

Papéis Avulsos de Zoologia

PAPÉIS AVULSOS ZOOL., S. PAULO, 29 (16): 111-119

12.IV.1976

ON THE LIZARDS OF A CERRADO CAATINGA CONTACT: EVOLUTIONARY AND ZOOGEOGRAPHICAL IMPLICATIONS (SAURIA)

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ABSTRACT

A field study of the lizards of an area of complex but sharp contacts between cerrados and caatingas confirms the idea that the caatingas have not a characteristic lizard fauna, but only a subset of the general fauna of the great cis-Andean diagonal of open formations. It is proposed that three mechanisms contribute to this homogeneity: (i) faunal exchange through interdigitations and small enclaves of cerrado and caatinga; (ii) substantial gene flow due to the large portion of the periphery of the domain of the caatingas occupied by this type of contact; (iii) turbulent mixing of faunas during climatic cycles, with complementary expansion and retraction of caatingas and cerrados.

INTRODUCTION

In a study of the ecological and geographical relationships of caatinga lizards (Vanzolini, 1974), I concluded that "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".

This is an important fact, and hard to explain *prima facie*, since cerrados and caatingas have practically nothing in common besides being open formations (Vanzolini, 1970). The morphoclimatic domain of the cerrados is fundamentally a mesic one, while the caatingas are characterized by extreme climatic irregularity, in frequent disaster years presenting a combination of very high temperatures and practically zero rainfall.

Naturally, these contrasting climatic regimes determine very distinct types of vegetation, thus enhancing the differences between the two areas from the viewpoint of animal life.

In order to verify and if possible extend the results of the previous work, I studied the lizards of an area of contact between cerrados and caatingas. This resulted in a confirmation of the original idea and in the proposal of a simple mechanism to explain the homogeneity of the lizard fauna of the two domains.

THE AREA

On the advice of Aziz N. Ab'Saber I chose the area around Valença do Piauí (ca. $6^{\circ}25'S$, $41^{\circ}45'W$) as the test site. This is the SSE sector of the Parnaíba Basin, on the backslope of the Serra Grande (locally Serra de Ibiapaba) escarpment, an area of tilted plateaux, consisting predominantly of Lower and Middle Devonian sandstones. The town of Valença is on the valley of the Rio Sambito, a tributary of the Poti. North and south of the town are two low mesas, Serra do Batista and Serra das Missões, maintained by the relicts of a formerly widespread but at present much dissected Cretaceous cover. These mesas should be more properly considered as cuesta outliers, but the regional dip of the Cretaceous strata is so little that they are practically table-like.

The area has been surveyed by "Projeto Radam" (see "Brasil" in the references).

I worked along the roads from Valença to Picos, to Teresina and to Pimenteiras, between 30 and 50 km in each direction (Map 1). Cerrados occur on all levels of the landscape, especially, as usual elsewhere, on top of the mesas (chapadas). In the neighborhood of Valença, typical caatingas, with cacti and other characteristic plants, were seen only on the Devonian sandstone. These caatingas vary from very sparse, over rock floors, through the usual types of semi-arboreal and arboreal caatingas, as seen in the core of their morphoclimatic domain, to patches of "agreste", i.e., much less xerophytic communities (Vanzolini, 1970).

Cerrados on the lower levels have usually a dense grass cover, a dispersed shrub layer and a weak arboreal stratum. On top of the mesas they are much more vigorous.

