

Papéis Avulsos de Zoologia

MUSEU DE ZOOLOGIA DA UNIVERSIDADE DE SÃO PAULO

ISSN 0031-1049

PAPÉIS AVULSOS ZOOL., S. PAULO 40(3): 65-85

23.V.1997

THE SILVESTRII SPECIES GROUP OF *AMPHISBAENA*, WITH THE DESCRIPTION OF TWO NEW BRASILIAN SPECIES (REPTILIA: AMPHISBAENIA)

P.E. VANZOLINI

ABSTRACT

Amphisbaena anaemariae, sp. n., from the Serra da Mesa, state of Goiás (14° 02' S, 48° 13' W) has two preanal pores, 156-170 body annuli, autotomy constriction between third and fourth or fourth and fifth caudal annuli, 18-20 tail annuli, 14-16/14-16 segments to a midbody annulus, dorsum lustrous brown, ventral parts checkered or piebald, tip of snout and chin region smudgy rose-colored.

Amphisbaena crisae, sp. n., from Cafeara, state of Mato Grosso (11° 50' S, 55° 20' W), has two preanal pores, 176-181 body annuli, 21-23 tail annuli, 10/10 (11) segments to a midbody annulus, dorsum brown, venter irregularly checkered.

Relationships among small two-pored species of *Amphisbaena* with spotted color patterns (here called the *silvestrii* species group) are briefly discussed, as well as a scenario for their speciation.

Keywords: *Amphisbaena*, Reptilia, *Amphisbaena*, *silvestrii* group.

INTRODUCTION

The group of graduate students in Herpetology at the Department of Zoology, University of São Paulo, under the leadership of Prof. Miguel

Museu de Zoologia, Universidade de São Paulo.

Recebido para publicação em 25.VI.96 e aceito em 11.VII.96.

Rodrigues, has been exploring a locality, Serra da Mesa, in the state of Goiás. The extremely valuable collections made there are being deposited in this Museum; deep appreciation is here emphasized. Their work is part of a program of faunal rescue, coordinated by Dr. Nelson Jorge da Silva, Jr, Pontificia Universidade Católica de Goiás, on the site of an intended hydroelectric dam.

During the 1995 campaign they collected, at a locality coded as "Point 2", a series of a small *Amphisbaena* which turned out to be new (*A. anaemariae*, below), and whose description entailed an examination of similar forms; this resulted in the discovery of another new species, that had stood misidentified in our collection for over 30 years, and is here described as *A. crisae*. Later a further specimen was collected at a nearby camp in Serra da Mesa (Ponto 3, 13°52'S, 48°23'W), and is here included as a paratype of *A. anaemariae*.

***Amphisbaena anaemariae*, sp. n.**

(fig. 1-4)

Holotype

MZUSP 80596, Brasil: Goiás: Serra da Mesa, Ponto 2 (14° 02' S, 48° 13' W), 2-22.xii.1995. Field number M. Rodrigues 95.7034.

Paratypes

MZUSP 80224, 80225, same locality as holotype, 4-9.xii.95, M.Rodrigues coll. MZUSP 80597-60601, same data as holotype, field numbers respectively M. Rodrigues 95.7150, 95.7178, 95.7196, 95.7263, 95.7295. MZUSP 80925, Serra da Mesa, Ponto 3 (13°52'S, 48°23'W), 18.ii-2.iii.96, field number M.Rodrigues 96.6035.

Referred specimen

AMNH 62155, Brasil: Goiás: Anápolis, v-ix.1936, R.M. Gilmore.

Etymology

Named in honor of Ana Maria Ramos-Costa, long time friend and co-worker.

Diagnosis

A small species (maximum total length 193 mm). Two preanal pores; 156-170 body annuli; 18-20 tail annuli; autotomy level between third and fourth or between fourth and fifth caudal annuli; 14-16/14-16 segments to a midbody annulus.

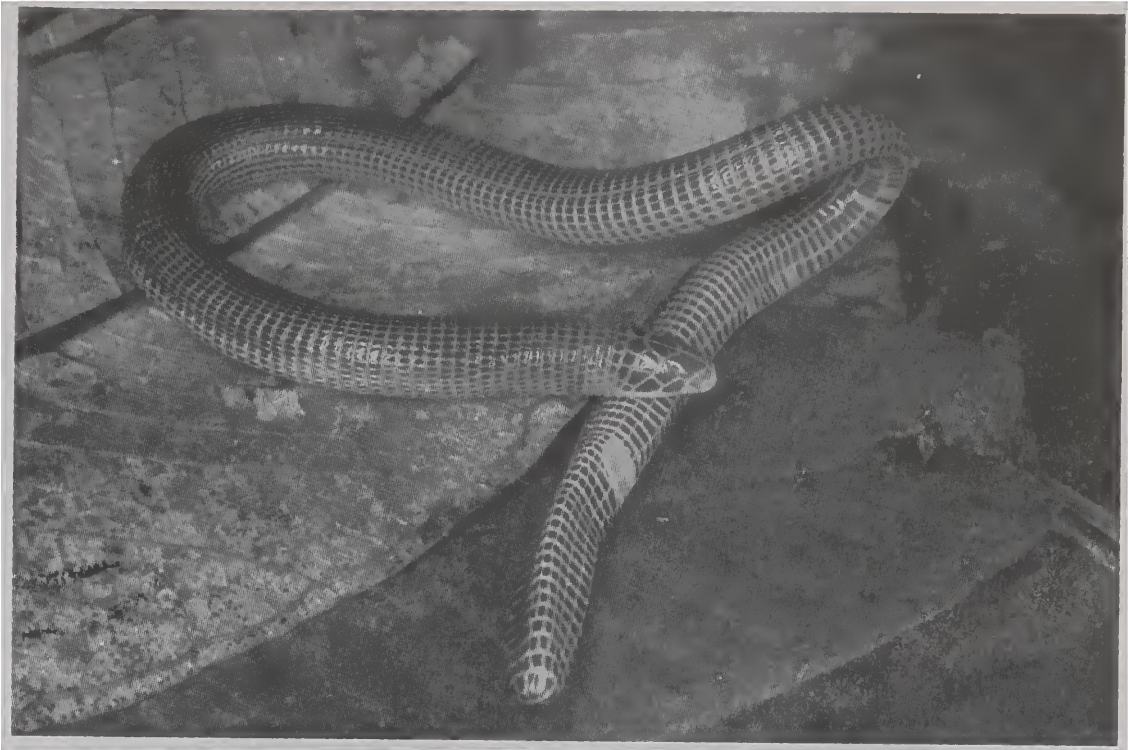


Plate 1. *Amphisbaena anaemariae*, sp.n., holotype, from life. Photo by Miguel T.U. Rodrigues.

