

Papéis Avulsos de Zoologia

ECOLOGICAL AND GEOGRAPHICAL DISTRIBUTION OF LIZARDS IN PERNAMBUCO, NORTHEASTERN BRASIL (SAURIA)

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INTRODUCTION

One of the most rewarding fields of study for the South American zoologist is that of the processes that have resulted in the highly diversified tropical faunas. It is now well established that cycles of expansion and retraction of the major morphoclimatic domains have played an important role in recent tropical evolutionary processes, and that the analysis of geographical differentiation is a fruitful method in the unravelling of patterns (for a brief summary of concepts, methods and results, as well as other matters dealt with in this introduction, see Vanzolini, 1970, 1972). On the other hand, it is becoming more and more evident that speciation mechanisms other than orthodox geographical isolation may have been operative in the genesis of tropical faunas; this is especially true of the existence of vicariant forms in adjacent morphoclimatic domains.

A necessary condition for speciation studies is a broad understanding of the ecological features of the forms involved, and especially of their degree of fidelity to the major types of plant formations and of their place within a given formation. In the present paper I report data pertaining to the domain of the caatingas and to its relationships with the cerrado, and with the Atlantic and Amazonian forests.

The large domain of the caatingas (ca. 1 million square kilometers) has a polygonal core area occupying most of the states of Northeastern Brasil, the so-called "polygon of droughts": Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia and part of Minas Gerais. It is a semi-arid, highly xerophytic region, with a climate characterized not so much by the insufficiency of rainfall but rather by its extreme irregularity. The characteristic plant formation, "caatinga", is well defined floristically, physiologically and physiognomically. To the east the caatinga meets the Atlantic forest, with diverse modes of contact; in the remainder it is encircled by cerrados, and the contact is usually in the form of a mosaic of interdigitations and mutual enclaves. The caatinga also contains, sometimes deep in the core, enclaves of forest; these are of particular importance as they are floristic and faunistic refuges, where differentiation by isolation may be studied in process.

My work on the patterns of differentiation of Guiano-Brasilian lizards has taken me to the point at which I feel the need to raise at least some preliminary hypotheses about the geographico-ecological relationships of caatinga lizards. As a first approach I decided to assemble, at some ecologically homogeneous localities, large collections of the common animals, backed by information on their immediate ecology, basically the type of plant formation and the gross structural niche. A second step would be to correlate the data so obtained with the store of distributional information in the literature and collections. A third phase would include going back to the field to investigate specific problems raised in the preceding stages.

The field work on which this report is based was part of a broader program on the ecology of the semi-arid Northeast of Brasil, undertaken by the Brazilian Academy of Sciences. The state of Pernambuco was chosen for the first trip for a series of reasons. Relevant to the present context are: (i) there are reasonable geobotanical maps (Vasconcelos Sobrinho, 1941, 1949; Lima, 1960); (ii) there are some remnants, spared by sugar cane agriculture, of the Atlantic forest and of forested enclaves; (iii) the contact between caatinga and Atlantic forest is through a well defined transitional formation, the "agreste"; (iv) to the west there are good interdigitations of cerrado and caatinga.

We had little experience of the area, and the trip had to be a short one; thus its results were expected to be no more than a general feeling of the ground. It happened, though, that some interesting patterns emerged, even at this early stage, which seem to deserve publication.

FIELD WORK

(Map 1)

Two Museum parties followed each other in Pernambuco in 1971. The first (May 6 to May 28) was composed of myself and my daughter Mariana (herpetology) and José Luiz Moreira Leme (malacology); the second (June 4-27) of Hélio F. A. Camargo (ornithology), Francisca Carolina do Val (entomology) and José Leopoldo da Silva Filho (taxidermist). At different times we had the help of personnel of the Federal University of Pernambuco: Aracilda Pereira de Farias, Maria do Carmo Arcanjo Leal, Paulo Leal and Artur Galileu Miranda Coelho.

The first party worked on remnants of the Atlantic forest around Itamaracá (Engenho Amparo, Engenho São João and Igarassu) from May 6 to 12; in the agreste at Agrestina (May 14-18); in the caatinga at Carnaubeira (May 20-24), and Sítio dos Nunes (May 26-28). It was initially intended that the second group would follow the steps of the first; given, however, the very poor results on the coast, the second group started work at an inland locality, Água Azul, near Timbaúba (June 3-9). They also worked in Agrestina (June 11-17); their caatinga locality was the Fazenda Campos Bons (June 19-27), some 20 km southwest of Carnaubeira.

Francisca Carolina do Val, of the second party, generously employed a significant part of her time at Agua Azul in herpetological collecting. I am indebted to her for an excellent collection,



Map 1. Plant formations of Pernambuco (adapted from Lima, 1960) and collecting localities. For the area of the Atlantic forest, see comment in the text. Agua Azul is not shown, since it is very close (ca 9 km) to Timbaúba.

accompanied by very adequate field notes. She also obtained a small collection at Fazenda Campos Bons.

The system of field work varied according to the localities. In the Atlantic forest all the time was spent in the woods, collecting and observing. In the agreste and caatinga, where lizards are enormously more abundant, a "lizard market" was established by the first party. Actual field work was limited to traverses of the areas worked by the local (child) collectors, in order to check the general distribution of the common species. No attempt was made at studying the rarer forms that turned up in the market.

As said, the area of the caatingas is characterized by extreme year to year variability of rainfall. We were lucky in doing our field work during a late but good "winter" (rainy season), and the results were very rewarding.

ATLANTIC FOREST LOCALITIES

In the region of Itamaracá and Igarassu, on the coast, some small but relatively productive remnants of forest existed until recently. Lately, however, these have been felled to give place to sugar cane plantations, and the only wooded areas left are short and narrow fringes on the steep sides of low hills. Even these fringes have been culled of hardwoods and a small amount of firewood is currently extracted.

The relict woods at Agua Azul (part of the Cruangi sugar mill) are much larger, several kilometers across, with reasonable stands of left-over rain forest on some hills. The area where most of F. do Val's collecting was done was one of somewhat disturbed forest, with a number of clearings.

The present relicts of the Atlantic forest are separated by plantations, by scrub and possibly by expanding agreste vegetation.