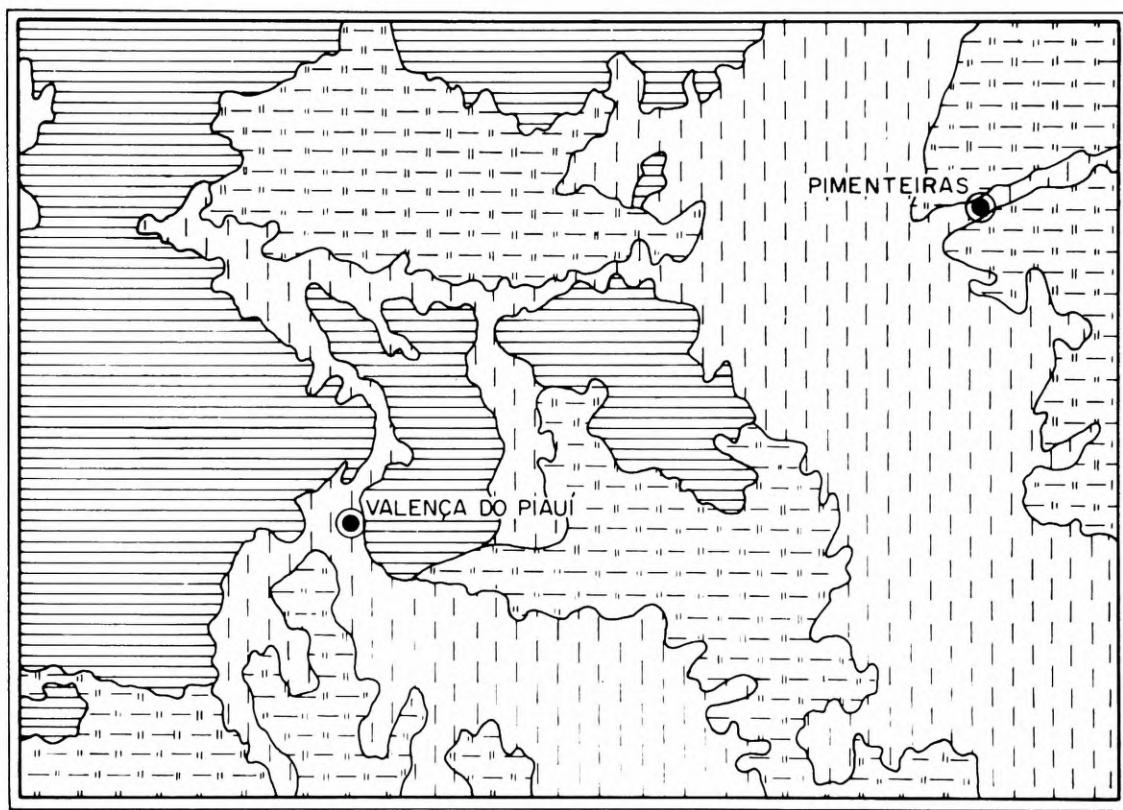
FIELD WORK

As cerrados predominate in the area, and the city of Valença do Piauí, where we stayed, is surrounded by them, I decided to start by assembling as rapidly as possible, by means of a "lizard market", a collection of cerrado lizards. Next I would check the distribution in caatinga and cerrado of the forms thought to be relevant.

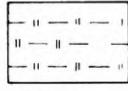
Response of the Valença children to the lizard market was enthusiastic. On the second day more than 700 specimens were brought

in, and we had to stop buying the common forms. After the third day there were no novelties, and in less than a week I had a fair idea of the fauna and of what to look for.

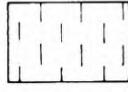
After the basic collection was assembled, I checked the presence of the common animals in two places in the cerrado: a few kilometers south of Valença on the road to Picos, and 30 kilometers northwest of Valença on the road to Teresina. Next I searched two caatinga-cerrado contacts until I saw all the relevant species; one place was about 35 km northwest of Valença, on the road to Teresina, the other 15 km northeast of town on the road to Pimenteiras.



Cerrados without caatinga enclaves



Cerrados with caatinga enclaves on the
mesa levels



Cerrados with caatinga enclaves on the
lower levels

Map 1. Interdigitation of cerrado and caatinga in the study area. Adapted from Projeto Radam, Levantamento de Recursos Naturais, vol. 2.

The following species were collected in the cerrado.

Gekkonidae

Briba brasiliiana Amaral, 1935 (3 specimens)
Hemidactylus mabouia (Moreau de Jonnès, 1818) (59)
Phyllopezus p. pollicaris (Spix, 1825) (8)

Iguanidae

Iguana i. iguana (L., 1758) (9)
Polychrus acutirostris Spix, 1825 (1)
Tropidurus semitaeniatus (Spix, 1825) (66)
Tropidurus torquatus (Wied, 1820) (222)

Scincidae

Mabuya cf. mabouya (Lacépède, 1789) (8)

Teiidae

Ameiva ameiva (L., 1758) (207)
Cnemidophorus ocellifer (Spix, 1825) (296)
Tupinambis teguixin (L., 1758) *sensu* Boulenger, 1885 (1)

Amphisbaenidae

Amphisbaena vermicularis Wagler, 1824 (7)
Leposternon polystegum (A. Duméril, 1851) (14)

Collected or seen both in the cerrado and the caatinga were the two *Tropidurus*, *Cnemidophorus ocellifer*, *Ameiva ameiva* and *Phyllopezus pollicaris*.

Comments on the list

Tropidurus, *Ameiva* and *Cnemidophorus* were bought only during two days, and no specimens refused; thus, their numbers in the collection afford a reasonable estimate of their local density. *Iguana* is under-represented, because we accepted only a couple of large specimens.

The *Mabuya* collected at Valença belongs to the group of forms currently lumped under the name *M.m. mabouya* (Rebouças-Spieker, 1974). Its exact identification is not important in the present context, as will be noted below.