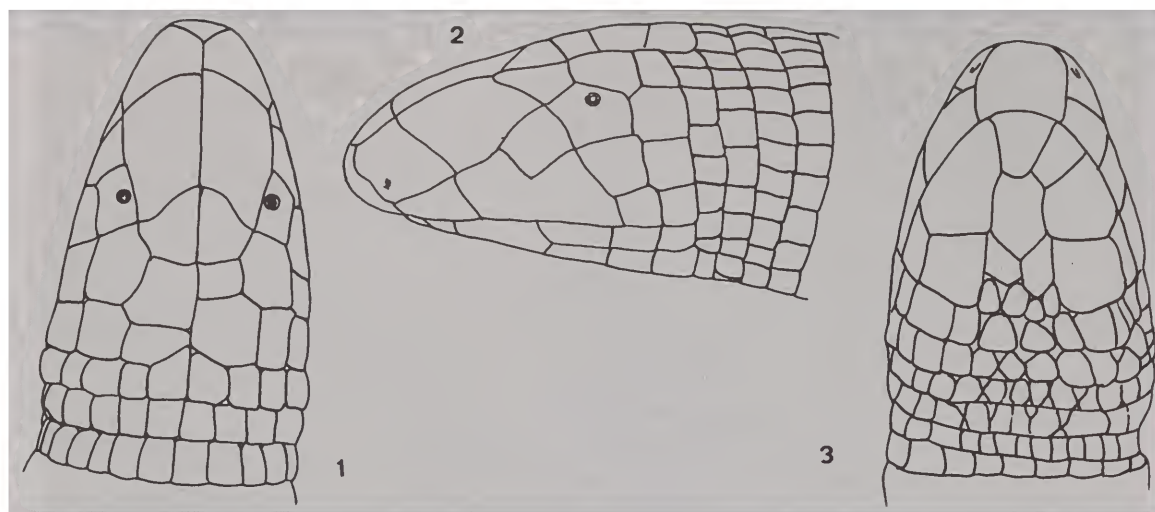
Description (Figs. 1-4)

Body moderately stocky. Tail slightly clavate. Lateral sulci little marked. No dorsal or ventral sulci.

Sutures on the dorsal aspect of the head in the following order of increasing length: nasal, frontal, prefrontal. Parietals and occipitals irregular. Nostril near the antero-inferior angle of the nasal. Upper labials four, second and third large, subequal. Behind the eye two successive rows of three scales each, becoming larger from the bottom up. Symphysial small, in some specimens irregular. Post-symphysial narrow, elongate, somewhat irregular. Lower labials four, the first small, the second very large, the third narrow and elongate, its posterior end sometimes pinched off to form a fourth lower labial. Two median genials (*sensu* Vanzolini, 1991): a variable number of post-genials; all of these very irregular; one large, regular lateral genial on each side.

Dorsal segments regular, narrow and elongate. Medio-ventral segments once and a half as wide as long. Preanal pores two, very small. Six preanal scales, the outer ones very small. Postanals forming a raised semicircle. The first median pair of ventral caudals in some specimens much enlarged. Autotomy constriction between the third and fourth or the fourth and fifth tail annuli.

Back a lustrous brown with slightly lighter intersegmental sutures, light enough to cause a just noticeable reticulate pattern. On the flanks and belly there are segments with a dark center and light edges, irregularly distributed



Figs. 1-3. *Amphisbaena anaemariae*, sp.n., holotype, head.

and varying in density: the general appearance of the belly varies from practically white to a brown checkerboard. The ventral aspect of the tail may also be a checkerboard, or may present longitudinal series of 5-10 light segments, or still be almost white. All this variation in eight specimens. Rostral, nasals, upper labials and chin region smudgy rose-colored.

Scale counts and body proportions: see Discussion.

***Amphisbaena crisae*, sp.n.**

(fig. 5-8)

Holotype

MZUSP 6418, Brasil: Mato Grosso: Cafeara (11° 50' S, 50° 20' W), July, 1950, H.Sick coll.

Paratypes

MZUSP 6415-6417, 6419-6423, same data as holotype.

Note on the type locality

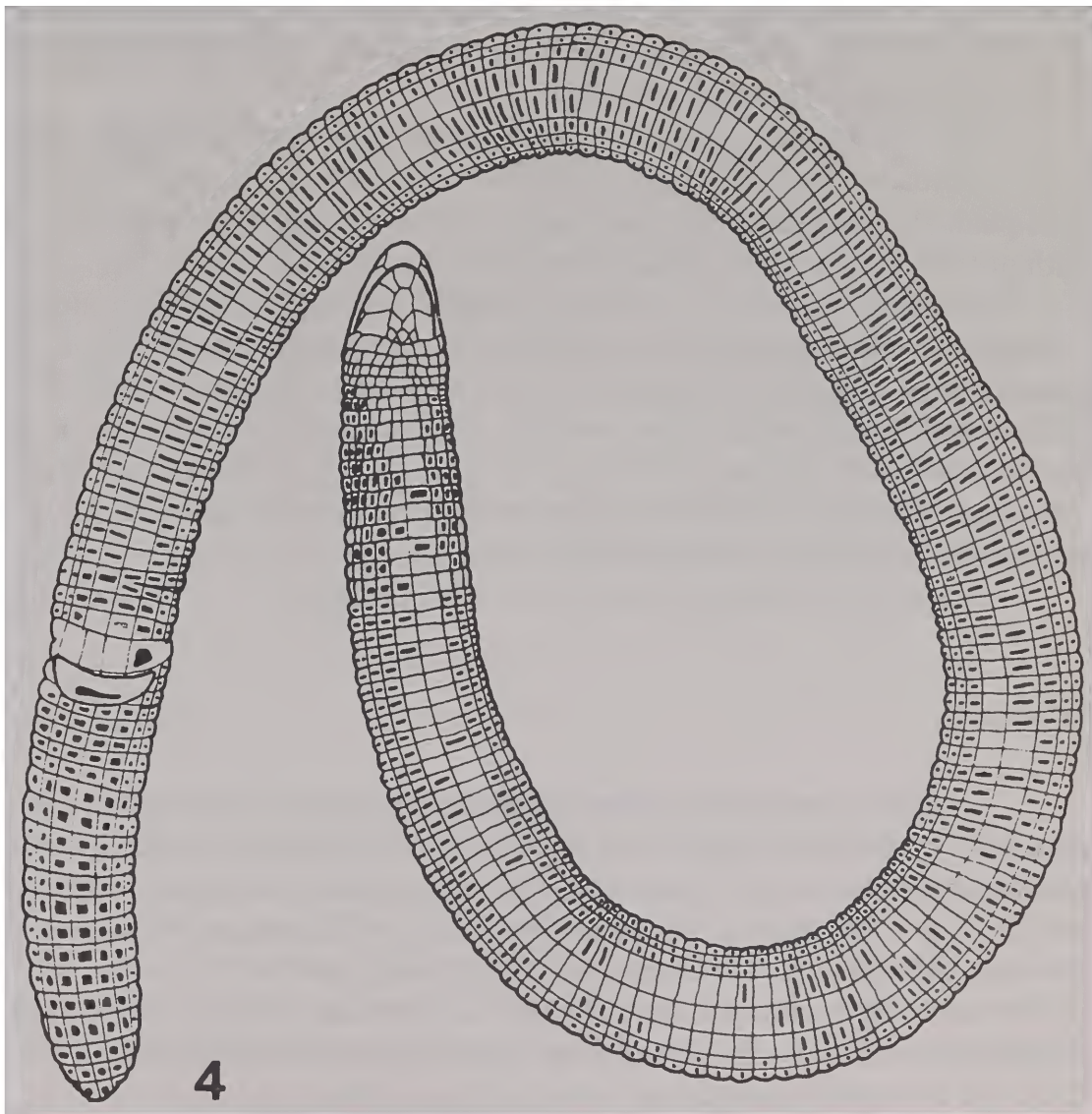
At the time of collecting the locality was a camp of the Central Brasil Foundation, a government agency in charge of establishing and maintaining emergency airfields on the Rio de Janeiro-Manaus route. It was then called Acampamento Teles Pires or simply Teles Pires (from the nearby river). There was the type series collected by the late Dr. Helmut Sick, an ornithologist then in the employment of the Foundation. When northern Mato Grosso was opened to colonization, the camp grew into a village and a town and was named Cafeara.