CAATINGA AND AGRESTE

Lima (1960) and Vasconcelos Sobrinho (1941, 1949) consider only one phytogeographic zone, "zona da caatinga", with two subzones, "agreste" and "sertão". I prefer to follow Egler (1941) and Ab'Saber (1967; see also Vanzolini, 1970) who restrict the word caatinga to the core area of the domain (sertão) and consider the agreste as a transition zone between the caatingas proper and the Atlantic forest.

Caatinga vegetation is characterized by some conspicuous physiognomic features, especially summer deciduousness and a high proportion of cacti and other succulent and thorny plants. The soils are shallow, though not infertile. There are many outcrops of bare rock (granite, gneiss and Mesozoic sedimentaries), frequently in the form of extensive floors ("lajeiros"). Extensive descriptions of large tracts of the domain of the caatingas, with photographs and lists of species, are found in Luetzelburg (1922-1923). However, they must be interpreted with care, because the terminology is not in agreement with modern usage. A good ecological summary is given by Alvim (1949). Egler (1941) discusses sub-types and local facies of caatinga.

Agreste is, in Lima's works, a "mitigated caatinga". Rainfall is more regular, the soils deeper, and the vegetation considerably less xerophytic — especially cacti are much less conspicuous. Land

is not as valuable as in the Atlantic forest, but is economically much more productive than in the core of the caatingas, and so the agreste is rather heavily exploited. The area is divided into numerous small farms, adjacent fields being separated by hedges of an introduced plant, *Euphorbia tirocalis*, "aveloz". Along these hedges there is great concentration of the lizard fauna.

It is interesting to note that the term "agreste" as here used is relatively recent in the literature. Luetzelburg (1922-1923), for instance, uses it with an entirely different meaning, and fails to recognize the individuality of the belt in Pernambuco. In reality, this, the Pernambucan agreste, is the only segment mapped; even its continuation in Paraíba can only be ascertained, and very vaguely so, by interpretation of local descriptions and through indirect evidence.

Agrestina, our only agreste locality, lies 20 km south of the city of Caruaru, on a plain through which runs a seasonal stream; all the land is tilled and there is a dense network of hedges. Some kilometers to the north of Agrestina there are some low hills (Serra da Quitéria, Serra das Vertentes) where, because of the steepness of the ground, the vegetation is less disturbed and hence the lizards can be seen in a more natural setting.

In Map 1 Agrestina seems closer to the Atlantic forest than it actually is. It must be kept in mind that Lima's chart, on which ours is based, does not portray the present and actual distribution of the forest, but an idealized pristine distribution, based not only on historical data, but also on geomorphic and analogical criteria. Our collecting area in Agrestina was homogeneous agreste, quite safely away from any other types of plant formations. It must also be said that at Agrestina we collected probably all species of lizards hitherto recorded from the whole agreste area.

All 3 caatinga localities explored, Carnaubeira, Fazenda Campos Bons and Sítio dos Nunes, are in the area called by Lima "sertão central". The ground is sand or nude rock, and in all three localities low hills occur. The density of the vegetation varies. Field observations were made only at Carnaubeira, where the caatinga is exceedingly dense and thorny.

SYSTEMATIC ACCOUNT

Here I give a list of the species collected, with the available field notes. All the forest specimens were collected by ourselves, and are accompanied by notes. As said, in the agreste and caatinga the overwhelming majority of the lizards were brought in by children; however, we saw and collected an adequate number of these forms that are commented on. The number of specimens obtained (1572 in all) is given within parentheses. No bibliographical citations are given in this systematic part, as a recent catalog is available (Peters & Donoso-Barros, 1970).

Family Gekkonidae

Brida brasiliiana Amaral, 1935

Carnaubeira (9). Fazenda Campos Bons (1).

Coleodactylus meridionalis (Boulenger, 1888)

Água Azul (2).

In leaf litter in the forest, as usual (Vanzolini, 1972).

Gymnodactylus g. geckoides Spix, 1825

Carnaubeira (9). Fazenda Campos Bons (4).

Gymnodactylus geckoides darwinii (Gray, 1845)

Água Azul (1).

Under a log in the forest.

Lygodactylus sp.

Carnaubeira (161). Fazenda Campos Bons (4).

This is a still undescribed species on which I have commented before (Vanzolini, 1968). In Carnaubeira it was very common during the day, both in town and outside, on thorny hedges, made of different plants.

Phyllopezus p. pollicaris (Spix, 1825)

Carnaubeira (20). Sítio dos Nunes (4). Fazenda Campos Bons (2).

All the Carnaubeira specimens of this nocturnal gecko, as well as all but one from Sítio dos Nunes, were collected in abandoned houses. The other specimen was found during the day, in a rock crack on the top of a low rocky hill.

Family Iguanidae

Anolis fuscoauratus D'Orbigny, 1837

Itamaracá (1). Água Azul (2).

The Itamaracá specimen was in the forest, near the edge, on the ground; chased, it climbed a trunk about 15 cm thick and was caught at breast level. One of the Água Azul specimens was also found on the ground on leaf litter, and tried to climb a tangle of sticks.

Anolis punctatus Daudin, 1802

Água Azul (1).

Inside the forest.

Enyalius catenatus (Wied, 1821)

Água Azul (1).

Inside the forest, low on a tree trunk.

Iguana i. iguana (L., 1758)

Carnaubeira (1). Fazenda Campos Bons (1). Sítio dos Nunes (2).

The specimen from Carnaubeira was caught in very dry caatinga; one from Sítio dos Nunes near an irrigation pond.

Polychrus acutirostris Spix, 1825

Agrestina (3). Carnaubeira (1).

Collected on low trees.

Polychrus marmoratus (Linné, 1758)

Agua Azul (1).

I am commenting elsewhere, in this same journal, on the relationships between these species and on some interesting evolutionary problems they pose.

Strobilurus torquatus Wiegmann, 1834

Itamaracá (1). Agua Azul (8).

The Itamaracá specimen was found inside the forest, on a tree trunk about 15 cm thick, at a height of 1 m above ground. It tried to escape upwards. The throat was rusty; there were yellow areas on the lower belly, on the anal flap and on the lower surface of the thighs. This color pattern reminds one of *Plica umbra* and *Uracentron azureum* (Vanzolini, 1972).

