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ENVIRONMENTAL TEMPERATURE AND NUMBER OF BODY ANNULI IN *AMPHISBAENA ALBA*: NOTES ON A CLINE (SAURIA, AMPHISBAENIDAE)

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ABSTRACT

Multiple regression analysis shows that absolute minimum temperature and average yearly temperature range explain approximately 54% of the variance of the number of body annuli of a subterranean limbless lizard.

INTRODUCTION

In 1955 I published a study of the geographical differentiation of the limbless subterranean lizard *Amphisbaena alba* in Brasil. Among the conclusions it was maintained that the number of body annuli, which varies more or less orderly along a north-south gradient (cline), depends principally on environmental temperatures: a crude demonstration was offered. Better materials and especially access to computing facilities now permit further analysis.

MATERIAL AND METHODS

SAMPLES

I have 122 specimens from 86 Brasilian localities, between Amazonia and Santa Catarina (Vanzolini, 1955; also Table 6). The general area is enclosed in a polygon whose vertices have approximate coordinates (to the nearest whole degree, latitudes South, longitudes West of Greenwich) 0-51, 4-70, 19-58, 26-49 and 8-35 (Map).

ECOLOGICAL DATA

Temperatures (in degrees centigrade) were obtained from the 1955 "Atlas climatológico do Brasil". The individual maps are on the scale of 1:15,000,000 for the country and 1:9,000,000 (inset) for the State of S. Paulo. Isotherms are spaced 2°C. For each locality were initially recorded the absolute minimum and maximum, the yearly average and the average maximum and minimum temperatures; average and maximum yearly ranges, used on a second stage, were obtained by subtraction.

The map of the Brasilian morphoclimatic domains is taken from Ab'Saber (1967).

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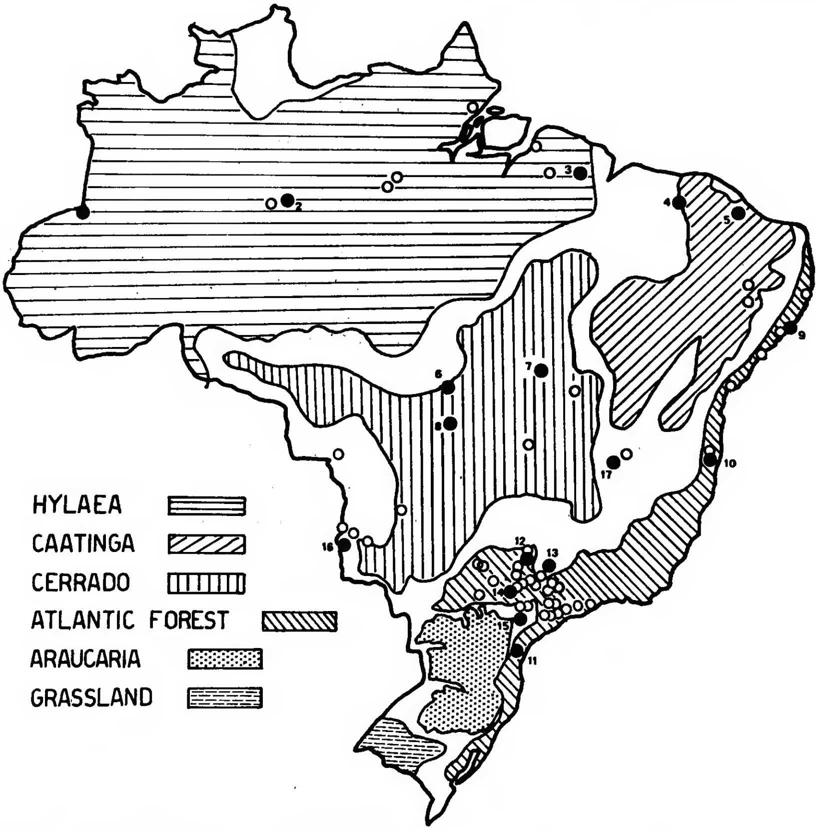
CRITIQUE OF THE DATA

There are two major areas of criticism of the present data. First is that they suffer greatly from imprecision. Locality records of museum specimens are per force very heterogeneous. To begin with, there are differences originating from collectors' pratices. Besides, standards of reference are not the same in the various parts of Brasil: in the south one may have the nearest railroad station; in the Amazon, a river; in Central Brasil, the nearest (often not very near) Indian Service post; and so on. Thus the plotting of each locality on the map includes an area of penumbra impossible to estimate.