Etymology

Named in honor of Maria Cristina Oliveira Lima Murgel, coordinator of an ongoing biological survey of Mato Grosso, instituted by the state's Secretariat of Planning (SEPLAN), that made it mandatory to publish the present species.

Diagnosis

A small species (maximum total length 170 mm). Two preanal pores; 180-185 body annuli; 20-22 tail annuli; autotomy level between fourth and fifth or between fifth and sixth caudal annuli; 10/10 (in one case 10/11) segments to a midbody annulus.



Figs. 4. *Amphisbaena anaemariae*, sp.n., holotype, ventral view.

Description (Figs. 5-8)

Body moderately stocky. Tail varying from cylindrical, slightly tapering, to clearly but not strongly clavate. Lateral sulci thin but distinct; no dorsal or ventral sulci.

Median scale sutures on the dorsal aspect of the head in the following order of increasing length: (nasal, parietal), frontal, prefrontal. Frontal irregular, with arcuate sides, at times quite elongate. Occipitals small but still differentiated. Upper labials four, second and third very large, fourth squarish, sizable. Behind the ocular an oblique row of two large polygonal scales sitting on the fourth labial. Symphysial small, with very short antero-lateral horns. Postsymphysial seven-sided, rather short and broad, fairly regular. Lower labials five, the second very large, the third to fifth forming an even longitudinal row of rectangular scales. Medial genials large. Postgenials three. Lateral genials large, with elongate anterior processes.

Dorsal segments squarish, very slightly swollen. Ventral segments variable, the broadest (median) 2 to 2.5 times as broad as long. Preanal pores two, well made. Preanal scales six. Autotomy constriction between the fourth and fifth or the fifth and sixth caudal annuli. Tip of tail plainly segmented.

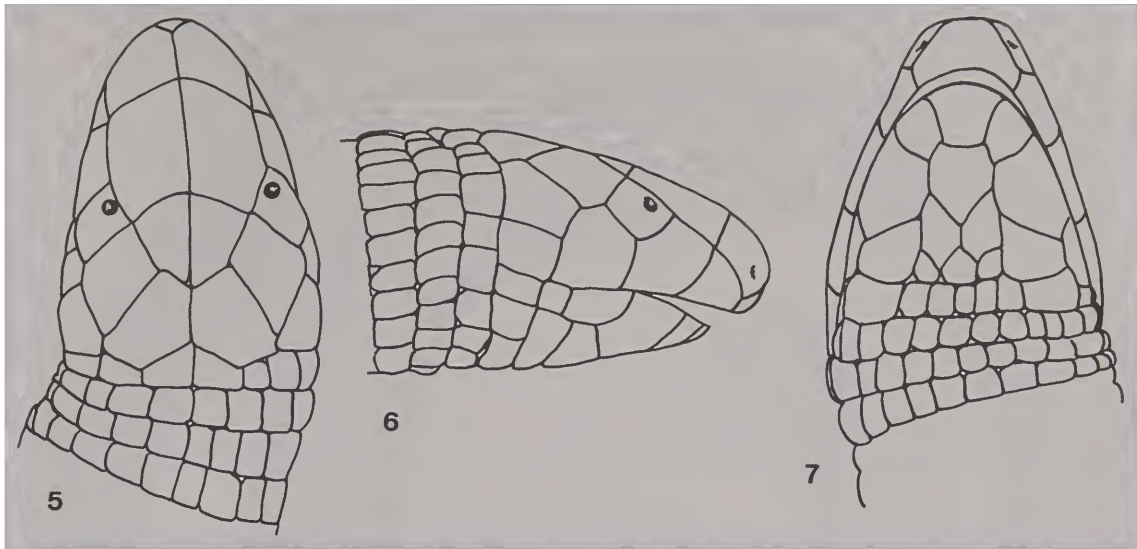
Dorsum medium brown. Intersegmental sutures lighter, from almost inconspicuously to distinctly so, resulting at the extreme in a finely reticulate pattern, more evident on the posterior third. The segments on the flanks tend to have dark centers with lighter margins; this pattern extends onto the belly, sparing anteriorly the four median segments, invading all the venter posteriorly. Ventral aspect of tail heavily checkered. Head dorsally and ventrally the same color as the body, without lighter areas.

Scale counts and body proportions: see Discussion.

Discussion

Amphisbaenas are somewhat paradoxical creatures. Their scale counts and body proportions, aided by a few details of scutellation, make specific identifications very easy. The structure of the genus, however, is a different matter. It is very speciose and covers smoothly a wide gamut of characters, making subdivision a hazardous job. The only genus to be split from *Amphisbaena* in recent times was *Cercolophia* Vanzolini, 1992; the other single satellite genus, *Bronia*, is quite convenient but not wholly convincing. In fact, there are no obvious outgroups.

It seems to me that the four species dealt with in this study may be said to constitute a species group, or the nucleus of one. They are small forms



Figs. 5-7. *Amphisbaena crisae*, sp.n., holotype, head.

without obvious cephalic or caudal specializations; all have two preanal pores, and a shared color pattern, characterized by the presence of dark (brown) and light (creamy) areas, with a stepped appearance, i.e., each segment is either dark or light, and there are no straight edges to the areas of main color; broad checkered areas are frequent. I propose to call it the *silvestrii* species group, after the first species described — also the most widely distributed and the most frequent in collections.

There are at present enough materials to discuss in a preliminary way the four known species, although the information on *A. neglecta* is not yet satisfactory.

Distribution

The four species are essentially Central Brazilian.

A. silvestrii Boulenger, 1902, was described from Cuiabá, in the state of Mato Grosso; the area is ecologically complex, comprising cerrados (“savannas”) and pantanal (large seasonally flooded depressions).

A. neglecta Dunn and Piatt, 1936, was described from Chapada dos Guimarães, some 45 km to the northeast of Cuiabá, in cerrado. Fox (1896) states that H.H. Smith, the collector, assembled under the name “Chapada” specimens from this locality and from a few neighboring ones.

