analyses of the differentiation of forest forms, aimed at revealing differences in evolutionary behavior between taxa, are now heavily dependent on the location of the refuges, which, as I see it, is the province of geomorphology and paleopalynology rather than systematics.

On the other hand, the matter of differentiation within isolates has received very little attention besides being taken for granted. It is manifest that new approaches should be tried. I here present the preliminary results of an investigation of existing refuges, not as

an attempt to prove their existence, but to gather data on the natural history of differentiation in forest isolates, and to probe for further lines of research.

### THE APPROACH

It is quite evident that the rain forests of Brasil are retreating; among other facts, the relationships between the faunas of the hylaea and of the Atlantic forest (Vanzolini, 1974) and the distribution of the vegetation in southern Brasil (Klein, 1975) show that we have recently gone past a climatic optimum, in terms of temperature and rainfall. For this reason the progress of speciation within refugia can be more conveniently studied in forest animals. The pace of climatic change, of the order of thousands of years, is fast in geological perspective, but still too slow in comparison with the human life span: to investigate the march of the process of differentiation one has to have recourse to indirect methods of observation. It is a natural choice to substitute a gradient in space for the gradient in time. Desiccation of the climate affects some areas before others, and with uneven severity. It should then be possible to find, in the midst of a broad area of open formations, relict patches of forest, proper and unequivocal refuges in the sense of the model, representing, by virtue of their peculiarities, diverse stages of the succession along the dry part of a cycle.