The *Tupinambis* collected in the cerrado of Valença is what used to be called *T. teguixin* (Linné, 1758). However, Presch (1973) saw the type of *teguixin* and concluded that the name should be applied to the form till then known as *T. nigropunctatus* Spix, 1825. Presch, fur-

thermore, synonymized what used to be *teguixin* with *rufescens* (Günther, 1871); he does not discuss his grounds for this drastic move, and I am not prepared to accept it before examining adequate materials; thus I adopt for the time being Boulenger's scheme.

The *Lygodactylus* mentioned is an unnamed species of which I have presented elsewhere a description and figure (Vanzolini, 1968).

DISCUSSION

General comparison

In Table 1 I list the caatinga species discussed in my 1974 paper and all the forms obtained in this trip.

Table 1

Ocurrence and relative abundance of lizards in the caatinga of Pernambuco (Vanzolini, 1974) and in the cerrado of Valença do Piauí (present collection)

	Caatinga (Pernambuco)	Cerrado (Piauí)
<i>Tropidurus torquatus</i>	+++	+++
<i>Tropidurus semitaeniatus</i>	+++	(++)
<i>Cnemidophorus ocellifer</i>	+++	+++
<i>Lygodactylus</i> sp.	+++	-
<i>Ameiva ameiva</i>	++	++
<i>Phyllopezus p. pollicaris</i>	++	++
<i>Gymnodactylus geckoides</i>	++	-
<i>Iguana iguana</i>	++	++
<i>Briopa brasiliiana</i>	++	++
<i>Polychrus acutirostris</i>	(+)	(+)
<i>Amphisbaena vermicularis</i>	(+)	(++)
<i>Mabuya mabouya</i>	-	++
<i>Tupinambis</i> sp.	-	+
<i>Leposternon polystegum</i>	-	(++)

The abundance scores mean: (i) three crosses indicate the truly dominant animals, of which hundreds could be collected in one day; (ii) one cross indicates animals only occasionally brought in; (iii) two crosses denote all intermediate levels of abundance; (iv) parentheses call attention to peculiarities or difficulties in scoring.

In the table parentheses are applied to: (i) *Tropidurus semi-taeniatus*, extremely abundant but only in specific situations, as discussed below; (ii) *Polychrus acutirostris*, a lizard very hard to see (see Vanzolini, 1974); (iii) the amphisbaenids, subterranean forms erratically found on the surface.

Distributional data

Table 1 confirms the hypothesis that the caatinga has not a characteristic lizard fauna.

The discrepancies between the two columns of the table are very few, especially if one takes into consideration how usual it is to find marked and unexplainable differences in the density of lizard species at neighboring and apparently very similar localities.

We must comment on two cases of species present in the Pernambuco materials and not here.

Lygodactylus sp. In all places where I have seen this gecko it has a strong anthropophilous bent, being especially attached to fences. Its absence in the large Valença collection, that covered backyards as well as uninhabited cerrados, thus very probably reflects a real situation. I did not see it either in the two caatinga localities explored, but good structural habitats were infrequent there. This continues to be a mysterious animal: a species of an otherwise African genus, with an enormously disjunct distribution in Brazil (Vanzolini, 1974: 79). I think it is urgent to investigate its status on the southwestern end of the range.

Gymnodactylus geckoides. The absence of *G. geckoides* in this collection does not harm the general argument, because authentic cerrado and caatinga specimens exist in collections. It is annoying, however, to have missed this species, of which additional materials are sorely needed, as its distribution and differentiation are unique and still insufficiently studied (Vanzolini, 1974: 73).

Among the forms reported from the cerrado and not from the caatinga is the *Mabuya*; this confirms previous data in that so far no *Mabuya* is known from the caatingas (this is why the exact identification of the species is not indispensable).

The case of *Tupinambis* is still a moot one. The two species that occur in Brasil are certainly sympatric and even possibly syntopic in the domain of the cerrado. They are both by preference riparian, but otherwise differ much in ecology (Vanzolini, in preparation). I have not seen undoubted caatinga specimens, but have heard from local people that they occur there. If this is true, most probably the species involved will be the teiú (*teguixin* *sensu* Boulenger).

Finally, there is the case of *Leposternon polystegum*. Its distribution (Gans, 1971) is bewildering, extending from Pará to the northeastern states. It is quite probable that a number of forms are lumped under this name; the present sample, potentially precious for taxonomic studies (it seems to be the first moderately large series to be collected) adds very little to the general problem of open formation distribution patterns.

Ecological data

In my 1974 paper I considered *Briba* as probably a cerrado-caatinga lizard, but wished for first hand information on cerrado specimens. This is now available: our Valença specimens were caught in the cerrado.