A. anaemariae is also from a typical cerrado area in Goiás. *A. crisae*'s type locality, Cafeara, is in northern Mato Grosso, in the transition from cerrado to Amazonian-type forest. The transition is not a gradual one, but rather a

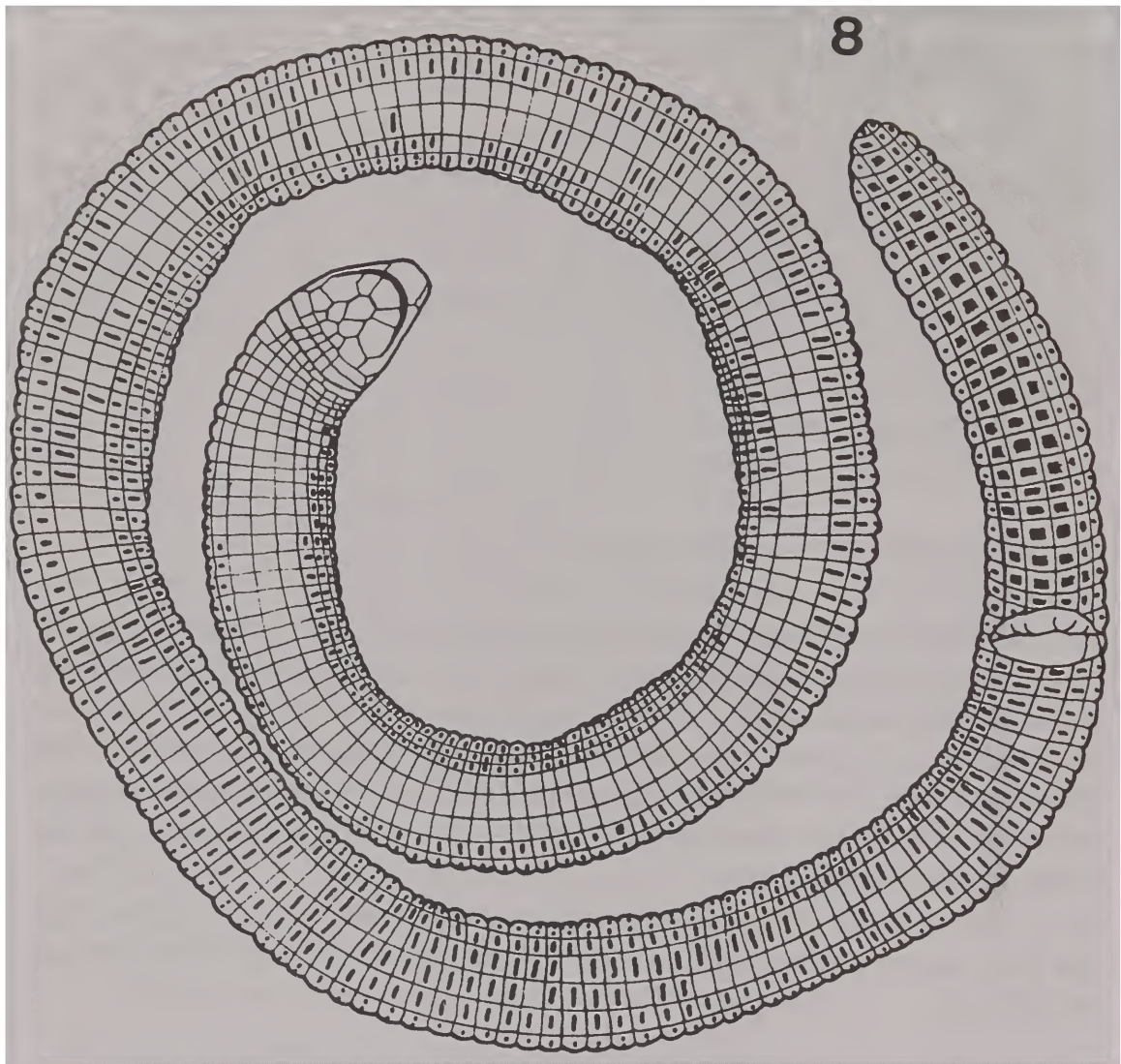
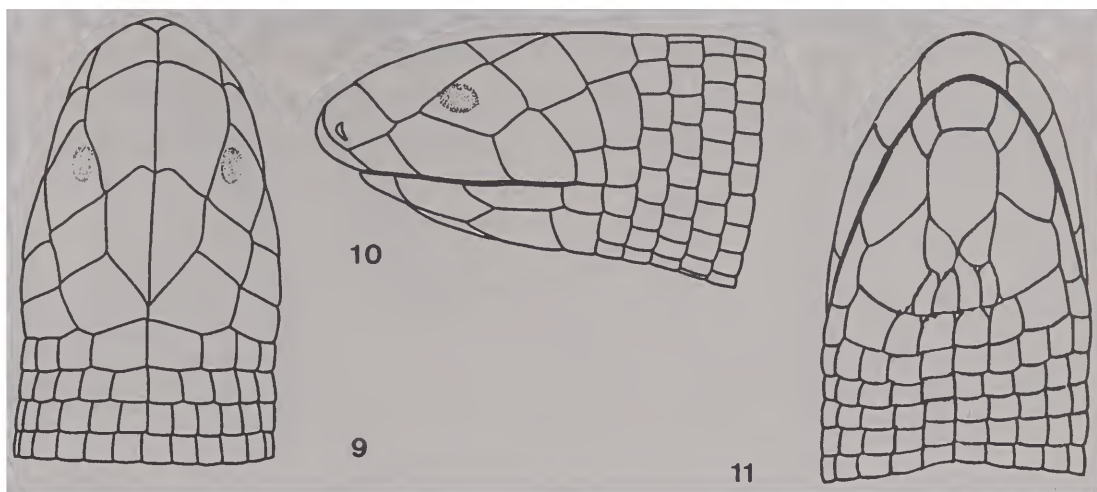


Fig. 8. *Amphisbaena crissae*, sp.n., holotype, ventral view.

serrated contact constituted of alternate “fingers” of the contrasting plant formations, sometimes cut off, forming border enclaves of varying importance. The ecology of *A. crissae* is an open matter and one of the few ones related to amphisbaenians that has a rational, immediate focus: is it basically a cerrado species or an euryecious one? Field work will hopefully tell.

Comparisons

Amphisbaena neglecta and *A. silvestrii* were compared by Gans (1962). He had at hand the type of *silvestrii* (not a very good specimen, according to



Figs. 9-11. *Amphisbaena silvestrii* Boulenger, 1902, holotype, head, after Gans (1962), by permission.