There are notes on 6 Agua Azul specimens. All were in the forest: 4 on fallen logs, 2 on thick trees, at a height of approximately 2 meters.

Tropidurus semitaeniatus (Spix, 1825)

Agrestina (87). Carnaubeira (75). Serra das Vertentes (1). Sítio dos Nunes (11).

This is, as already noted (Vanzolini, 1972), strictly a rock lizard. It is very abundant in the facies locally called "caatinga de lajeiro", where not only boulders abound, but also broad flat floors of bare rock. On these lajeiros it coexists peacefully with *Tropidurus torquatus*. I spent 40 minutes observing a place where some 6-8 *torquatus* and 4-6 *semitaeniatus* were feeding together; I saw no conspicuous interactions between the two species.

Tropidurus torquatus (Wied, 1820)

Itamaracá (5). Agua Azul (11). Agrestina (126). Carnaubeira (82). Fazenda Campos Bons (1). Sítio dos Nunes (101).

It is well known that this is a very versatile lizard. In Itamaracá it was seen sunning itself on thick trunks on the edge of the forest; one specimen was caught 5 m inside the forest, on the ground.

In Agrestina and Carnaubeira it was very common on rock outcrops (with *T. semitaeniatus*, above) and in edificarian situations. It was not seen in the "general" Agrestina situation, i.e..

around *Euphorbia* hedges. I watched several lajeiros where it was present and saw no specimens enter the area from the surrounding sandy caatingas, or vice versa. It is striking that in this region *T. torquatus* does not frequent fences, one of its preferred habitats in the cerrados of Central Brasil.

Family Teiidae

Ameiva ameiva (Linné, 1758)

Itamaracá (3). Agua Azul (1). Agrestina (29). Carnaubeira (6). Fazenda Campos Bons (1). Sítio dos Nunes (5).

Ameiva is not as abundant in this area as in other open formations, where it is the dominant lizard (Vanzolini, 1972).

In Itamaracá it was seen in the open, in second growth, and occasionally inside the forest. In the agreste and caatinga it seemed to avoid rock outcrops, preferring sandy areas.

Anotosaura sp.

Agrestina (3).

This seems to be a new species, although rather close to the type of the genus, *A. collaris* Amaral, 1933. The specimens were forwarded to James R. Dixon, who is revising the group. I did not see the species in the field.

Cnemidophorus ocellifer (Spix, 1825)

Agrestina (45). Carnaubeira (250). Fazenda Campos Bons (2). Sítio dos Nunes (151).

This was the most abundant ground lizard in sandy areas, especially in the caatinga.

Gymnophthalmus multiscutatus Amaral, 1933

Agrestina (19).

This form is certainly a vicariant and possibly a subspecies of *G. rubricauda* Boulenger, 1902, from which it differs apparently only in the condition of the prefrontals and in scale counts.

I collected one specimen under a mat of dried cut grass, on the edge of a field. The remaining specimens were said to have been found in the hedges.

Kentropyx calcaratus Spix, 1825

Itamaracá (2). Agua Azul (6).

These Atlantic forest populations are widely disjunct from the Amazonian ones. The general ecology seems to be exactly the same (Vanzolini, 1972): the lizard is a heliophil of the forest, living mostly on the ground but climbing on fallen trees and vine tangles, in places where the sun comes through the canopy.

Stenolepis ridleyi Boulenger, 1887

Agua Azul (1).

Francisca do Val caught one specimen, on the ground, inside the forest at Agua Azul. The dorsal parts were very dark, and the belly intense orange. This seems to be the first specimen recorded after the original description; it shows a very curious anomaly, complete fusion of the scales on top of the head.

Family Scincidae

Mabuya mabouya (Lacépède, 1789)

Agua Azul (1).

Regarding the application of this name, see Rebouças-Spieker (in press).

The specimen was found on the ground, in the forest.

Mabuya heathi Schmidt & Inger, 1951

Agrestina (286).

Abundant along the hedges, on the ground.

Family Amphisbaenidae

As usual, no ecological data are available on amphisbaenids, except that they were found crawling along, during the day.

Amphisbaena alba L., 1758

Agrestina (3).

Amphisbaena carvalhoi Gans, 1965

Agrestina (2).

Amphisbaena pretrei Duméril & Bibron, 1839

Agrestina (15).

Amphisbaena vermicularis Wagler, 1824

Floresta (1).

Floresta (do Navio, not dos Leões) was not one of our collecting localities, but, passing through, F. do Val picked up the present specimen dead on the street. The area is extremely dry caatinga, through which passes the large seasonal river Pajeú.

FOREST FORMS

Twenty seven species of lizards in all were obtained, 12 of which in Atlantic forest localities. Three will be omitted in what follows: *Ameiva ameiva* and *Tropidurus torquatus* are not forest animals; the *Mabuya* of the *mabouya* species group was found (one specimen) inside the forest, but other specimens have been collected in the area in open situations and I am unsure both about the taxonomic situation and the ecological preferences of the populations involved. The remaining 9 forms seem to be strictly forest animals, and I will briefly comment on their geographical patterns.

The distribution of *Coleodactylus meridionalis* is very special and must be considered separately; it is an extremely spotty distribution, which I have discussed elsewhere (Vanzolini, 1957, 1968a). It is sufficient to say here that it seems to be a relict from a time when the area of forests in Brasil was much larger and more continuous than now, and that the lizard has been able to survive in small relictual woods. The fact that populations are known north of the Amazon Valley, glaringly separated from the southern members by the area of a more advanced congener, *C. amazonicus*, bears witness to the relatively old age, in terms of paleoclimatic cycles, of the original continuous distribution.

The remaining distributions must be analyzed in terms of relationships with the hylaea and with the open formations. The data are summarized in Table 1.