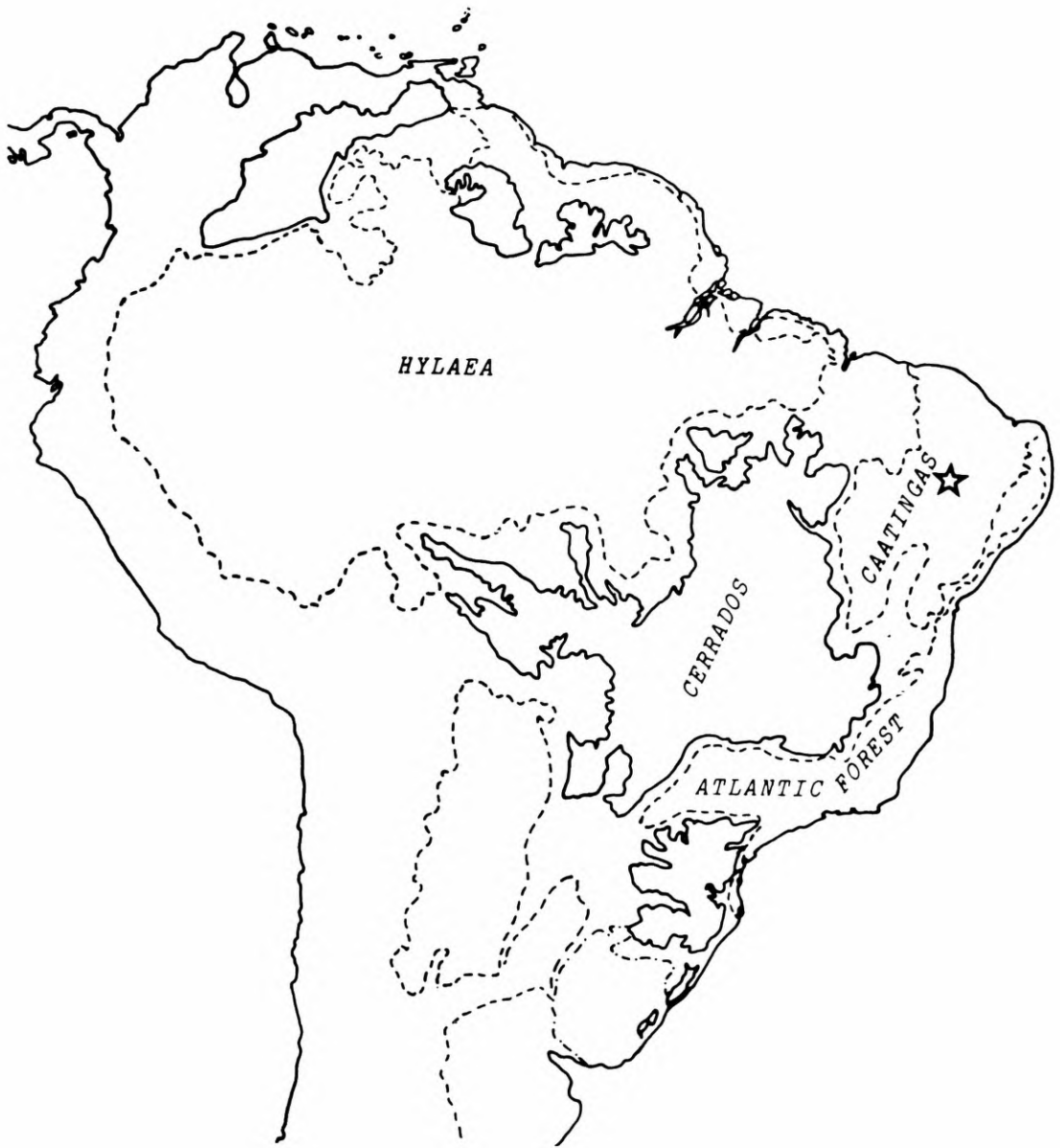
### THE AREA

The great morphoclimatic domain of the Brazilian caatingas (Ab'Saber, 1977, 1980; Hueck, 1966; Map 1) constitutes, at present, the most favorable area for the type of research contemplated. It is a continuous, well-defined area of approximately 800,000 square kilometers, covered by a very characteristic set of xerophytic plant formations, the caatingas. The climate, though not actually desertic, is semi-arid (Nimer, 1972; Reis, 1976). The annual rainfall varies locally from 300 to 800 mm; evaporation exceeds precipitation during a significant part of the year. Mean humidity can be as low as 50% or 60%. Mean annual temperatures vary roughly from 24° to 26° C, with small seasonal departures; this hot climate enhances the humidity deficit. A very important feature of the climate is its irregularity, both in time and space. There are frequent and disastrous drought years, some of which have entered history: to this day people talk about the "two sevens", the "three eights" and the "fifteen" (1877, 1888, 1915). These droughts seldom affect simultaneously the whole domain; it is not uncommon for a given region to experience severe drought and another a "good winter" or even floods. In some years the drought marches across the land, successively afflicting different areas.

All the autochthonous rivers of the domain are intermittent. The drainages are, however, exorrheic, and this absence of centripetal basins, and consequently of concentration of salts in the soil, prevents serious deterioration of the landscape.

The keynote of the vegetation is the conservation of water, and this is reflected in its physiognomy: thorny and succulent plants prevail; leaves, if present, frequently show hairs and wax; almost all species are summer deciduous. Daily and yearly rhythms are geared to the water economy. There is a striking contrast between the gray, leafless caatinga of the dry season and that "on the green" of the good winters, that has considerable biomass.

The core areas of the Brazilian morphoclimatic domains are separated by belts very diversified in width and constitution (Ab'Saber, 1977). The caatingas are widely separated from the hylaea to the north by a broad corridor of complex vegetation, including an area of buffer palm forests in Maranhão and Piauí, so large as almost to constitute a proper domain. To the west of this area cerrados intervene between caatinga and hylaea. The relationships between caatingas and cerrados are intimate, frequently taking the form of complex interdigitations (Vanzolini, 1976). In the case of the transition from the caatingas to the Atlantic forest, there are two intervening sub-types of plant formations.



Map 1. Cis-Andean morphoclimatic domains of South America (adapted from Ab'Saber, 1977), showing the position of the Cariri.

On the south (state of Bahia), there is a peculiar type of low, scrubby, tangled forest, the "mata de cipó" (literally "vine forest"). On the north, characteristically in Pernambuco (Vanzolini, 1974), there is instead a narrow belt of less harsh caatinga, the "agreste".

In the middle of this fairly homogeneous domain there are many enclaves of forest, usually called "brejos" (this use of the term is purely regional; elsewhere in Brasil it means a small swamp). They are determined by strictly local features, usually topographic, and may be situated on any level of the landscape. In fact, the current classification of the brejos, first proposed by Ab'Saber in the 1955 meeting of the Association of Brazilian Geographers, takes into account exactly the topographic situation: at the foot of mountains or ridges, on the slope, on the top. For example, on some of the higher elevations (ca. 1000 m), the milder temperatures may bring about more mesic conditions. In other cases, the orientation of the relief relative to the prevailing winds may cause regular

orographic rains, and forest to exist at mid-slope or at the foot of the relief. Finally, geological and geomorphological structure may result into a concentration of permanent springs, capable of supporting forest by natural irrigation, even in the face of low or irregular rainfall.

My working hypothesis is: if it is true that the hylaea and the Atlantic forest have been recently connected, and that the mesic enclaves of the Northeast are relicts of this connection, then their fauna should bear witness to the fact, and a comparative study of enclaves should help in understanding the natural history of speciation in refuges.

If this research were to be undertaken 250 years ago, the situation would have been perfect. We would have had a wide choice of enclaves of all sizes and kinds, with a practically undisturbed fauna. But it is easy to understand that mesic enclaves in a semi-arid region are at a premium, and that human occupation from early times has taken its toll of their native vegetation. Even so, there still remain some suitable areas, protected by design, or too steep for cultivation, that repay investigation. It will also be seen that some elements of the fauna have proved remarkably resilient to deforestation, and that their study yields valuable insights into the problem.

There is still one other, complementary approach. The Atlantic forest has been very extensively reduced by agriculture, and so preserved stands, encroached upon by open formations strongly influenced by the caatingas, function exactly as refuges and provide good opportunities for research.

## MATERIALS

When I first thought of this project, some ten years ago, looking for a meaningful continuation of the research began in Amazonia in collaboration with E. E. Williams (e. g. Vanzolini & Williams, 1970), reasonable information existed only in the case of the reptiles of the eastern hylaea, much work remaining to be done in the caatingas and in the northern Atlantic forest. A program to collect the missing information was started with the support of the Brazilian Academy of Sciences.

The method chosen was to establish a grid of localities, and to collect fast and intensively in them, establishing "lizard markets".

A series of transects was undertaken, and collections made at intervals, all the way from the coast to the cerrados on the west. To check the validity of the survey and to gather coherent basic ecological information, we had a colleague, Laurie J. Vitt, stationed for one year at Exu, (07°31'S, 39°43'W) in the caatingas of Pernambuco. Vitt will publish individually the results of his work, that went much beyond the basic needs of this research, but it is possible to say here that he confirmed our species lists and general data on habitat preferences. I think we now have a fair idea of the reptiles of the caatingas (Vanzolini, Ramos-Costa & Vitt, 1980). Much work still has to be done in the Atlantic forest, especially with respect to the snakes, but even there the information available is already sufficient to start work on the enclaves.