The climatic data are also imprecise. No actual records are available for the individual localities, only values extracted from isotherm maps, based on broad averages for the general area;



Map of the Brasilian morphoclimatic domains (after Ab'Saber, 1967), with the localities represented in this study. Black dots, localities whose temperature data are listed in Table 3.

details of topography, plant cover, and other important factors are forcibly ignored. The averages themselves are not very reliable, as the Brasilian network of meteorological stations is rather thin and incomplete, and much interpolation and guesswork is included in the maps. Furthermore, these are based on time series of variable length, and the ecology of many places has changed drastically in the period covered by the collections (some 60 years). For instance, soil temperatures are affected by changes in plant cover, and these have been rapid and extreme in many areas of Brasil.

However, keeping in mind that our interest lies in broad ecological patterns of geographical differentiation, not in the physiological mechanisms involved, I think this heavy load of imprecision in no way invalidates the study — quite the contrary. The imperfections of the data add to the variance but introduce no bias: significant correlations obtained against such odds are that much more impressive.

Another criticism would be that I have limited my study to Brasil. Guianan specimens are available that would extend the territory covered a further 7 degrees of latitude to the north, but I could not get the necessary climatological information. However, this is not a serious drawback: the samples as they stand cover 27 degrees of latitude, which is quite ample for the present purpose of evincing broad dependences, and include the southern (coldest) limit of the distribution.

Table 1

Distribution of the samples among the Brasilian morphoclimatic domains

Region	Localities	Specimens
Amazonia (hylaea)	10	15
Northeastern caatingas (xerophytic)	4	10
Central cerrados (savanna-like)	8	19
Pantanal of Mato Grosso (seasonally flooded)	5	5
Atlantic forest		
northeastern coastal	6	7
southern coastal	6	6
inland S. Paulo (agricultural)	47	60
	86	122

On the other hand, the diversity of the localities represented ensures a broad inductive basis to the analysis. All the Brasilian morphoclimatic domains and their principal subunits and transitional areas are represented (Table I and Map); the addition of the Guianas would not have markedly increased the diversity of environments sampled.

Also contributing to a solid inductive basis are the ranges of temperatures represented (Table 2), and the diverse way in which they are associated, in individual localities, due to the diversity of plant cover, topography and distance from the sea (Table 3).

Table 2

Ranges of environmental temperatures

	Lowest	Highest
Average minimum	13	22
Average maximum	24	34
Annual average	18	26
Absolute minimum	- 7	18
Absolute maximum	34	42
Average range	6	16
Extreme range	18	46

PRELIMINARY ANALYSIS

In the ideal study of geographical differentiation one would have a perfect network of localities, with a good sample from each, so that reliable isophenes would tell their own story. In actual practice one is led to test empirical models against the existing data. In the case of South America, two general methods are of primary importante: the consideration of the morphoclimatic domains and the search for linear trends.

Table 3

Temperature data for representative localities

Locality *	A	B	C	D	E	F	G
1 Benjamin Constant	20	30	24	12	37	10	25
2 Manaus	22	32	26	17	39	10	22
3 Canindé	20	31	26	13	40	11	27
4 Periperi	22	34	26	16	39	12	23
5 Maranguape	22	31	26	18	38	9	20
6 Jacaré, Alto Xingu	19	32	24	1	40	13	39
7 Barra do Tapirapés	20	32	24	6	42	12	36
8 Xavantina	19	32	24	1	40	13	39
9 Maceió	22	29	26	14	36	7	22
10 Santa Leopoldina	18	28	22	6	38	10	32
11 Joinville	18	24	20	- 7	39	6	46
12 Barretos	16	30	21	- 5	39	14	45
13 Guapuã	14	26	20	0	36	12	36
14 Batalha	14	28	21	- 1	38	14	39
15 Cerqueira Cesar	14	27	20	- 2	39	13	41
16 Serra do Urucum	18	30	24	1	42	12	41
17 Lagoa Santa	14	25	20	2	36	11	34

* The numbers identify the localities in the Map.