A note should be made on the use of the word "vicariant" in the table. This word means, etymologically, a substitute or replacement, and has been used in ecology and zoogeography with nuances of meaning, but mostly (e.g. Hesse, Allee & Schmidt, 1937) referring to the situation where "the corresponding species of a genus or the subspecies of a species represent each other in the corresponding environments of the two areas, without occurring anywhere together". I prefer to extend the term also to the case in which the taxa replace each other in different morphoclimatic domains. Emphasis is thus placed on occurrence in a different geographico-ecological unit, against complementarity within the same continuous unit (in our case morphoclimatic domain). Ambiguity is easily avoided by mention of one of the areas of vicariance. In the present case, since we are dealing primarily with Atlantic forest forms, "vicariant in the hylaea" and "vicariant in open formations" seem to me unambiguous and useful expressions.

Table 1 shows that two monotypic genera are endemic to the Atlantic forest. *Stenolepis ridleyi* is so far known only from Pernambuco. Of *Strobilurus torquatus* there were previously Alagoas, Bahia and Espírito Santo materials and a single Pernambuco specimen, collected at Igarassu ("Iguarasse", Boulenger, 1888). I suspect the latter is British Museum number 88.4.18.6, cited by Etheridge in his generic review (1968: 62) as from "Pernambuco, no specific locality". It is now clear that the species is not rare in the right kind of habitat in Pernambuco.

As to the groups that occur both in the hylaea and the Atlantic forest, the *Anolis fuscoauratus* species group extends at least from

Table 1

Distributional relationships of Pernambuco Atlantic forest
lizards with other relevant areas

Atlantic forest	Also in the hylaea	Vicariant in the hylaea	Vicariant in open formations
<i>Strobilurus torquatus</i>	-	-	-
<i>Stenolepis ridleyi</i>	-	-	-
<i>Anolis fuscoauratus</i>	+	-	-
<i>Anolis punctatus</i>	+	-	-
<i>Kentropyx calcaratus</i>	+	-	+
<i>Polychrus marmoratus</i>	+	-	+
<i>Enyalius catenatus</i>	-	+	-
<i>Gymnodactylus g. darwini</i>	-	-	+

northwestern Colombia to the state of Rio de Janeiro; the status of the eastern Brazilian populations needs to be ascertained. E. E. Williams and I are working on the species group.

Anolis punctatus ranges from western Amazonia to the coast of São Paulo (Williams & Vanzolini, 1966; Vanzolini, 1972).

Kentropyx calcaratus is said by Peters & Donoso-Barros (1970) to occur in the "Northern part of Amazonian basin of South America". It certainly does occur there, but also to the north and much to the south. The type locality itself is in Maranhão (Peters & Donoso-Barros, 1970). The southernmost records I know of are Misiones Mosetenes in Bolivia (Boulenger, 1898) and Espírito Santo in eastern Brasil (specimens in our collection). Previous published Atlantic forest records are by L. Müller (1927: Penha, near Cabo Branco, Paraíba) and Schmidt & Inger (1951: Recife).

The systematics of *Kentropyx* in the Amazon is confusing. Several names are currently accepted, but none of them has been submitted to critical analysis. The situation in the open formations is not better — in fact it is worse, because Amazonian specimens in museums are probably sufficient for a review, but much remains to be collected in Central Brasil and southern Mato Grosso before the open formation forms can be studied.

Polychrus marmoratus, as *Kentropyx calcaratus*, is widespread in Amazonia and forests to the north; along the Brazilian coast it reaches S. Paulo. The vicariant open formation species is *Polychrus acutirostris* (see the systematic account).

Enyalius catenatus is limited to the Atlantic forest, but the genus, as reviewed by Etheridge (1969), has one Amazonian species, the seemingly rare and somewhat aberrant *Enyalius leechii* of the Tapajós valley (Vanzolini, 1973).



Map 2. Approximate distribution of *Gymnodactylus geckoides*. Triangles, *G. geckoides*; squares, *G. amarali*; circles, *G. darwini*.

Gymnodactylus geckoides, forest and caatinga (Map 2)

Many years ago (Vanzolini, 1953) I studied the geographical differentiation of this lizard, and defined three ecologically vicariant subspecies, *geckoides* in the caatinga, *amarali* (a rather variable form) in the cerrado, and *darwinii* in the Atlantic forest. The latter is sharply distinguished from the others by color pattern and meristic characters. I chose at the time to call them subspecies because they were closely related allopatric forms, but no proper study of intergradation was made.

The materials I used in 1953 left a broad geographical gap, 6.5 degrees of latitude wide, between the northernmost locality of *darwinii* (Sooretama, in Espírito Santo) and the southernmost one of *geckoides* (Salvador in Bahia). Now Francisca do Val has collected *darwinii* in a typical situation (within a rotten log in the forest) at Agua Azul, at the same latitude as the nearest *geckoides* locality, Custódia, 300 km to the west.

The Agua Azul specimen agrees perfectly with the available southern samples (Vanzolini, 1953): it has 2 tubercles on a paramedian row, 16 rows of ventrals and 15 lamellae on the fourth toe. Additionally, it shows the very characteristic nuchal band of *darwinii*. On the other hand, the present caatinga specimens agree with previous *g. geckoides* samples: 42-48 tubercles on a paramedian row, 6 tubercle rows, 19-23 ventrals, 15-18 lamellae.

Thus, there is now ample latitudinal overlap between the two forms, and *darwinii* 11.5 degrees of latitude north of the previously known range keeps its identity perfectly well.

It will be discussed below that not one single gecko was found among the several hundred lizards collected at Agrestina. I consider this a strong indication of the absence of *G. geckoides* in the agreste area investigated; the two forms are probably not in contact at this latitude. If it is proved that this is the case, one must look for evidence of contact further south in Bahia, where the transitional plant formation between caatinga and Atlantic forest is a peculiar type of dry forest ("mata de cipó", vine forest), very different from the agreste (Tricart, 1958).

Even if the two forms are found to be in contact, this may happen in such a way that the possibility must be faced that we have actually two parapatric species, *darwinii* on one side and *geckoides* plus *amarali* on the other. A good study of intergradation and the use of experimental methods are necessary for a firm conclusion. Neither being presently available, nor the materials for them, here I treat *Gymnodactylus* in two ways: in the present context as a species with 3 races, and below, in the study of caatinga-agreste relationships, *geckoides* and *amarali* together, with *darwinii* omitted.