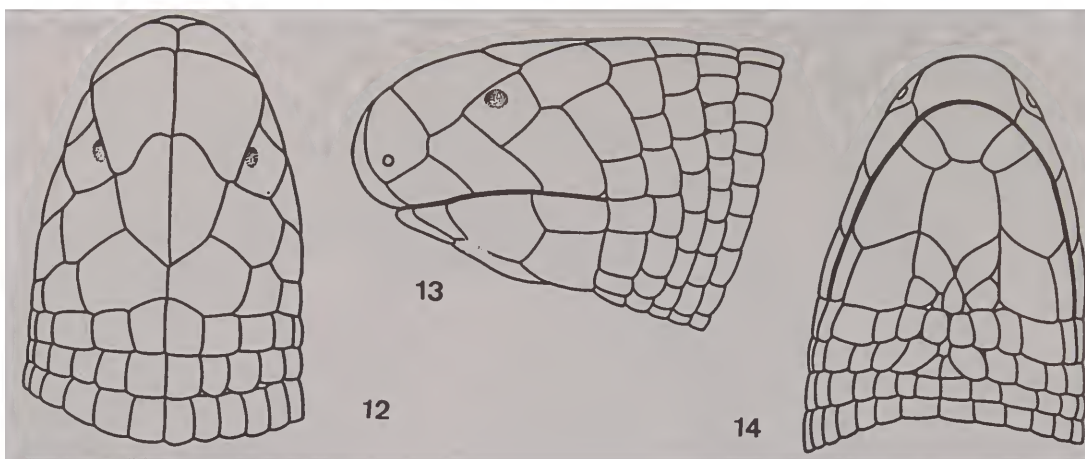
Capocaccia, 1961) and one more specimen from “Middle Xingú”, a rather vague locality (the Xingu is over 2,000 km long). Of *A. neglecta* he had the type series and one further specimen (AMNH 62155) from Anápolis, Goiás (on which more below). He reached the conclusion that they could be told apart as follows:

	<i>A. silvestrii</i>	<i>A. neglecta</i>
Body annuli	179-181	151-161
Dorsal segments	10 (possibly 12)	12-14
Ventral segments	10-11 (possibly 12)	12-14
Precloacal segments	4	4-6
Color	Segments brown with a clear lighter edge	Segments brown but without sharply lighter edges

In 1964 Gans, on the occasion of describing *A. leeseri* from the pantanal of the Corumbá region, state of Mato Grosso do Sul, presented data on additional specimens of *A. silvestrii*: (i) 5 from Barra do Tapirapés, Mato Grosso; (ii) 1 from Aruanã, Goiás; (iii) 2 from “Garapá” (actually Garapu), Mato Grosso; (iv) 7 from “Tacaré” (actually Jacaré), Mato Grosso; (v) 1 from Chavantina (present spelling Xavantina), Mato Grosso; (vi) 10 from Teles Pires (now Cafeara), Mato Grosso (my new *A. crisae*). These localities are shown on the map 1.

The new materials enabled Gans to set new ranges for the scale counts of *A. silvestrii*: body annuli 173-185, tail annuli 20-22, segments 10 (12)/10-11 (14). The characterization of *A. neglecta* of course did not change.

This is the substantive literature, subsequent to the original descriptions, on this group of amphisbaenas.



Figs. 12-14. *Amphisbaena neglecta* Dunn & Piatt, 1936, holotype, head, after Gans (1962), by permission.

When I started studying the small two-pored creature from the Serra da Mesa, I found it necessary to examine the geographical differentiation of *A. silvestrii*, which covered a vast and ecologically diversified territory. I counted on the following materials (specimens also used by Gans marked *): Barra do Tapirapés, 7 specimens; Cafeara*, 9; Gurupi do Tocantins, Tocantins, 1; Jacaré*, Mato Grosso, 6; Utiarití, Mato Grosso, 1; Garapu*, Mato Grosso, 2; Xavantina*, Mato Grosso, 1; Aruanã*, Goiás, 2.

Comparing Gans's scale counts and measurements with ours of the same specimens the differences were found to be insignificant, so I am using in some cases his data on specimens I have not seen, without further comment.

Scale counts

Body annuli: Table 1 presents the relevant distributions of frequencies. Inspection clearly indicates the presence of four kinds, characterized by ranges of the variable: *A. neglecta*, range 151-154; *A. anaemariae*, 160-170; *A. silvestrii*, widespread and geographically variable, 170-181; *A. crisae*, 180-185.

It seemed evident to me (Table 1), from the beginning, that the Anápolis specimen (AMNH 62155) was not *A. neglecta*, but belonged with *A. anaemariae*, which is geographically quite plausible. I borrowed the specimen, and, although the color pattern is blackened by preservation, it is indeed *A. anaemariae*. Since we have a sufficient number of well preserved specimens from the type locality, I am not designating this specimen as a paratype. *A. neglecta* continues to be known only from the type series, and its range of body annuli now falls to 151-154. Table 2 presents the statistics of the distributions of frequencies; there is no need of further analysis to conclude that the kinds seen on Table 1 are good species.

Tail annuli: Table 3 shows the data. *A. neglecta* again stands out with very few annuli (14-16). *A. anaemariae* is intermediate (18-20). *A. crissalis* and *A. silvestrii* have identical ranges (20-22); their distributions of frequencies, tested through the chi-square and the Mann-Whitney tests, do not differ sig-



Map 1. Localities cited, over the background of the Brazilian morphoclimatic domains. *hyl*, Amazonian hylea; *caa*, caatingas; *cer*, cerrados; *Af*, Atlantic forest. (Adapted from Ab'Saber, 1977). 1, Barra do Tapirapés (1039, 5036). 2, Cafeara (1150, 5520) 3, Gurupi do Tocantins (1143, 4904). 4, Jacaré (1205, 5324). 5, Utiriti (1302, 5817). 6, Garapu (1313, 5139). 7, Xavantina (1440, 5221). 8, Aruanã (1454, 5106). 9, Chapada dos Guimarães (1526, 5545). 10, Cuiabá (1536, 5605). 11, Anápolis (1620, 4858). 12, Serra da Mesa (1402, 4813). 13, Salitre (1901, 4648). Coordinates abbreviated; all latitudes South, all longitudes West.

TABLE 1. Number of body annuli, distributions of frequencies

	<i>anae</i>		<i>negl silvestrii</i>								<i>crisae</i>		
		apl		gur	tap	aru	jac	gar	xav	uti	type	all	
151			3										
152			-										
153			-										
154			1										
155													
156													
157													
158													
159													
160	1												
161	-	1											
162	1												
163	1												
164	1												
165	2												
166	-												
167	-												
168	-												
169	1												
170	1												
171							1						1
172							-						-
173							1						1
174					1		1						2
175					1		1		1				3
176					1		1			1			3
177					2								2
178					2	1							3
179											1		1
180													-
181				1				1					2
182													1
183													-
184													1
185													5
	8	1	4	1	7	1	6	1	1	1	1	19	9

anae, *Amphisbaena anaemariae*; apl, Anápolis; *negl*, *A. neglecta*; gur, Gurupi; tap, Tapirapés; aru, Aruanã; jac, Jacaré; gar, Garapu; xav, Xavantina, uti, Utiariti; all, sum of all *A. silvestrii*; *crisae*, *Amphisbaena crisae*.

TABLE 2. Number of body annuli, statistics of the distributions of frequencies

	N	R	M	s	V	I (M)
<i>anaemariae</i>	8	160-170	164.8 ± 1.19	3.37	2.05	161.9 - 167.6
<i>silvestrii</i>	19	170-181	176.0 ± .67	2.92	1.61	174.6 - 177.4
<i>crisae</i>	9	180-185	183.2 ± .55	1.64	.90	182.9 - 184.5

N, individuals in sample. R, range of the variable. M, mean ± its standard deviation. s, sample standard deviation. V, coefficient of variation. I (M), 95% confidence interval of the mean (mean ± t times its standard deviation).