A, average minimum
B, average maximum
C, annual average
D, absolute minimum

E, absolute maximum
F, average range
G, maximum range

MORPHOCLIMATIC DOMAINS

Ab'Saber (1967) has defined and mapped the core areas of 6 morphoclimatic domains in Brasil. These are regions in which there is coincidence of geomorphic, climatic and vegetational characteristic features. He of course designates the domains by rigorous geographic terms, but I prefer, for zoological usage, to name them after the characteristic plant formations, as more suggestive to naturalists. The six domains are (Map): (i) the Amazonian hylaea; (ii) the northeastern semi-arid, summer deciduous caatingas; (iii) the savanna-like cerrados of Central Brasil; (iv) the Atlantic forest; (v) the Araucaria forest; (vi) the southernmost mixed prairies.

The transition belts are differently constituted. At times (as between cerrado and hylaea in northern Mato Grosso) one has a peculiar type of "buffer" vegetation. Other times, as in the contact between caatinga and cerrado, there is a complex interdigitation, topographically determined. In one specific case, that of the Paraguay valley, the transition belt is extremely complex, due to the recency of the alluvional phenomena, and the area (the seasonally flooded "pantanal") shows very peculiar ecologic features.

I have assembled samples constituted by specimens from the core areas and from the pantanal and no general ecological or geographical pattern is discernible (Table 4 and Graph 1).

Table 4

Number of body annuli of samples representing the morphoclimatic domains

Sample		N	R	M	V
Amazonia		14	223 - 247	231,3 ± 1,89	3,1
Caatinga		10	223 - 236	229,7 ± 1,19	1,6
Cerrado		13	207 - 231	217,9 ± 1,94	3,2
Pantanal		5	214 - 227	221,2 ± 2,31	2,3
Atlantic forest:	north	7	222 - 244	234,9 ± 2,62	3,0
	south	6	210 - 223	215,3 ± 2,08	2,4
	inland	32	198 - 223	212,7 ± 1,02	2,7