A note on *Iguana iguana*

The scarcity (perhaps absence) of *Iguana iguana* in the Atlantic forest must be commented. *Iguana* reaches Paraguay on the west (Krieg, 1936; Hellmich, 1960) and northern Minas Gerais on the east (Griffin, 1917; several skins in our collection). In this trip we obtained specimens only in the caatinga, where it has been frequently collected, but there are numerous records from the

cerrado, and some from the agreste. From the area of the Atlantic forest, however, I know of no recent specimens and of only two references. Boulenger (1885) cites one old specimen from Recife; L. Müller (1927), in the list of Bresslau's collection, cites 4 Pernambuco specimens, with the note (in the introduction of the paper) that "Pernambuco" really meant Recife.

Recife is the capital and port of Pernambuco, and thus the British Museum record might perhaps be interpreted as a "shipping locality".

On the other hand, the Atlantic forest area where Bresslau worked (Dois Irmãos) is a small one in the city, and it is possible that his specimens were caught elsewhere and brought to him. In addition, it would be possible to raise doubts about two or three of his specimens, as he was away from Recife, in the interior, on the day 2 of them were collected, and hadn't arrived there yet on the date of the third one (Bresslau, 1927). Relatively intensive recent collecting in the area has failed to turn up any specimens. But, conceding that all or some of these Recife records are authentic forest records, they are still very meager compared with the abundance of the species in the other types of environment. It is puzzling to me that an animal that is extremely common all over Amazonia, that at the same time flourishes in the harshest environment that separates the hylaea from the Atlantic forest, that furthermore reaches in eastern Brasil a latitude of 16 degrees South (remember the forest extends from 7° to 27°) still remains very rare or possibly does not even exist in the Atlantic forest.

Of the 8 lizard species of Table 1, 4 occur also in Amazonia, and one has a congener there. These 5 species extend in the Atlantic forest much to the south of Pernambuco. Of the remaining 3, one is so far endemic, and the other 2 extend considerably to the south. It is quite clear that the ensemble represents one single forest fauna stretched out along more than 30 degrees of latitude, and that the gap that now separates the hylaea from the Atlantic forest has not always existed; on the contrary, at some recent time traffic must have been easy between the two areas.

It is debatable whether this traffic obtained through a sizable continuous body of forest, or through gallery forest corridors longer and thicker than today. I am strongly inclined to accept broad continuity, because the number of elements in common is large. Of course it is possible that both types of relationship existed, in different climatic cycles.

If we compare (Table 2) the forest lizards, 21 species in all, that occur in similar environments in Belém and Pernambuco, the following pattern emerges:

1. Nine species that occur in Belém do not occur in Pernambuco and have no close relatives there: *Gonatodes humeralis*, *Lepidoblepharis festae*, *Thecadactylus rapicauda*, *Anolis ortonii*, *Plica umbra*, *Alopoglossus carinicaudatus*, *Arthrosaura kockii*, *Leposoma percarinatum* and *Prionodactylus oshaughnessyi*.
2. Three species that occur in Pernambuco do not occur in Belém and have no close relatives there: *Gymnodactylus geckoides darwini*, *Strobilurus torquatus* and *Stenolepis ridleyi*.

3. Six species are common to the two areas: *Anolis fuscoauratus*, *Anolis punctatus*, *Polychrus marmoratus*, *Kentropyx calcaratus*, *Tupinambis* sp., and *Mabuya mabouya*.

4. One genus, *Coleodactylus*, has a different species in each area.

5. *Enyalius* does not occur in Belém, but has a congener farther west in Pará.

So 8 out of 20 forms (40%) are either common to the two areas or represented by close relatives. I consider this a large proportion,

Table 2

Forest lizards occurring in Pernambuco and in similar environments
at Belém (data in part from Crump, 1971)

	Pernambuco	Belém
<i>Gonatodes humeralis</i>	-	+
<i>Lepidoblepharis festae</i>	-	+
<i>Coleodactylus meridionalis</i>	+	-
<i>Coleodactylus amazonicus</i>	-	+
<i>Gymnodactylus geckooides darwini</i>	+	-
<i>Thecadactylus rapicauda</i>	-	+
<i>Anolis fuscoauratus</i>	+	+
<i>Anolis ortonii</i>	-	+
<i>Anolis punctatus</i>	+	+
<i>Enyalius catenatus</i>	+	-
<i>Plica umbra</i>	-	+
<i>Polychrus marmoratus</i>	+	+
<i>Strobilurus torquatus</i>	+	-
<i>Alopoglossus carinicaudatus</i>	-	+
<i>Arthrosaura kockii</i>	-	+
<i>Kentropyx calcaratus</i>	+	+
<i>Leposoma percarinatum</i>	-	+
<i>Prionodactylus oshaughnessyi</i>	-	+
<i>Stenolepis ridleyi</i>	+	-
<i>Tupinambis</i> sp.	+	+
<i>Mabuya mabouya</i>	+	+

especially if some circumstances are taken into account. First, an area effect: the Belém forest is part of the vast hylaea, and the Pernambuco belt in its best days was never quite 100 km broad. More, the Pernambuco forest fauna we know is that of the very depleted remains of the primitive area, as this was one of the first regions of Brasil to be opened for agriculture, and collecting there started relatively very late. If we add the difference in latitude, we must conclude that the number of elements in common is too large to be explained by gallery forest corridors, with their unavoidable filtering effects.

As to the location of the forest bridges, several possibilities exist, and it will be a fascinating task to look for their traces.

CAATINGA AND AGRESTE

Table 3 lists the 16 lizard species obtained in the caatinga, in the agreste, or in both, scored as to relative abundance.

The limited time spent in the field and the lizard-market system did not permit anything remotely resembling an accurate estimation of species abundance, so I am using a rough and purely impressionistic approach, and keeping my analysis within the bounds of this approach.

Four crosses denote lizards constantly seen in large numbers, i.e., those that, after a short time, we had to stop buying, because the task of preparing them would become unmanageable, and because we had to stimulate the collecting of less easily obtainable forms. These four-cross species represent the truly dominant animals. One cross indicates species only occasionally brought in. Two crosses indicate moderately abundant species, within a rather ample range, as reference to the figures in the systematic section will show. Finally, 3 crosses were reserved for *Mabuya heathi*, that turned up in large numbers but only after we stopped buying the most common forms, and were paying an attractive price for it.