No small enclave has been studied in depth yet, but several have been prospected, and their salient features noted. This information, added to that gathered in the relict patches of Atlantic forest, has made it possible to use incidental collections made in the past by Museum ornithological parties, and to plan future work.

As to the large enclaves, two visits have been made to one of the largest, the Cariri, in the state of Ceará. The results have been fascinating (a short account has been published by Williams & Vanzolini, 1980) and, although confirmatory field work remains to be done, the main pattern is definite enough.

## THE SMALL ENCLAVES

A first characteristic of the lizard fauna of the small enclaves (information on the snakes is still scanty), and one to be expected (Preston, 1962), is the reduced number of

forest species, no more than three or four being obvious at any place, against 12 to 15 in the main body of the Atlantic forest and 20-odd in the eastern hylaea. This impoverishment is selective: each small enclave has its own set of forms.

A second important characteristic is the "Belém Park effect" of Williams (1977): some of the species are found in abnormal abundance. For example, in a small relictual woods at Arauaris, in Sergipe (Vanzolini & Gomes, 1979; Williams & Vanzolini, 1980) both *Anolis ortonii* and *punctatus* were very common; the former had just recently been recorded from the Atlantic forest and the latter, although less rare, had never been found in abundance. In another relict woods, at Água Azul, Pernambuco, *Strobilurus torquatus* was unusually frequent, and my colleague Francisca do Val obtained, in two days, two specimens of the microteiid *Stenolepis ridleyi*, thus far known only from the type, in spite of considerable time spent looking for it. These abnormal densities may very possibly bring the involved species into competition, which is rather unlikely in the sparsely inhabited main forests (Heyer, 1976).

A third important feature is that the fauna of the surrounding open formations penetrates the small enclaves of forest, at least to forage. This is a phenomenon that will probably be better observed in birds, but, even among the lizards, *Ameiva ameiva* and *Tropidurus* of the *torquatus* species group are frequently found deep in the woods. At Arauaris a specimen of *Coleodactylus meridionalis*, a small forest leaf litter gekkonid, was found in the stomach of a *Tropidurus hygomi* caught in the open.

These features of the lizard fauna of small enclaves indicate clearly that a small refuge is not a random sample of the primitive forest, but has a personality of its own. The forest species surviving in it live in an entirely different context than in the original habitat. Their survival means adaptation, i.e., change, under very strong selective pressures. Rapid differentiation is to be expected.

A very interesting, if incidental, consequence of the interactions of the fauna of the refuges with that of the surrounding open formations is that it precludes the direct application to small enclaves of the concepts of "insular biogeography", which makes no provision for fishes foraging on trees.

### THE CARIRI, A LARGE ENCLAVE

That large enclaves have existed, capable of supporting, during a dry episode, a sizable portion of the fauna of the forest at its optimum is made necessary by the very nature of the Amazonian lizard fauna, extremely diversified at the generic level but much less so at the specific one. There are no intact large forest enclaves left in the northeast of Brasil; they have been decimated by agriculture. (It is possible that some will be found in the large domain of the cerrados, but information on this area is still inadequate and hard to obtain). It was in a spirit of adventure that I first went collecting in the Cariri, one of the largest and best known mesic areas of the Northeast. (Northeast, with capital N, is a straight translation of Nordeste, the traditional Brazilian designation for the coastal states from Piauí to Bahia — an usage analogous to the American "West").

Cariri was the collective name of a large and strong group of Indian nations that inhabited the Northeast at the time of European occupation. Their name survives as a toponym in two regions: the old "Cariris Velhos", in the state of Paraíba, and the new "Cariris Novos" or simply "The Cariri" in southern Ceará, the area with which we are concerned.

Roughly speaking, our Cariri is delimited to the south by a very large mesa, the Serra or Chapada do Araripe, that runs from East to West; in the other directions the Cariri merges gradually with the adjoining caatingas.

The Chapada is responsible for the existence of the enclave. Its midline follows more or less the parallel of 07° 30'S; it is some 200 km long and on the average, about 30 km wide; the maximum height is around 1000 m above sea level, the lowlands around it lying between 400 and 450 m. Geologically, the Chapada is constituted by almost horizontal

strata; the top 200 m are made of a soft, very permeable sandstone, underlaid by about 50 m of impermeable limestones of the Cretaceous Santana Formation (well known for its nodules containing fossil fishes), that forms a gentle syncline within the mesa. Below the limestones there are further sandstone beds, and finally the crystalline rocks of the Brazilian shield. The water imbibed by the topmost sandstone runs along the limestone and flows out of the northern and eastern flanks of the mesa in a series of permanent springs, at the approximate height of 725 m (Small, 1923). Above the line of springs the flanks of the mesa are sheer; below it they form dissected spurs, with rounded, convex contours, characteristic of the milder climates. This area is the heart of the enclave. Additionally to the water supplied by the springs, the Cariri enjoys better rainfall, ca. 1000 mm, less irregularly distributed in time, than the adjacent areas (Nimer, Filho & Amador, 1971). It must be stressed that the conjunction of hydrogeological and meteorological factors is an essential feature of the Cariri.