In the same paper (p. 85) I stated that *Tropidurus semitaeniatus* "may be called a caatinga lizard". The possibility remained, however, that the fidelity of *semitaeniatus* would be to exposed rock, not to the caatinga proper. In this trip we saw in several pure cerrado localities dense populations of *T. semitaeniatus* on sandstone exposures, in the usual relationship with *T. torquatus*. I consider this as an extremely important fact. It is not impossible that *T. semitaeniatus* enters deeper into the domain of the cerrados than presently known. This is not very important, however, given the impediments to its spread consequent upon the scattering of suitable environments. On the contrary, its presence in the cerrados of Valença, a contact area, I consider indispensable to my argument.

THE ROLE OF THE CONTACT AREA IN THE EVOLUTION OF THE FAUNAS

In my 1974 paper, dealing with the Atlantic forest and the agreste, I briefly analyzed the role of transitional areas in the evolution of faunal assemblages. The present study was undertaken to look at the other extreme of the spectrum, at abrupt, linear contacts.

The Radam vegetational chart (1:1,000,000) of the area shows only unbroken cerrados with a few very large caatinga enclaves. This is a matter of scale, and if one turns to the sketch accompanying the description of sheet SB.24-X-A (p. IV/88), or to my Map 1, adapted from that sheet, one has an adequate idea of the nature of the contacts. There are numerous interdigitations, some cut off, forming small enclaves, very frequently on the same topographical level. The Radam phytogeographers do not mention the presence of agrestes, but I think this may be a matter of nomenclature. I prefer to call "agreste", according to the northeastern usage, the caatingas with no cacti and few thorny plants that occur in wetter areas. The local rainfall (ca. 800 mm) is certainly sufficient.

It is obvious that the complex pattern seen can only be attributed to edaphic factors, and that not even very local topoclimates can be invoked to explain it. In fact the best cases I saw were quite clearly due to soil differences.

I must say that when I use the term "linear contact", I am being literal. Not only in the areas of rock floors (lajeiros) but also in those of arboreal caatinga, the transition between caatinga and cerrado is a matter of a few steps.

This sharp mosaic pattern seems to me the most favorable configuration for the exchange of faunistic elements without consequent differentiation. The proximity between the contrasting plant formations is on the spatial scale of the foraging routine of an individual ground lizard. Natural selection will tend fatally to favor those that do equally well in both habitats. These are interfaces that lead to homogenization, not to vicariance.

This basic mechanism is necessary to the causation and maintenance of faunal homogeneity, but is not sufficient. We must add spatial and temporal dimensions.

The domain of the caatingas measures some 800 thousand square kilometers. Any mechanism capable of maintaining uniformity within such a large area must have proportionate geographical expression. That is, the belt of intricate linear contacts must have enough length to ensure sufficient gene flow to counter the genetic effects of mere distance; only a few gates on a fence several thousand kilometers long would not be enough. We have detailed charts (Radam, 1:250.000) of the area north of 6° ; it is quite obvious that interdigitation patterns by far predominate. Numerous accounts of local situations, as well as personal experience in Bahia and Minas Gerais, to the south, tend to confirm this.

By the same token, even in the presence of an extensive interface, capable of maintaining substantial gene flow, it is to be expected that nuclei of differentiation will appear in the heart of the caatingas. These can only be diluted by what might be called "turbulent mixing", i.e., faunal movements consequent upon biogeographical upheavals of some magnitude. Of such we have ample evidence, in the shape of climatic cycles, during the drier phases of which the caatingas have undergone enormous expansion and retraction, alternately replacing and being replaced by cerrados (Vanzolini, 1970).

As a final comment, it must be remembered that the present area of the domain of the cerrados is much larger than that of the caatingas, and covers a much broader latitudinal (and climatic) span, very diversified but in general a mesic one, without the extremes of drought that characterize the caatingas. It should thus have a richer fauna than the latter. This is true, but that the difference is so small (Table 1) testifies to the efficiency of the homogenizing mechanism outlined above.

ACKNOWLEDGMENTS

The Academia Brasileira de Ciências fully supported the field work. The team included Dalcy de Oliveira Albuquerque (Museu Nacional, Rio de Janeiro, who took time off from his own research in order to help me), Mariana Vanzolini, and Dorival de Souza (on loan from the University of São Paulo Museu de Arqueologia e Etnologia).

The authorities of Projeto Radam, Departamento Nacional da Produção Mineral, Ministério das Minas e Energia, kindly permitted the adaptation and publication of Map 1.

Aziz Ab'Saber as usual gave me indispensable help with geomorphological matters, and Ernest E. Williams criticized the manuscript.

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