Parentheses in the table emphasize extra difficulty in meaningfully scoring a species for abundance. *Polychrus*, for instance, is a procryptically colored twig and probably crown animal, that spends long periods motionless and moves sluggishly (in places it is nicknamed "sloth beast", in others "blind lizard"). The number of specimens obtained in different localities varies enormously, and one never knows whether that reflects actual abundance, or seasonal, or even local variations in behavior; numbers of specimens randomly collected probably bear little relationship to actual abundances.

In the case of the amphisbaenids, as of all subterranean animals, again random collecting is chancy, and abundance practically impossible to estimate.

Table 3 shows 3 groups of animals: present in either and in both formations.

Three of the 5 species present in both environments — *Tropidurus torquatus*, *Cnemidophorus ocellifer* and *Ameiva ameiva* — are very common wherever they occur, which is in open formations in general: I explicitly include the cerrados and the open formations in Amazonia and north of it (where *Cnemidophorus* is represented by *C. lemniscatus*, see Vanzolini, 1970a). This is also the case of

Table 3

Occurrence and observed relative abundance of lizards
in caatinga and agreste

	Caatinga	Agreste
<i>Tropidurus torquatus</i>	+ + + +	+ + + +
<i>Tropidurus semitaeniatus</i>	+ + + +	+ + + +
<i>Cnemidophorus ocellifer</i>	+ + + +	+ + + +
<i>Ameiva ameiva</i>	+ +	+ +
<i>Polychrus acutirostris</i>	(+)	(+)
<i>Lygodactylus</i> sp.	+ + + +	-
<i>Phyllopezus p. pollicaris</i>	+ +	-
<i>Gymnodactylus g. geckoides</i>	+ +	-
<i>Briba brasiliiana</i>	+ +	-
<i>Iguana iguana</i>	+ +	-
<i>Amphisbaena vermicularis</i>	(+)	-
<i>Mabuya heathi</i>	-	+ + +
<i>Gymnophthalmus multiscutatus</i>	-	+ +
<i>Amphisbaena pretrei</i>	-	(+ +)
<i>Anotosaura</i> sp.	-	+
<i>Amphisbaena carvalhoi</i>	-	(+)

Iguana iguana, as explained above. *Polychrus acutirostris*, probably the most common arboreal lizard in open formations, is a species of the great diagonal to be discussed below. *Polychrus marmoratus* is left for another paper, as it involves many matters foreign to the present argument.

Tropidurus semitaeniatus is not known from the cerrado; it is very abundant in the rocky facies both of caatinga and agreste.

Turning to the species that were obtained in only one of the formations, we omit from the discussion *Amphisbaena vermicularis*, widely distributed in caatinga, agreste, cerrado and forest (Gans & Amdur, 1966). This is an animal that needs further study.

This species apart, we see that 4 species of geckos were collected in the caatinga, while instead no geckos, but one skink, two microteiids and two amphisbaenids were collected in the



Map 3. Approximate distribution of *Lygodactylus* sp.

agreste. This is a stark and striking pattern, but one that, given the wide geographic range of many of the forms involved, cannot be taken at face value, but has to be analyzed in terms of the separate elements. Using materials in this museum's collection and data from the literature, I shall attempt to study the general distribution of the forms in question, keeping in mind that some locality records permit reliable inferences about the ecology of the animal, while others have little information from this viewpoint.

The 4 geckos found in our caatinga localities have broad distributions (Vanzolini, 1968, 1968a), but are not known from any agreste or coastal locality.

The distribution of *Lygodactylus* sp. (Map 3) continues to be disjunct. We have now 4 localities on the northeast: Senhor do Bonfim and Barreiras (Vanzolini, 1968) and the two new ones of Fazenda Campos Bons and Carnaubeira. There are now several hundred specimens from the general area. On the southwest, besides the previous locality of Urucum, we have now a not very well preserved juvenile from S. Luis de Cáceres, on the upper Rio Paraguay, Mato Grosso. I have for the purposes of this paper re-examined these two and only southwestern specimens, and, as far as I can see, they all belong to the same species.

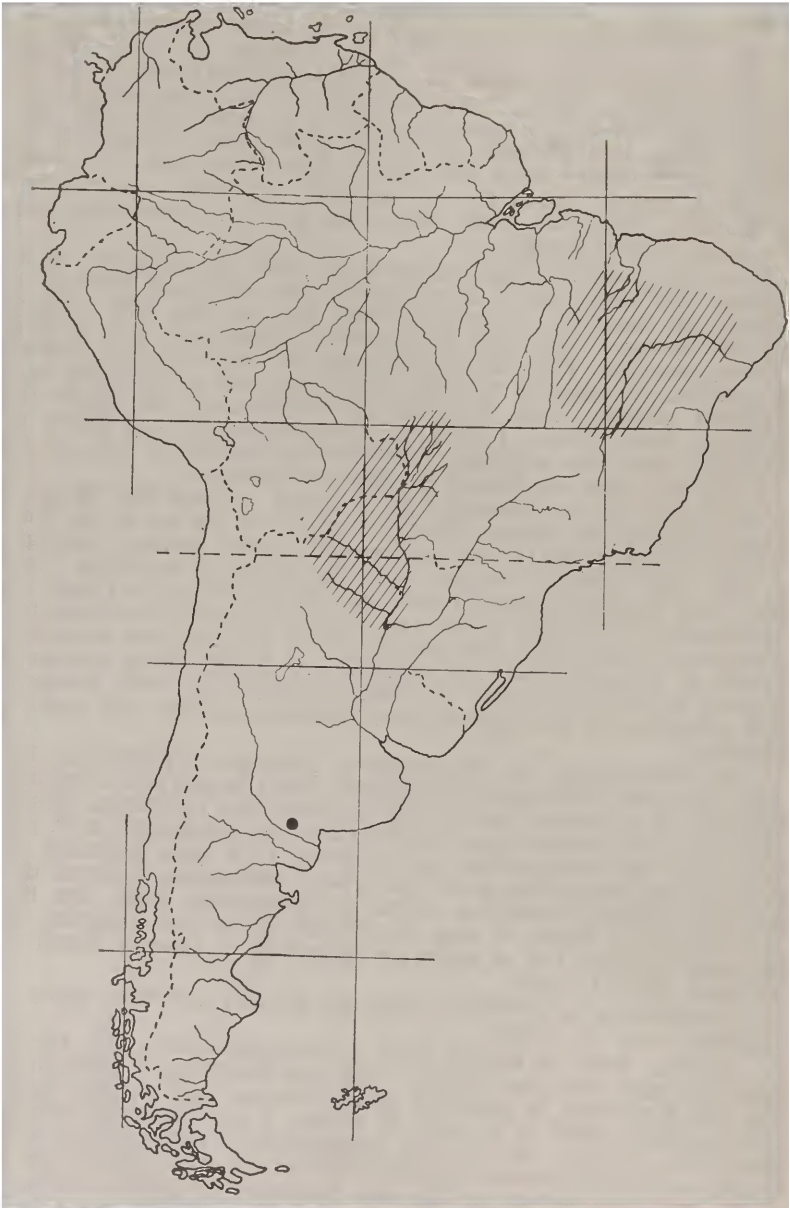
This type of distribution I have called in 1963 the "diagonal of open formations". Before that, and unnoticed by me at the time, Schmidt & Inger (1951) had stressed this same pattern, calling it (p. 440) "the savanna corridor", or "the chain of savannas extending from the Paraguayan Chaco and Mato Grosso to Ceará and Pernambuco". The true limits are a little different (northwestern Argentina to Maranhão), but this is trivial and the idea essentially correct; it is regrettable that Schmidt and Inger's term cannot be adopted, as "savanna" may be used (although not very properly) with reference to the cerrado, but never to cerrado and caatinga together.