I know of no estimates of the area under mesic conditions, since it grades, as said, into the normal caatingas around; my personal guess would be between 3 and 4000 square kilometers.

Given the mild climate and the availability of running water for irrigation, the Cariri was soon settled (in the middle 18th century) and its native vegetation, from the level of the springs down, substituted by cultivation. The earliest comment on the vegetation I could find was made in 1860 by a professional botanist (Freire-Allemão, 1862), who wrote of the springs: "It is these waters that maintain there, on a belt two or three leagues [12-18 km] wide, a luxuriant vegetation and the admirable fertility of this blessed spot. The Cariris used to be, in early times, shaded by imposing forests, to which nowadays some remains bear witness." (My own free translation).

There is much published information on the Cariri (e. g., SUDENE-ASMIC, 1967), but apparently no specific account of the vegetation. Loeffgren (1910) and Ducke (1958) deal with it incidentally and briefly; Luetzelburg (1923) has more data, but is much less reliable.

An interesting point is that the top of the mesa is covered with harsh sandy caatinga, except for a few kilometers on the eastern end (near the city of Crato) where there is an area considered by Loeffgren (loc. cit.) to be a type of "cerradão", a cerrado predominantly arboreal, with a canopy (Rizzini, 1963). The more mesic areas around Exu where *Coleodactylus* has been collected (see below) may have been in the very recent past cerradão enclaves.

I report here mainly on a first collection of reptiles made at Arajara (07°21'S, 39°23'W), a village of some 50 houses located on an indentation of the northeast flank of the Chapada, just below the line of the springs. These flow out of a network of rather roomy caves and passages in the sandstone; the water is from the start diverted through numerous carefully designed irrigation ditches, that end up by running into the Salamanca, a small tributary of the Jaguaribe, which is the largest, but still intermittent, river of Ceará. As elsewhere in the enclave, all the land is divided into small farms and tilled, sugar cane and orchards predominating. We stayed 10 days in Arajara and, almost exclusively through the efforts of the local children (the "lizard market"), obtained 729 reptiles, comprising 26 species. This was not a random sample: the common, easily identifiable species were accepted only at the beginning, and the children instructed to look for forms new to the collection. It turned out to be a surprising one.

## CARIRI LIZARDS

The information we have on lizards (including, for convenience, the amphisbaenids) is much better, in amount and kind, than what we have on the snakes. The two groups must be treated separately.

The following species of lizards and amphisbaenians were obtained at Arajara:

## Gekkonidae

- Coleodactylus meridionalis* (Boulenger, 1888)  
*Gymnodactylus g. geckoides* Spix, 1825  
*Phyllopezus p. pollicaris* (Spix, 1825)

## Iguanidae

- Anolis chrysolepis brasiliensis* Vanzolini & Williams, 1970  
*Platynotus semitaeniatus* (Spix, 1825)  
*Polychrus acutirostris* Spix, 1825  
*Tropidurus torquatus* (Wied, 1820)

## Scincidae

- Mabuya heathi* Schmidt & Inger, 1951  
*Mabuya arajara* Rebouças-Spieker, 1980

## Teiidae

- Ameiva ameiva* (L., 1758)  
*Cnemidophorus ocellifer* (Spix, 1825)  
*Micrablepharus maximiliani* (Reinhardt & Luetken, 1862)

## Anguidae

- Diploglossus lessonae* Peracca, 1890

## Amphisbaenidae

- Amphisbaena pretrei* Duméril & Bibron, 1839  
*Leposternon polystegum* (A. Duméril, 1851)

The main elements for discussing the present collection are my papers on the lizards of Pernambuco and on the lizards of a caatinga-cerrado contact (Vanzolini, 1974, 1976); the excellent collection made by Laurie Vitt in the caatingas at and around Exu, some 40 km of Arajara, on the opposite, southern side of the Chapada; and one collection made at Santana do Cariri, 80 km NW from Arajara, at the foot of the Chapada, just outside the mesic area. The procedure at Santana was identical to that used at Arajara. Vanzolini, Ramos-Costa & Vitt (1980) may be used as a general reference.

Three species of geckos are easily obtained in the caatingas: *Gymnodactylus g. geckoides*, *Phyllopezus p. pollicaris* and *Vanzoia klugei* Smith, Martin & Swain, 1977 (referred to as *Lygodactylus* sp. in my 1974 paper). All three were abundant at Exu and Santana. At Arajara *Vanzoia* was not found; of the others, only two specimens of each. *Coleodactylus meridionalis*, which was obtained, is well known from the Atlantic forest and from forest enclaves in the open formations; however, Vitt found it also at Exu, in situations more mesic than typical caatinga, but by no means forested (possibly much devastated remains of cerradão — see above).

Four iguanids are frequent in the caatingas: *Platynotus semitaeniatus*, *Tropidurus torquatus* (sensu Vanzolini & Gomes, 1979), *Polychrus acutirostris* and *Iguana iguana* (L., 1758). The latter was not present at Arajara. Immensely interesting was the series of 20 *Anolis chrysolepis brasiliensis*, discussed in some detail by Williams & Vanzolini (1980).