TABLE 3. Number of tail annuli, distributions of frequencies

	<i>anae</i>	<i>negl</i>	<i>silvestrii</i>					
				tap	jac	xav	type	all
14		2						
15		1						
16	1	1						
17	-							
18	3							
19	2							
20	1				1	1	1	3
21			6					6
22					1			1
	6	4	6	2	1	1	1	10
								7

anae, *Amphisbaena anaemariae*; *negl.*, *A. neglecta*; tap, Tapirapés; jac, Jacaré; xav, Xavantina; all, sum of all *A. silvestrii*; *crisae*, *A. crisae*.

nificantly from each other; they do from the other species.

Segments to a midbody annulus: Table 4 shows the distributions of frequencies of the sum of dorsal and ventral segments. As in the case of caudal annuli, there are three groups: *anaemariae* (range 28-32), *neglecta* (25-26) and *A. silvestrii* plus *A. crisae* (respectively 20-24 and 20-21). The two latter do not differ significantly (Mann-Whitney test). The Anápolis specimen confirms its relationships with *anaemariae*, rather than with *A. neglecta*.

Body proportions

Tail length x body length: This is a measure of relative elongation, i.e., attenuation. Table 5 and Graph 1 show the data on this regression. The coefficients of determination are good, all above .92. Analysis of variance shows that the three lines may be considered parallel, but that the intercepts are not homogeneous:

Origin of variance	df	mean square	F
General regression	1	332.3198	293.034***
Intercept	2	6.9478	6.126**
Slope	2	.0789	.070 ns
Error	17	1.1341	

** , significant at the 1% level; *** , significant at the .1% level; ns, not significant.

The result of Tukey's test (as prescribed by Zar, 1984: 191, 303), is not conclusive. As explained by Zar (l.c.: 190) this is certainly due to the fact that the analysis of variance is more powerful than the multiple comparison test; the remedy would be to enlarge the samples, which is a matter for the future. Inspection of Graph 1 shows that *A. silvestrii* is consistently longer-tailed (i.e., more attenuate) than *A. anaemariae*, and that *A. crisae* is intermediate. There are not enough specimens of *A. neglecta* to compute a regression; the individual points plotted on Graph 1 indicate that it probably has the shortest tails in the group.

Head width x body length: This is another measure of attenuation, head width being easier to measure and a much more reliable proxy for body diameter. Table 5 and Graph 2 show the pertinent regressions. Again analysis of variance shows heterogeneity of the intercepts:

Origin of variance	df	mean square	F
General regression	1	9.3258	140.7559 ***
Intercept	2	.5261	7.940 **
Slope	2	.0438	.661 ns
Error	27	.06869	

In this case Tukey's test shows that the three samples differ significantly, *A. anaemariae* being relatively the stoutest and *A. crisae* the slenderest. Combining the data on relative tail length and head width, it is evident that *A. anaemariae* is the least attenuated of the three species, the other two being more slender.

TABLE 4. Total number of segments to a midbody annulus, distributions of frequencies

	anae		negl	silvestrii							crisae		
	apl			gur	tap	aru	jac	gar	xav	uti	type	all	
20					3	2	6	1	1	1		14	8
21					-							-	1
22				1	-							1	
23					1						1	2	
24					3							3	
25			1										
26			3										
27													
28	1	1											
29	-												
30	3												
31	1												
32	3												
	8	1	4	1	7	2	6	1	1	1	1	20	9

anae, *Amphisbaena anaemariae*; *apl*, Anápolis; *negl*, *A. neglecta*; *gur*, Gurupi; *tap*, Tapirapés; *aru*, Aruanã; *jac*, Jacaré; *gar*, Garapu; *xav*, Xavantina; *uti*, Utiariti; *all*, sum of all *A. silvestrii*, *crisae*, *A. crisae*.

Pholidosis

As far as cephalic scutellation goes, these are rather conventional, ordinary species of small amphisbaenas. They all conform to the same general plan, with the following exceptions:

The parietals are in general large and regularly polygonal; only in *A. anaemariae* they are small and irregular. There are also differences in the genial region: *A. anaemariae* has two rows of postgenials, the other forms have only one. These are, it can be seen, really very minor differences.

Color pattern

From Gans's description and photograph, *A. neglecta* seems rather similar to *A. anaemariae* and to *A. silvestrii* in having a solid or finely reticulated brown dorsum and a rather melanistic venter. *A. crisae* has a light front half of the belly. The differences are just of degree of melanism, within a same general pattern.

TABLE 5. Body proportions, statistics of the regressions

Tail length x body length							
	N	R (x)	R (y)	b	a	F	r ²
<i>A. anaemariae</i>	6	96-172	12-22	.13 ± .019	-.72 ± 1.554 ns	49.852 ***	.9257
<i>A. silvestrii</i>	10	80-143	11-20	.14 ± .015	-.43 ± 1.196 ns	195.258***	.9225
<i>A. crisae</i>	6	65-149	9-21	.15 ± .012	-.92 ± 1.909 ns	159.175***	.9755
Head width x body length							
<i>A. anaemariae</i>	8	96-172	3.5-4.6	.012 ± .00286	2.39 ± .123***	18.577*	.7559
<i>A. silvestrii</i>	17	80-165	2.5-4.2	.017 ± .00320	1.42 ± .131***	26.721***	.6401
<i>A. crisae</i>	8	65-149	2.2-3.9	.018 ± .00189	1.12 ± .179***	90.464***	.9378

N, individuals in sample. R (x), R (y), range of the variables. b, regression coefficient (slope) ± its standard deviation. a, regression constant (intercept) ± its standard deviation. F, Fisher's quotient of variances (significance of the regression). r², coefficient of determination. ns, not significant. *, significant at the 5% level. ***, significant at the .1% level.

Conclusion

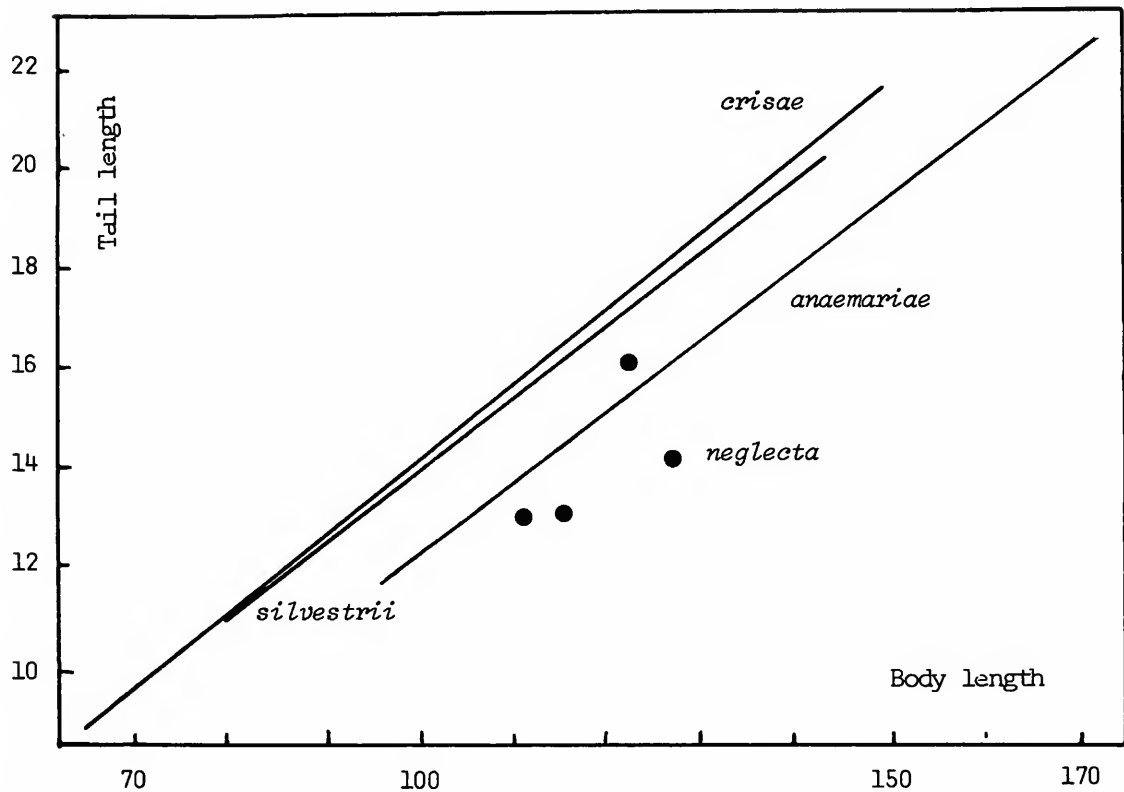
All in all, this is a fairly compact group of species, in general morphology, scutellation, body proportions and color pattern. From a taxonomic viewpoint, the diagnostic characters, as usual in small species of *Amphisbaena*, are the scale counts.