N, number of individuals

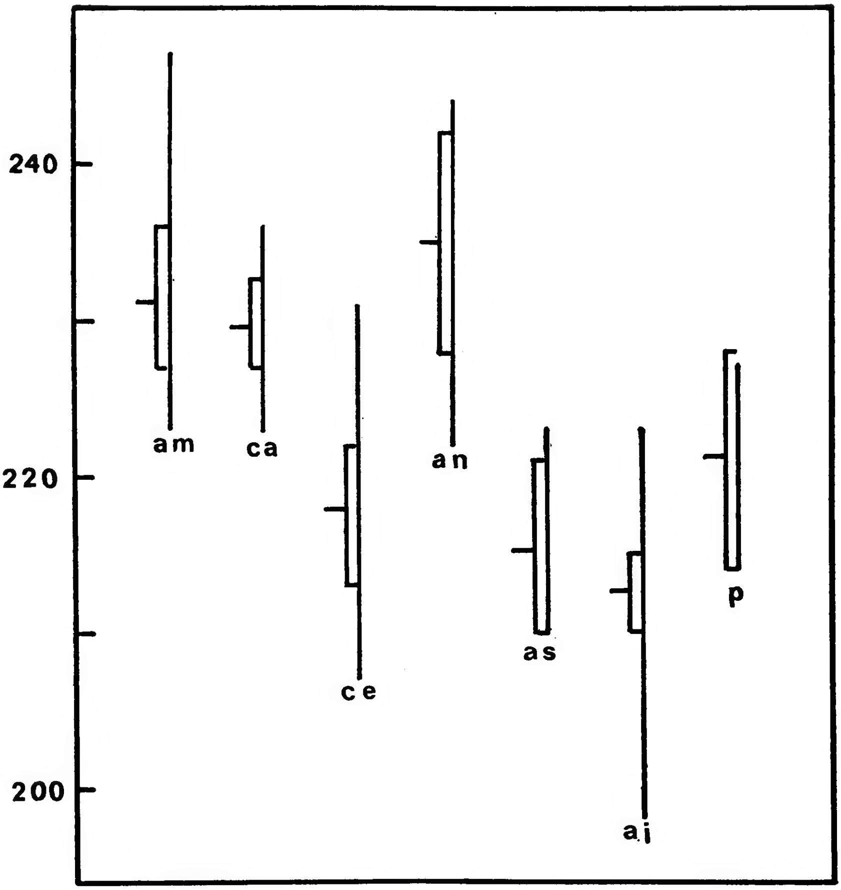
R, observed range

M, mean ± t (Student's) times its standard deviation

V, coefficient of variability

LINEAR TRENDS

Procedure in the search for linear trends is very much a matter of circunstance and expediency. For instance, in my study of *Amphisbaena fuliginosa* (1951) the available materials could be analysed along several meaningful transects, and areas of character stability and intergradation thus identified. In the present case



Graph 1. Number of body annuli (range, mean and confidence interval of the mean) of samples representing the morphoclimatic domains: *am*, Amazonia; *ca*, caatinga; *ce*, cerrado; *an*, Atlantic forest, northern half; *as*, Atlantic forest, southern half; *ai*, Atlantic forest, inland (S. Paulo); *p*, pantanal. Data from Table 4.

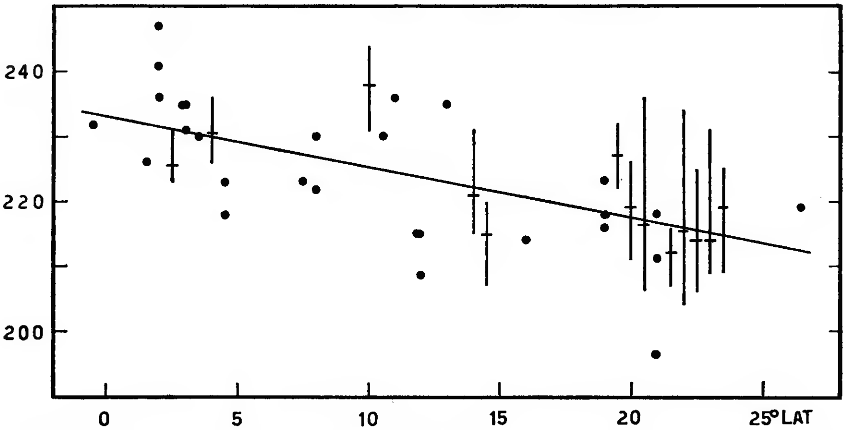
such an arrangement is not feasible, but the inspection of Graph 1 suggests the presence of a latitudinal cline. In fact, we have 3 groups of samples: (i) Amazonia, caatinga and north Atlantic forest, with high counts; (ii) cerrado, south Atlantic forest and pantanal, with intermediate counts and (iii) inland Atlantic forest with the lowest values.

In order to test this model I assigned to each specimen a number corresponding to the latitude of the nominal locality, to the nearest half degree (Graph 2). In the graph are shown individual annuli counts for latitude samples with 3 or fewer specimens, observed ranges and means for larger samples. The dependence is unmistakable, as can be seen from the fitted regression line, which afforded a correlation coefficient of .63, meaning that approximately 40 per cent of the variance of the number of body annuli is explained by the latitude of the locality.

According to current concepts (Mayr, 1963), this may be considered a very good case of clinal variation.

STUDY OF THE CLINE

Since it was first proposed by J. Huxley in 1939, the term cline has had a very broad meaning, being applied to any spatial or temporal gradient in any type of character. It covers thus a very broad spectrum of situations, going, in taxonomical practice, from sharp gradients across narrow belts of intergradation to broad continent-wide patterns such as the presently studied. To me, this excessive inclusiveness tends to reduce the efficiency of the term, even if modifying prefixes (topocline, geocline, etc.) are adopted. Further obscurity is caused by the fact that, as discussed by Mayr (1963), very diversified mechanisms are potentially involved in the causation of gradients.



Graph 2. Number of body annuli against latitude. Explanation in the text.

Actually, classifying a pattern of differentiation as a cline means only that the hidden ecological factor (or factors) most relevant to the expression of the character must have a more or less orderly geographical distribution. Once the relevant ecological factors are identified, the purely geographic gradient loses importance, as it contains less information than the regression of the character on the factor. Isophenes, which take as much art as science to draw, are thus substituted by points and intervals of confidence on a regression line.