There is no need to repeat the full argument, but the following points should be stressed in the present context. *Anolis chrysolepis* is one of the species that most clearly show a pattern of differentiation and distribution shaped by the last cycle of forest pulsation. The northeastern race, *A. chrysolepis chrysolepis*, is extremely distinct, but the narrow area of intergradation with its western neighbor, *planiceps*, is a textbook case; some misidentifications of localities, made by Vanzolini & Williams (1970) and discovered by Hoogmoed (1973) did not change the picture at all, a test of robustness. The race *planiceps* is the strongest argument I know against authors (e. g. Endler, 1977) who advocate the view that present day subtle ecological barriers can account for the patterns of differentiation, without recourse to paleoclimatic cycles. *A. c. planiceps* extends from the Cordillera de la Costa in Venezuela to the northern bank of the Amazon, ignoring and bypassing the Venezuelan llanos, not exactly a subtle ecological barrier. The western race *scypheus* reflects in its morphology the necessarily complicated history of the forest on the tortured Andean slopes and passes. In this general framework, an important role is assigned to *brasiliensis*: it is the form that followed the expansion of the hylaea southward, and should show in its present distribution the signs of the post-optimum retreat, i. e., it should behave as an animal "left behind". Previous data on its distribution suggested so; the Arajara record, in such a far place, so completely surrounded by caatingas, is a most welcome confirmation.

The relatively large size of the sample might be construed as an example of the Belém Park effect; in the eastern hylaea it would have been very difficult to assemble twenty specimens in ten days. However, the conditions of visibility are different, and it is better to keep the matter in abeyance.

So far only one species of *Mabuya*, *M. heathi*, has been found in the caatingas. The find of *Mabuya arajara* is extremely interesting.

As noted by Rebouças-Spieker (1980) in her description, and as it will be further discussed in a revision she and I have in preparation of the Brazilian lizards currently lumped under the name *M. m. mabouya*, it is a close relative of *M. bistriata* (Spix, 1825). The latter has a disjunct distribution: it is widespread in Amazonia and occurs on the northern end of the Atlantic forest (Pernambuco and Alagoas). There are no noticeable differences between eastern hylaeal and Northeastern materials, but *arajara*, represented by over one hundred specimens, is undoubtedly different. The case is very probably one of speciation in a refuge, where morphological differentiation was faster than in the large forested areas.

The ecological situation of *M. arajara* is also very interesting. Amazonian mabuyas are heliophils not totally committed to forest life; they are found in small clearings, on fallen trees and other places where sunshine pierces the canopy, but also in large clearings and plantations. If *M. arajara* is indeed derived from *bistriata*, it must have experienced an ecological reversal, returning to life in the open.

The teiids and anguids obtained at Arajara are exactly what can be expected from a caatinga locality. The contrary occurs with the amphisbaenids. *Amphisbaena pretrei* and *Leposternon polystegum* are not known from the caatingas. The former (Gans, 1965, and data from our collection) occurs in the Northeast in coastal localities and in the agreste, the transitional area between caatinga and northern Atlantic forest (Vanzolini, 1974). *Leposternon polystegum* has a bewildering pattern of distribution and variation (Gans, 1971, and data from our collection). It occurs in eastern Pará in full hylaea, in non-forested areas of the coast of the Northeast, and in several cerrado localities. It varies much, both in cephalic lepidosis and in scale counts: one may have ranges of 40 or 50 annuli within a sample and of more than one hundred annuli between samples. It has not been possible so far to find a geographic rationale for the variation, and our good Arajara sample (24 specimens) is no help in this regard.

The case of *L. polystegum* is another one that might be taken as an example of the Belém Park effect; when Gans (1971) revised the genus he was able to assemble 21 spec-

imens. However, the number of amphisbaenids one obtains at a given locality is not necessarily proportionate to the actual abundance.

*Comments.* The lizard fauna of Arajara is predominantly mesic in character. There are two characteristic forest elements, *Anolis chrysolepis brasiliensis* and *Mabuya arajara*, and both indicate that the Cariri can be considered a refuge for the fauna of a retreating forest, and that this refuge has functioned as a site of differentiation.

The two amphisbaenids indicate that it has functioned also as a refuge for elements from open formations milder than caatingas. The influence of the caatinga fauna, as shown by the geckos, is not too marked, in spite of deforestation.

To check these indications that historical factors are really important in shaping the fauna of such a site, I studied the lizards of a comparable locality, Catinga do Moura (10°58'S, 40°45'W) in Bahia.

This is an oasis maintained by a tributary of the upper valley of the Rio Salitre. The bedrock is the Salitre Formation limestone, of the Precambrian Bambui Group (Almeida, 1977), which has many karstic features (Bley, 1965). The river that maintains the enclave, Rio da Catinga do Moura, runs on the surface for a little more than 20 km, from some bubbling springs to a sink hole. Except for the relief, the area has important points in common with Arajara. The water is extensively used for irrigation, the native vegetation has been substituted by cultivation (garlic, castor beans, etc); the contrast with the surrounding caatingas is even sharper. By using again the lizard-market system, supplemented this time by intensive field work by Miguel T. Rodrigues, one of our party, 435 specimens, comprising 10 species, were rapidly assembled. The collection was very different in kind from the Arajara one; it was in fact a typical caatinga sample.