It is impressive that three of the four species are geographically confined to the part of the domain of the cerrados usually known as "Central Brasil", and the fourth occurs in the transition between this area and the Amazonian forest.

Speciation

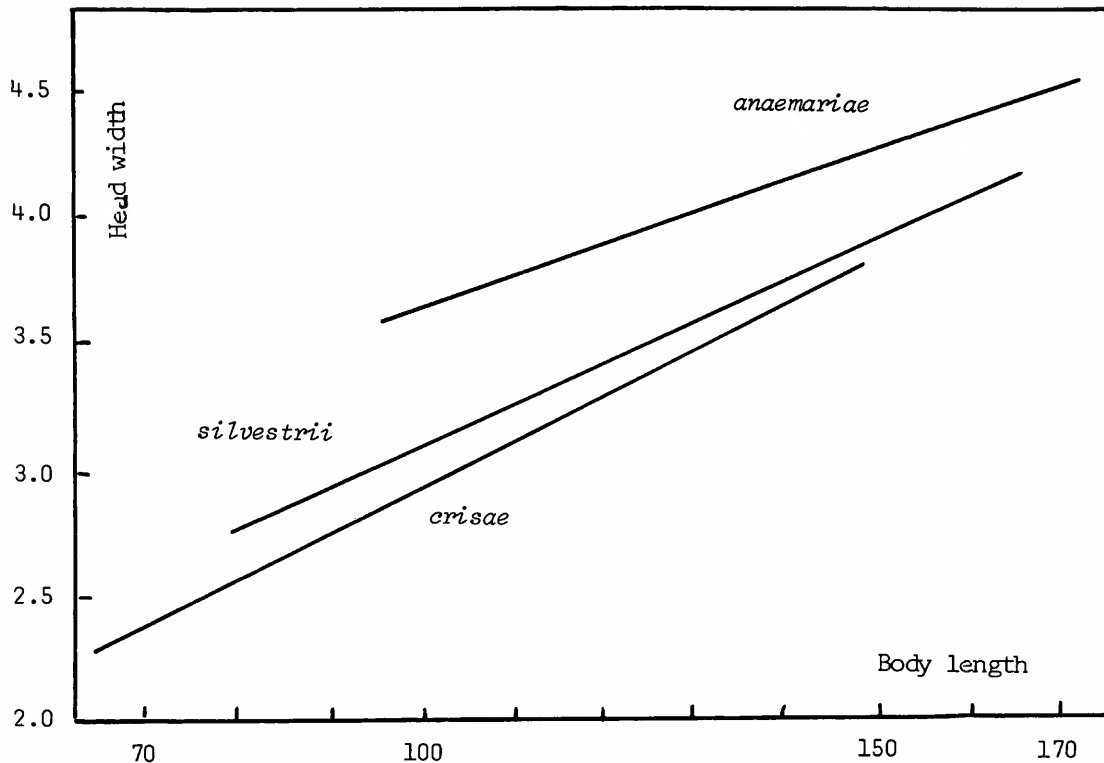
The presence of four closely related species in the domain of the cerrados, one widespread and three apparently rather local, is not easy to explain. In fact I do not know of any analogous case argued in the literature.

It is obvious to me that a strictly geographical model of speciation should be applied. Such models, old and tested, have been in recent times unnecessarily, in fact incorrectly, called "vicariance" models. They have as conceptual basis that speciation happens in geographical isolates of species with formerly



Graph 1. Regression of tail length on body length.

continuous distributions, i.e., by disruption and dissection of broad relatively uniform areas. The actual agency of disruption is immaterial. It can be, as frequently invoked, a physical barrier, but, in tropical continental lowlands, ecological fragmentation is the rule, consequent upon severe climatic shifts. There has been a tendency, espoused mainly by zoologists of a more theoretical bent, to adopt a "central-peripheral" model, in which a nuclear forested area would successively expand and retreat, leaving behind, at each retreat, peripheral isolates, sites of speciation. I cannot imagine, in the case of South America, any mechanism that would cause these orderly cycles of pulsation. On the contrary, as first demonstrated by Haffer (1969), fragmentation of broad forest areas can be much more drastic than this mild pulsating model predicts. Unmistakable signs of much drier climates (paleopalynological, geomorphological, vegetational) show that, instead of pulsating, the large forested areas have been deeply dissected and dismembered, the landscape at the height of the dry episodes consisting of forest enclaves ("refuges") surrounded by very large areas of open formations. In certain cases it is possible to associate the location of the refuges with environmental features. The clearest one is, for me, that, first explored by Haffer (1969), of the eastern façade of the Andes, mountains where whatever moisture the winds carry is checked and dropped.