The distribution of *Phyllopezus pollicaris* (Vanzolini, 1968, 1968a; Gallardo, 1971; Sage & Capredoni, 1971) is still more extensive (Map 4), as it extends beyond the diagonal into La Pampa, eastern Argentina. The relationships between the two subspecies of *P. pollicaris* have not been worked out properly. It is quite probable that they are real subspecies, given the type of differences between them and their relative constancy within the respective areas. But here, as in all other cases of taxa distributed along the diagonal belt, the need is badly felt of adequate collecting in Central Brasil and southern Mato Grosso.

Gymnodactylus geckoides does not go very far west along the diagonal: only to Goiás.

Finally, *Briba* is known from 2 localities outside the Pernambuco caatinga: the type locality (Rio dos Pandeiros, a tributary of the São Francisco in northern Minas Gerais) and Jatobá, said in the specimen label to be also in Minas. I am, however, doubtful about this locality, as it could be Jatobá in Pernambuco, which would have very different implications. On the other hand I am not sure about the ecology of Rio dos Pandeiros: I do not know the area, but there is both cerrado and caatinga in it.

So *Briba* may finally turn out to be either another diagonal species, or a true caatinga form; obviously, better data are needed.



Map 4. Approximate distribution of *Phyllopezus pollicaris*. On the northeast, *pollicaris*; in the southwest, *przewalskii*; circle, Loventuel, La Pampa.



Map 5. Approximate distribution of open formation *Gymnophthalmus*.
Circles, *G. multiscutatus*; hatching, *G. rubricauda*.

As to the forms obtained only in the agreste, *Amphisbaena carvalhoi* is known from only two localities, Poção and Agrestina. This I find still too slim an inductive basis for any decision.

Gymnophthalmus multiscutatus (Map 5), taken either as a vicariant or a subspecies of *G. rubricauda*, has a distribution extremely similar to that of *Phyllopezus pollicaris*, and presents the same type of problems of coverage in Central Brasil and Mato Grosso. We have in our collection specimens of *multiscutatus* from Ceará (Açudinho, near Baturité), Paraíba (Açude Soledade; Umbuzeiro; Piancó), Pernambuco (Pesqueira; Agrestina) and Bahia (Senhor do Bonfim, the type locality). We also have one specimen, apparently the northernmost one, of *G. rubricauda* from near Três Lagoas, Mato Grosso; the remainder of the distribution of this form can be gathered from Gallardo (1951, 1969) and Hellmich (1950). We cannot be sure that *G. multiscutatus* does not occur in the caatinga. While Pesqueira, Agrestina, Açude Soledade, Umbuzeiro and Baturité are certainly not caatinga, Piancó almost certainly is. The type locality does not permit reliable inference, as it is in an area of complex interdigitations (Tricart, 1958). As a further note on *Gymnophthalmus*, two Amazonian forms are known, *lineatus* (L.) and what is currently called *speciosus* (Hallowell, 1961).

The *Anotosaura* from Agrestina is so far known only from the present small series. If we take into account *A. collaris*, from Senhor do Bonfim, the distribution comes to resemble that of *Gymnodactylus*, *Briba* and *Gymnophthalmus multiscutatus*. A third, very distinct, species of *Anotosaura* has been collected recently in central Minas Gerais (also forwarded to J. R. Dixon for review), and this locality would tend to confirm the general "short diagonal" pattern.

Finally, *Mabuya heathi* and *Amphisbaena pretrei* show another and very distinct type of distribution: they occur on the northeastern coast, in the agreste and in the cerrado, but so far not in the caatinga.

Mabuya heathi (Map 6) was described from Ceará (Fortaleza), Rio Grande do Norte (Baixa Verde; Ceará Mirim) and Paraíba (Independência, the present Guarabira). We have specimens from Maranhão (Itapicuru-Mirim; Barra do Corda), Ceará (Pacajus; Coluna, near Justiniano Serpa; Itapipoca), Paraíba (Mamanguape), Pernambuco (Ponta de Pedras; Recife; Agrestina; Pesqueira), and Alagoas (Quebrangulo). Extremely diversified plant formations are involved, but definitely not caatinga. In fact, a search of the literature and of our collection failed to reveal any specimens of the genus *Mabuya* from the domain of the caatingas.