#### Gekkonidae

*Briba brasiliana* Amaral, 1935  
*Gymnodactylus g. geckoides*  
*Phyllopezus p. pollicaris*  
*Vanzonia klugei*

#### Iguanidae

*Tropidurus torquatus*

#### Scincidae

*Mabuya heathi*

#### Teiidae

*Ameiva ameiva*  
*Cnemidophorus ocellifer*

#### Anguidae

*Diploglossus lessonae*

Additionally were collected some *Hemidactylus mabouia* (Moreau de Jonnés, 1818) a peri-anthropic species, not abundant in the caatingas (Vanzolini, 1978) but found in several localities, among them Exu.

I am not prepared at this time to discuss eventual past connections of the Catinga do Moura oasis with forested areas, but its lizards fauna clearly indicates that mesic conditions by themselves are not sufficient to warrant the presence of a mesic fauna.

#### CARIRISNAKES

The following species of snakes were obtained at Arajara:

##### Colubridae

- Dromicus reginae* (L., 1758)
- Dromicus poecilogyrus* (Wied, 1825)
- Liophis joberti* (Sauvage, 1884)
- Lygophis lineatus* (L., 1758)
- Oxybelis aeneus* (Wagler, 1824)
- Philodryas olfersii* (Lichtenstein, 1823)
- Sibynomorphus mikanii* (Schlegel, 1837)
- Waglerophis merremii* (Wagler, 1824)

##### Elapidae

- Micrurus ibiboboca* (Merrem, 1820)

##### Viperidae

- Bothrops atrox* (L., 1758)

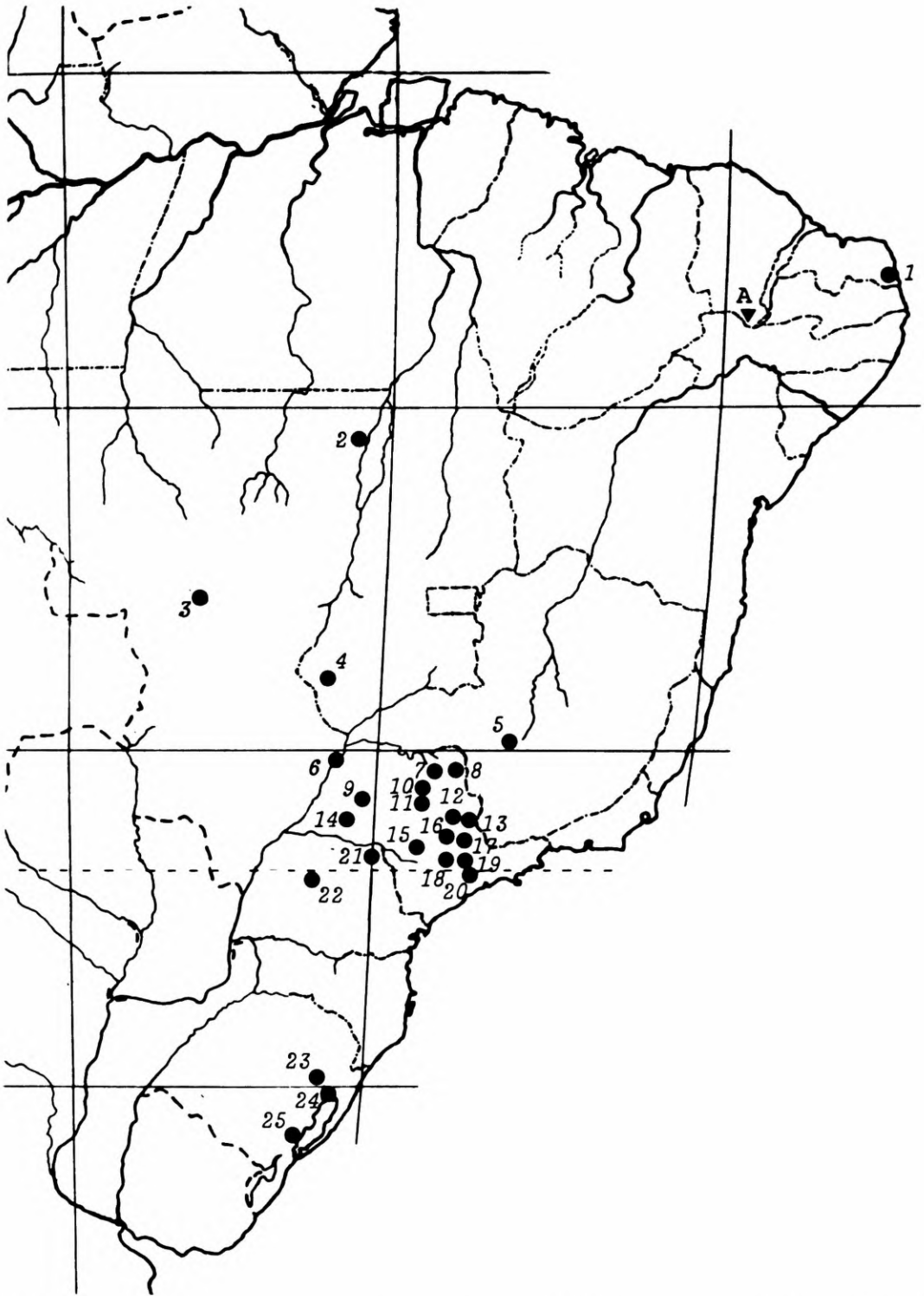
In the following discussion I have used data from the Museu de Zoologia collection, and drawn freely from the literature, citing formally, however, only in the case of very specific points. To only one paper I made constant reference, Cordeiro and Hoge's (1974) uncommented list of the snakes of Pernambuco, which reveals much useful information once the localities are placed in proper ecological perspective.