Graph 1 has some very suggestive aspects. The broad agreement between the two forested areas and the caatinga indicates that humidity and plant cover have little if any importance in determining the cline. This is in keeping with what is known of the causality of Brasilian climates, which depend on the interplay of air masses (Monteiro, 1963) rather than on strict latitudinal zonation. One is thus led to consider the role of temperature.

The number of body annuli in the genus *Amphisbaena*, and specifically in *Amphisbaena alba*, is directly related to the number of somites (Alexander & Gans, 1966), which is well known to be very sensitive to environmental temperatures. It is one of the characters that present most geographical differentiation in snakes and limbless lizards, and its phenotypical expression in cold-blooded vertebrates can be influenced by manipulation of temperatures at some critical stages (Fox, Gordon & Fox, 1961; Orska, 1962). In selecting which temperatures to test, I was led in part by choice, in part by circunstance.

Initially, a closer inspection of Graph 2 affords some clues. The samples of latitudes 12° (Jacaré) and 14.5° (Xavantina) show values much lower than those of adjacent latitudes (Maceió, Aracaju and Barra do Tapirapés) which belong into the general trend. A first check of climatic maps showed that the most important difference between the two groups of places was in the absolute minimum temperature (Table 3). It must be remembered that Jacaré, Xavantina and Barra do Tapirapés are all in the cerrado (Map).

It can also be seen that the southernmost samples are very variable, both within and among latitudes. A verification of what happens in the state of S. Paulo, where more detailed climatic data are available (Setzer, 1946) showed that the lowest values seemed to be associated with areas in the north and west of the state where the lowest minima, - 5° and - 6°, are found.

Thus, the inclusion of absolute minimum temperature was mandatory, as well as of its symmetrical, absolute maximum.

On the other hand, *Amphisbaena alba* being a burrowing lizard, I had the impression that average temperatures would be more important than extremes, as the subterranean environment is thermally buffered (Vanzolini, 1948). Thus I included also the average maxima and minima and the yearly average.

Plotting the number of body annuli against these temperatures showed regression in the case of the two minima, but not of the other temperatures. However, since the different temperatures are correlated among themselves, it was clear that the choice method for analysis was that of multiple regression.

The data were submitted to multiple regression analysis, by the "stepwise" method, in a IBM-1620 computer, at the Center of Electronic Computation, Institute of Mathematical Research, University of S. Paulo, thanks to the kindness of dr. Isu Fang. The results are shown in Table 5.

The correlation observed is very good, since approximately 54 % of the variance of the number of body annuli is explained by the joint consideration of 3 relevant temperatures; the improvement over the regression on latitude is about 35%.

Since the average maximum temperature was also found significant, and with signal opposite to that of the minima, it became necessary to test the relevance of temperature ranges. The maximum and average ranges were added (without omission of the previously studied variables) and a new analysis performed; the results are also shown in Table 5.

Table 5

Results of multiple regression analysis
(step-wise method, last significant step)

Variable	Regression coefficient	Student's t	Correlation coefficient
First analysis			.73
Absolute minimum	0.726	3.581***	
Average maximum	- 1.148	2.188*	
Average minimum	1.105	2.024*	
Second analysis			.73
Absolute minimum	0.741	8.054***	
Average range	- 1.040	3.497***	

*** Significant at the 5% level. ***at the 0,1% level**

It is remarkable that there was no improvement of the fit; the new correlation coefficient is exactly equal to the first. But besides absolute minimum, average range was now the only variable significant; signs were again opposed.

COMMENTS

These data suggest that temperature influences the number of body annuli through selection, pleiotropic mechanisms determining at the same time some physiological adaptive character and the number of somites. It would be necessary to pursue the analysis, and to check which part of the life cycle is preferentially affected by selection: sperm, egg, embryo or newborn. For such a study we lack ecological information. When this becomes available, a multiple regression analysis including the temperatures of the ecologically relevant months, instead of the yearly indexes used here, may very possibly increase the portion of the variance of the number of body annuli explained by temperature.

Otherwise, comparison of samples of very young specimens with samples of adults from the same area may help to ascertain the stage at which selection acts.