As to *Amphisbaena pretrei*, supplementing Gans's (1965) data with two further specimens from our collection, we have: Rio Grande do Norte (Natal; Lagoa Papará), Paraíba (Campina Grande; João Fessoa), Pernambuco (Ponta de Pedras; Recife; Igarassu; Pesqueira; Poção, Agrestina), Alagoas (Maceió), Sergipe (Cotinguiba; Maruím), Bahia (Queimadas), Minas Gerais (Rio Arassuaí). One specimen from "Rio de Janeiro: coast of (?)" in the Vienna Museum, cited by Gans (1965), I am inclined to discard. Among all these localities only one, Queimadas, is in the general domain of the caatingas, but the immediate ecology is not certain, as the area is diversified.



Map 6. Approximate distribution of *Mabuya heathi*.



Map 7. Approximate distribution of *Amphisbaena pretrei*.

DISCUSSION

The distributional patterns described above are based, on the ecological side, on large series from a small number of localities; on the geographical side, in a majority of cases, on a reasonable number of reliable records, given that the forms involved are common or relatively so, and easy to identify, several of them having been recently reviewed. I think they permit a first approach to the problem of what, zoogeographically speaking, the caatinga and the agreste are.

It is quite apparent that the caatinga, in spite of its strong ecological personality, does not harbor an individualized lizard fauna (Vanzolini, 1963). Of the species included in this study only one, *Tropidurus semitaeniatus*, may be called a caatinga lizard. The other possible case, *Briba brasiliama*, remains open.

What really exists is a fauna of the open formations, specifically of the great NE-SW diagonal belt, of which *Lygodactylus* sp., *Phyllopezus pollicaris*, *Gymnodactylus geckooides* (*g. geckooides* plus *g. amarali*), *Gymnophthalmus multiscutatus* (plus *rubricauda*), *Anotosaura* sp. (plus *collaris*), *Polychrus acutirostris*, *Cnemidophorus ocellifer*, and, eventually, *Briba brasiliama*, are members.

As we turn to the agreste we see that, from the viewpoint of lizard distribution it is not transitional between the caatinga and the Atlantic forest, but rather between the caatinga and the open coastal formations to the east and the cerrados to the north, as clearly indicated by *Mabuya heathi* and *Amphisbaena pretrei*. It is possible that this role of the agreste be a recently acquired one, consequent to the destruction of the Atlantic forest and its substitution by cultural steppe, scrubby second growth, and possibly by expanding agreste vegetation.

A possibility remains of an endemic agreste species, *Amphisbaena carvalhoi*. Even if this comes to be proved, this case should not be given too much weight, as narrow distributions in *Amphisbaena* are common, and this would be rather a local than a specifically agreste phenomenon.

We must now turn to Table 3, and analyze the striking patterns of mutual exclusion there shown. I see no gross ecological reason for the absence in the agreste of geckos that are abundant both in caatinga and cerrado. I do not think their absence can be explained in terms of insufficient negative evidence, because the collections are sizable. I propose that the most plausible explanation follows from the rather obvious fact that a transitional zone even when transiently "over-populated", i.e., harboring more species than either one of the primary areas, simply cannot accommodate *all* the species of both, and that some will have to be excluded. This would have two consequences of interest.

One is that, as the type of contact between morphoclimatic domains varies from place to place, as does the ensemble of interacting species, a strong chance element is to be expected in the choice of the forms excluded, and consequently that the faunal composition of transitional belts will show a marked degree of local variation. The diverse contacts of the caatinga with the surrounding areas, when studied, must perforce reveal a pattern of this type.

Another consideration is that transition belts may come to reverse roles, functioning first as bridges and then as barriers between populations of the same species that occupy more than one plant formation. Imagine that one species from an open formation has invaded a forested area through the intermediate transitional belt, where it coexists with forms otherwise limited to the open formation or to the forest. Any change in conditions may result in chance extinction within the belt. One victim may happen to be the local population of the species that is both within and outside the forest, which will then be split into two population narrowly but effectively separated. This could eventually lead to what has been called parapatric speciation.

Returning to the mutual exclusions in Table 3, the case for the geckos, backed by good collections, seems to be stronger than that for the microteiids. These now collected in our area seem to skip the caatinga. Further field work may show that they in fact live in agreste and caatinga, and that their absence in the present collection has no zoogeographical weight. On the other hand, if they turn out to be actually absent from the caatinga, or restricted to small favorable pockets inside it, the simplest hypothesis to explain their distribution would be that they originated in the Central Brazilian cerrado and reached their present range in times of milder climates, when more favorable conditions prevailed in the area of the present sertões. Alternatively, a circuitous route around the edge of the caatingas from the north would also be feasible; this would explain the case of *Gymnophthalmus*, but not that of *Anotosaura*, not known from the northern cerrados.

Thus it seems clear that the cases of mutual exclusion are not all part of a single pattern, rooted in competition, but are due to convergence from a variety of basic situations through a diversity of mechanisms.

CONCLUSIONS

We started with collections from a few ecologically well defined localities and followed the distribution of the species present, with basis on museum specimens actually seen and literature records thought to be reliable.

The following conclusions are drawn, to be tested as working hypotheses:

1. The Atlantic forest lizard fauna of Pernambuco is a latitudinal element of a single general forest fauna, reaching from the Amazon to Rio Grande do Sul. It is thought that there was broad continuity between the Atlantic and Amazonian forests in relatively recent times.
2. There is no lizard fauna characteristic for the caatingas. From the viewpoint of lizard distribution, the caatingas are part of a great diagonal belt of open formations extending from northwestern Argentina to Maranhão.
3. The agreste, although phytogeographically transitional between the caatinga and the Atlantic forest, does not function as such for

lizards. It is in fact transitional between the caatinga and other open formations to the east and to the north. This may be a recent pattern, consequent on the destruction of the Atlantic forest.

4. The absence from the agreste of forms (such as the geckos) that would seem ecologically suitable, since they occur in both caatinga and cerrado, is more probably explained by an insufficiency of carrying capacity of the agreste. If this explanation is valid, two possible consequences may be thought of: (i) great local variations in the faunistic composition of transitional belts and (ii) the possibility that transitional belts may come to function as barriers between populations of the same species occurring on both sides of the belt: a sort of gate effect.

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Top, agreste at Agrestina, showing rock floor (lajeiro). Habitat of *Tropidurus semitaeniatus*. Bottom, caatinga at Fazenda Campos Bons, near Carnaubeira. (Both photographs courtesy of H elio F. A. Camargo).