Of the snakes collected at Arajara three are not known to occur in caatingas: *Dromicus reginae*, *Sibynomorphus mikanii* and *Bothrops atrox*. The most interesting case is that of *S. mikanii*, of which 21 specimens were obtained, definitely an abnormally high frequency.

In his revision of the dipsadines, Peters (1960) divided *S. mikanii* in two subspecies, one distributed along the coast and the other in the interior of Brasil. The range of the nominate race would be "Internal drainage areas of southeastern Brazil, not including coastal areas except in north, in states of Mato Grosso, Minas Gerais, Paraná, Rio Grande do Norte, Rio Grande do Sul and São Paulo." And that of *S. m. newwiedi*, "South-eastern coastal strip of Brazil, from Bahia on the north to the state of Rio Grande do Sul on the south."

These statements do not describe correctly Peters' own distributional data. In the case of *mikanii* the mention of "internal drainages" is unfortunate. Peters uses the term not in the sense of centripetal, endorrheic drainages, but referring to rivers that arise near the coast and run inland, reaching the sea deviously, such as the tributaries of the Paraná. The concept is zoogeographically irrelevant, and is misapplied in the case of the Minas Gerais and Rio Grande do Sul specimens.

In the case of *newwiedi* the inadequacies are more serious. The term "coastal strip" does not make sense applied to large stretches of coast of very variable morphology. But it happens that the majority of Peters' localities are not coastal. Curitiba, for instance, occupies a site extremely similar to that of São Paulo, a *mikanii* locality: the headwaters of a tributary of the Paraná. More regrettable still is the omission, from the map and from the



Map 2. Localities of *Sibynomorphus mikanii*. A, Arajara. 1, Nisia Floresta (= "Papery"). 2, Porto Velho, Rio Tapirapés. 3, Chapada (dos Guimarães). 4, Jataí. 5, Lagoa Santa. 6, Ilha Solteira. 7, Barretos. 8, Franca. 9, Araçatuba. 10, Andes. 11, Taquaritinga (= "Jaquaritinga"). 12, Emas; Pirassununga. 13, Aguai (= Cascavel). 14, Rinópolis. 15, Botucatu. 16, Piracicaba. 17, Campinas; Valinhos. 18, Itu. 19, Jundiá. 20, São Paulo; Osasco; Barueri; Santo André. 21, Jacarézingo; Leoflora. 22, Maringá. 23, Montenegro. 24, Porto Alegre; Campo Bom; Gravataí; Viamão. 25, São Lourenço (do Sul). Records from Peters (1960); Hoge, Romano, Federsoni & Cordeiro (1975); Fundação Zoobotânica do Rio Grande do Sul (1976); collection of the Museu de Zoologia, USP.

description, of the locality "Tambos" (actually Tombos) in Minas Gerais: this locality makes the two subspecies broadly sympatric. Peters extends *neuwiedi* to Rio Grande do Sul, but his southernmost specimens are from Santa Catarina, and there are no records from Rio Grande in the literature he cites.

Peters does not discuss intergradation between the subspecies, either from the morphological or from the geographical viewpoint. In fact he gives no explicit reason for calling them subspecies; I suspect his incomplete view of the distributional pattern led him to that position.

Examination of specimens leaves no doubt that two taxa are involved, most probably two full species, largely but not entirely allopatric. In my personal experience, the best diagnostic characters between the two are the number of subcaudals, much lower in *mikanii*, and the color pattern of the head, well described by Peters. According to these criteria, the Arajara materials belong to *mikanii*. Geographically, *neuwiedi* would also be plausible. Peters gives Bahia as its northernmost locality, but Boulenger (1896: 454) cites specimens from Pernambuco (no further data) with the right color pattern and high subcaudal counts.

The color pattern of head and body of our Arajara specimens agrees very well with that of materials from Central and southeastern Brasil. So does the number of subcaudals, 41 to 55; Peters has 37 to 62 (sexes combined); our best sample, 16 specimens from the state of São Paulo, has values between 40 and 56; the inclusion of a few specimens from Rio Grande do Sul and Central Brasil does not broaden the range.

Arajara shows a definite difference in the number of ventrals. Peters has a range (sexes combined) of 153 to 177; our inclusive sample goes from 156 to 172; Arajara has 148 to 163. Testing the difference between our general sample and Arajara, by means of the test of the median, it is found to be significant at the level of  $6 \times 10^{-7}$  (Fisher's exact test for 2 x 2 tables).

Arajara is outside the known geographical range of *S. mikanii*, but partly encompassed by it. The closest locality is "Papery" (Schmidt & Inger, 1951), a misprint for Papary, now Nisia Floresta, on the coastal plain of Rio Grande do Norte, some 500 km from the Cariri. This specimen was identified by Peters (1960: 154) as *mikanii* and its meristic data, 161 ventrals and 48 subcaudals (Schmidt & Inger, *loc. cit.*) are quite plausible. All the other localities lie much to the south, far inland. The nearest one, Porto Velho, Rio Tapirapés, almost on the left bank of the Araguaia, is about 1300 km away; however, this distance will very probably be reduced when the northern cerrados become better known.