Table 6

Number of body annuli of specimens not reported in Vanzolini (1955). All in the collection of the Departamento de Zoologia

222	Rio Pratagi, Al	236
374	São Miguel, Al	231
378	Santarém, Pa	231
3304	Salvador, Ba	235
3308	Sta. Bárbara, Sa. Caraça, BM	226
3467	Xavantina, Mt	207
3468	Xavantina, Mt	213
3469	Xavantina, Mt	220
3470	Xavantina, Mt	219
3499	Jacaré, Alto Xingu, Mt	215
3500	Jacaré, Alto Xingu, Mt	209
3501	Jacaré, Alto Xingu, Mt	215
4717	Tomé-Assu, Pa	223
6452	Periperi, Pi	231
6453	Periperi, Pi	226
6454	Periperi, Pi	236
6470	Manacapuru, Am	230
6471	Tomé-Assu, Pa	224
6482	Guapuã, SP	212
6684	Maranguape, Ce	234
6686	Maranguape, Ce	230
6687	Maranguape, Ce	231
6688	Maranguape, Ce	229
6689	Maranguape, Ce	227
6821	Belém, Pa	226
6899	Jaborandi, SP	206
6900	Recife, Pe	222
7670	Uberlândia, Mg	216
7696	Sera do Urucum, Mt	218
7706	Pto. Esperança, Mt	224
8150	Aracaju, Se	236
8359	Benjamin Constant, Am	223
8360	Benjamin Constant, Am	218
8813	Sta. Teresa, ES	223
9768	Barra do Tapirapés, Mt	230
10345	Rio Tracajátuba, Ap	232
11949	Canindé, Pa	224

REFERENCES

AB'SABER, A. N.

1967: Domínios morfo-climáticos e províncias fitogeográficas do Brasil. *Orientação (Dept. Geogr. Fac. Fil. Ci. Letr. Univ. S. Paulo)* *3*:45-48.

ALEXANDER, A. A., & C. GANS

1966: The pattern of dermal-vertebral correlation in snakes and amphisbaenids. *Zool. Med. Leiden* *41*(11):171-190.

BRASIL, Conselho Nacional de Geografia e Serviço de Meteorologia.

1955: *Atlas climatológico do Brasil.* Vol. 1, 2 parts, 221 maps. Rio de Janeiro.

FOX, W., C. GORDON & M. H. FOX

1961: Morphological effects of low temperatures during embryonic development of the garter snake, *Thamnophis elegans. Zoologica N. York* *46*(2):57-71.

HUXLEY, J. S.

1939: Clines: an auxiliary method in taxonomy. *Bijdr. Dierk.* *27*:491-520.

MAYR, E.

1963: *Animal species and evolution.* XIV + 797 pp. Cambridge, Mass.

MONTEIRO, C. A. F.

1963: *Clima* in *Geografia do Brasil, Grande Região Sul.* Bibl. Geogr. Brasil 4 (1): VIII + 215 pp. Rio de Janeiro: Conselho Nacional de Geografia.

ORSKA, J.

1962: The influence of temperature on the developement of meristic characters of the skeleton in *Salmonidae.* Part I. Temperature-controlled variations of the number of vertebrae in *Salmo irideus* Gibb. *Zool. Poloniae* *12*(3):309-339.

SETZER, J.

1946: *Contribuição para o estudo do clima do Estado de S. Paulo.* 239 pp. S. Paulo.

VANZOLINI, P. E.

1948: Notas sôbre os ofídios e lagartos da Cachoeira de Emas, no município de Pirassununga, Estado de S. Paulo. *Rev. Brasil. Biol. Rio de Janeiro* *8*(3):377-400.

1951: Contributions to the knowledge of the Brazilian lizards of the family Amphisbaenidae Gray, 1825. 6. On the geographical distribution and differentiation of *Amphisbaena fuliginosa* Linné. *Bull. Mus. Comp. Zool.* *106*:1-67.

1955: Contribuições ao conhecimento dos lagartos brasileiros da família Amphisbaenidae Gray, 1825. 5. Distribuição geográfica e biometria de *Amphisbaena alba* L. *Arq. Mus. Nac. Rio de Janeiro* *42*:683-706.