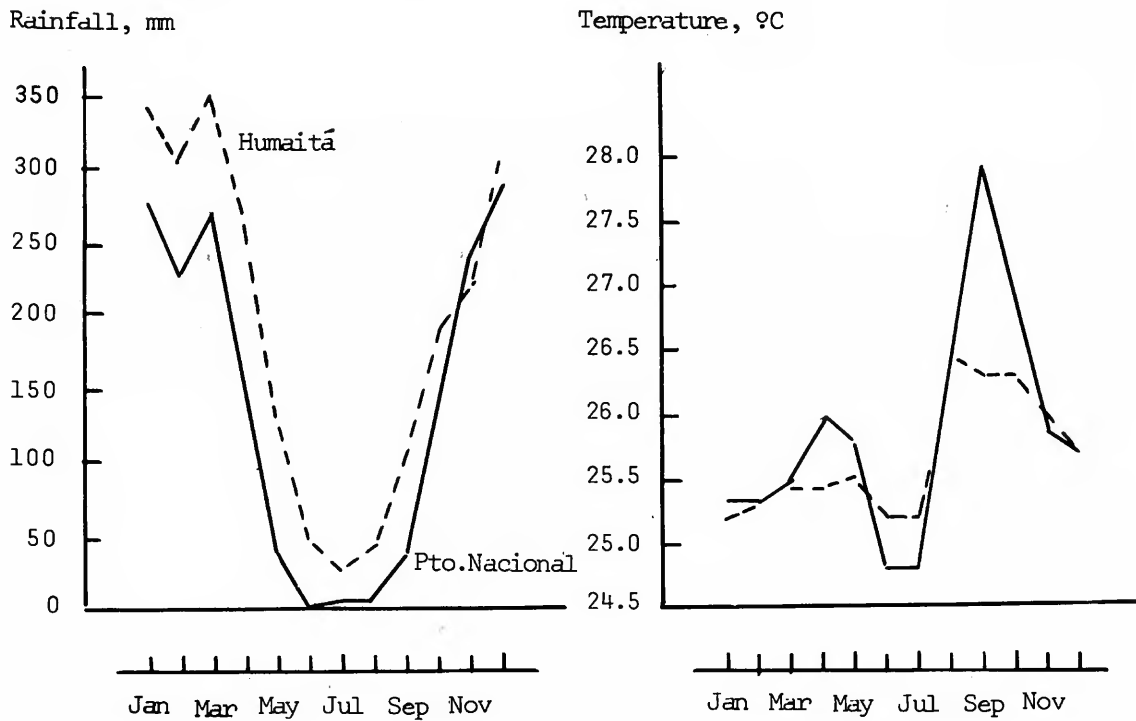


Graph 2. Regression of head width on body length.

This type of refuge is doubly interesting because, major land forms being longer-lived than climatic cycles, the same areas, conserving their topography, are prone to function again as refuges in successive cycles, originating a process that can be called "resonance" (Vanzolini & Williams, 1970).

A fair amount of work, including both confirmation and contestation, has been done in the case of the presently forested areas; practically none in the case of the open formations. I myself (Vanzolini, 1986), did discover in the state of Rondonia, in the middle of Amazonian terra firme forest, some very small isolates of caatinga-like open formations, inhabited by lizard species characteristic of cerrado and caatinga; but I have not had yet the chance of pursuing these studies. In the present circumstances, however, it seems possible to take some initial steps towards establishing ecological and time frames for speciation in and restricted to the domain of the cerrados. A spatial context would of course require much better geomorphological and paleopalynological mapping than now available.

The time frame must be restricted to the period during and since the last glacial (Wisconsinan). This was a time of very active speciation, which tends to blur the signs of former events; these can at present be revealed only by experimental methods (Heyer and Maxson, 1982). It is also unavoidable to confine consideration to climatic aspects, as there is no history of the soils in tropical South America.



Graphs 3 and 4. Monthly average temperature and rainfall, Humaitá and Porto Nacional.

Essentially, it is necessary to look for conditions favoring the formation of cerrado enclaves inside a very broad area of forests. A model can be found in southwestern Brazilian Amazonia, in the Humaitá-Labrea region, on the divide between the rivers Purus and Madeira, where well characterized middle sized spots of cerrado are found today, surrounded by vigorous terra firme forest (Braun & Ramos, 1959; Kuhlmann, 1959: map facing page 112).

In Graphs 3 and 4 I contrast the two available (and anyway paramount) elements of the climate temperature and rainfall, for Humaitá, in the state of Amazonas ($07^{\circ} 31' S$, $63^{\circ} 02' W$), and Porto Nacional, in the state of Tocantins ($10^{\circ} 42' S$, $48^{\circ} 25' W$), a locality in the core of the domain of the cerrados.

It is easy to see that the two rainfall patterns are quite similar, and that Humaitá shows the dry winter characteristic of cerrado climates. There is however, more precipitation in Humaitá, whose climate is about average for Amazonia in this respect. As for temperature, Humaitá is more isothermic, and this is very possibly a feature to be taken into consideration, but there are at present no criteria to judge, or to elaborate.

All in all, not forgetting the sketchiness of this preliminary approach, it would take a cerrado locality an increase of about 50% in its rainfall to become, given the right kind of soils, a mosaic of cerrado isolates inside a forested area.

Next should be considered the only paleoclimatic study in the area of the cerrados, Ledru (1993). It is fortunately a very competent work, and the area of the borings, Salitre, in the state of Minas Gerais ($19^{\circ} 05' S$, $46^{\circ} 48' W$),

is geographically and ecologically relevant in the present context. Ledru characterized and dated eight palynological periods, covering from approximately 30,000 to 3,000 yr B.P. Three of these periods are described as having as predominant vegetation broad-leaved forest. I take dates from her graph. Period VII (from at least $32,030 \pm 2020/ - 1620$ yr to $16,800 \pm 440/ - 420$ B.P.) shows undeniable floodplain forest of a clear (if amazing) Amazonian cast. Sub-period IIIa ($6,510 \pm 310/ - 300$ to $5,560 \pm 370/ - 360$ yr B.P.) had semideciduous forest, and a cold winter (10° - 15° C). Period I ($4,350 \pm 540/ - 500$ to $3,060 \pm 210$ yr) had about the same ecology as IIIa.

These data may be confronted with those of Absy *et al.* (1991) on the palynological history of the Serra dos Carajás, in the state of Pará ($06^{\circ} 20' S$, $50^{\circ} 25' W$). They found, in the time frame of the last 30,000 yr B.P., three periods of forest expansion: C (in full at $28,660 \pm 450/ - 450$), E1 (from $10,460 \pm 850/ - 770$ to $7760 \pm 590/ - 550$) and E3 ($2,950 \pm 470/ - 440$). Phase C undoubtedly corresponds to Ledru VII; E1 is Ledru IIIa. These two phases are, as I see it in a first, simplistic way, the more attractive candidates for the round of speciation in the cerrado leading to the split of the *silvestrii* species group. As a matter of opinion, I prefer the older episode. In spite of amphisbaenids, as subterranean animals, being to some extent buffered by the soil against environmental temperature changes, I do not like, in this picture, winters, i.e., extended periods, months long, with temperatures between 10° and 15° C; these end by being felt in the subterranean environment, and are too cold for Central Brazilian faunas.

ACKNOWLEDGEMENTS

Professor Miguel Trefaut Urbano Rodrigues, Department of Zoology, University of São Paulo, and his graduate students are to be thanked once more for their contributions to the Museum collections. Dr. Nelson Jorge da Silva jr., Pontifical University of Goiás, in charge of the biological survey at Serra da Mesa, has agreed as to the destination of the specimens.

Professor Carl Gans and Copeia permitted the reproduction of Figures 9 to 14.

Dr. Francisca Carolina do Val did the drawings of heads; Sergioberto Gomes, under her supervision, did the ventral views. Dr. May Christine Modenesi, Geological Institute of the state of São Paulo, was kind enough to help with the palynology. Drs. W.R. Heyer and C.W. Myers, U.S. National Museum and American Museum of Natural History, have read and improved the manuscript. Dr. Myers has also loaned the Anápolis specimen of *A. anaemariae*.

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