There are few definite data on the ecology of *S. mikanii*, one reason being that many specimens were collected in disturbed environments. Several specimens are recorded from Lagoa Santa (Jensen, 1900; Peters, 1960), and these are certain to have been collected in cerrado. On the other hand, we have specimens collected in small woods inside the city of São Paulo. Thus it is only possible to say that the Cariri is functioning as a refuge for *S. mikanii*, without advancing any guesses about the snake's primitive ecology in the area. There is also an indication, in the low number of ventrals, that it is undergoing differentiation, but the available materials from other areas are not sufficient for analysis at the level needed.

*Bothrops atrox* belongs to a poorly known group of species, badly in need of comprehensive study; I have hesitated (Williams & Vanzolini, 1980) in thus naming the present specimen. The name *atrox* proper is presently applied to populations from the "Equatorial forests of Colombia, Venezuela, Guianas, Brasil, Peru, Ecuador and Bolivia" (Hoge & Romano, 1973). We have from the Atlantic forest (Mamanguape, Paraíba; Areia Branca, Sergipe) specimens that agree in color and scale counts with those from the eastern hylaea, and that I think should be called *atrox* until a good revision is available.

From the Cariri we have two specimens, one half-grown from Arajara and one adult from the cerradão at the top of the eastern end of the mesa (Floresta Nacional do Araripe). They agree both with hylaeal and Atlantic forest materials. Thus although the

*atrox* group occurs also at least in the cerrados (*B. moojeni* Hoge, 1966), I think the present specimens should be considered as representing a forest element isolated and sheltered in the Cariri enclave.

Under the name *Dromicus reginae* are certainly lumped several forms, spread across an enormous range, all of cis-Andean South America from Trinidad to Argentina. A form of the group is relatively common in the Northeast, but has been found so far only in the Atlantic forest and in small enclaves. At present it seems that the only thing to do is to record its presence in the Cariri.

The other snakes found at Arajara are too euryoecious to have a place in an argument on forest refugia. As a matter of procedure I checked their scale counts and color pattern for possible geographic regularities, but found nothing worth mentioning.

*Comments.* The Arajara snakes confirm the pattern found in the case of the lizards: we have one forest element, two species with less stringent habitat preferences but not occurring in caatingas and a group of euryoecious species.

Repeating the caveats that we know little about snakes and that snake collecting is chancy, it is worthwhile to list what we obtained at Catinga do Moura.

#### Leptotyphlopidae

*Leptotyphlops albifrons* (Wagler, 1824)

#### Boidae

*Epicrates cenchria* (L., 1758)

#### Colubridae

*Dromicus poecilogyrus*

*Drymarchon corais* (Boie, 1827)

*Mastigodryas bifossatus* (Raddi, 1820)

*Oxybelis aeneus*

*Drymoluber brazili* (Gomes, 1918)

*Philodryas nattereri*

*Waglerophis merremii*

#### Viperidae

*Bothrops erythromelas* Amaral, 1923

There are a few interesting points here, not directly related to our theme, but useful in understanding the fauna of the caatingas.

I use *Leptotyphlops albifrons* as a name of convenience for a little understood group of forms (Vanzolini, Ramos-Costa & Vitt, 1980). We have another specimen, practically identical to the present one, collected at Junco do Seridó, Paraíba, in very rough caatinga.

*Mastigodryas bifossatus* is known from one locality, a few kilometers south of Chorózinho, Ceará (04°18'S, 38°29'W), not far from caatinga, but definitely outside it. This being characteristically a swamp and pond snake, it will possibly be found around reservoirs in the caatinga.

*Drymoluber brazili* is relatively rare in collections; it was originally described from the cerrados of southwestern Minas Gerais. We have another specimen from the Serra do Teixeira, in Paraíba.

The remaining species are common in the caatingas, and *Bothrops erythromelas* is the characteristic crotaline of the domain.

## CONCLUSION

I would say the work done in the Northeast in the last nine years has resulted in some relatively firm conclusions, to be used as stepping-stones for on-going research.

The small enclaves indicate that they are not samples of the primitive forests, but definite entities with a context very much of their own, involving altered population densities, interaction with forms from the open formations, and random reduction of the number of species.

The Cariri shows that, even in much disturbed circumstances, it is possible to find the footprints of the forest fauna in its advances and retreats. Accelerated differentiation relative to the core areas of the domains is made probable by *Mabuya arajara*. It is evident that many normally stenoeious species are tolerant, in certain places, of extensive habitat change; this opens interesting possibilities with regard to the origin of vicariant forms, the "vanishing refuge" model, that E. E. Williams and I are currently exploring.

Certain things we already knew, but there is no harm in reasserting them on fresh evidence: that refuges existed and exist, that differentiation occurs inside them, that Ceará was included in the forest bridge uniting the hylaea to the Atlantic forest, and that historical factors are very important in determining the faunal features of any given area.

Some points arise for immediate consideration. The relicts of the northern Atlantic forest must be worked in some depth, both to reconstruct as much as possible of its pristine features and to gather data on the ecology of small isolates, especially on the partition of resources. The same, of course, has to be done to a series of brejos, where additionally one must look for correlates of area, topography, etc. Populations showing the Belém Park effect should be studied from the viewpoint of genetical variability.

The Cariri has to be further explored, to verify and to expand the data already gathered. And the work has to be extended to other large enclaves, both in sedimentary and crystalline areas; information at hand points to the Serras of Ibiapaba and Baturité as targets of high priority.

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