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On *Gymnodactylus amarali* Barbour, 1925, with the description of a new species (Sauria, Gekkonidae)

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ABSTRACT

Gymnodactylus amarali Barbour, 1925, was previously considered to be a subspecies of *G. geckoides*, with a wide distribution in the Brasilian cerrados. Examination of a specimen from Alto Parnaíba, Maranhão, near the type locality (Engenheiro Dodt, Piauí), indicates that it is a proper species, apparently limited to the upper Parnaíba basin. The form previously identified as *G. geckoides amarali* is described as a new species, *G. carvalhoi*, type locality Ipueiras, State of Tocantins, thus diagnosed: color pattern plain or, more often, with moderately contrasted ocelli; dorsal tubercles in 13 – 16 poorly organized longitudinal rows (mode 14, 72%); 31 – 49 tubercles in a paramedian row; 17 – 22 transverse rows of ventral scales; 13 – 18 infradigital lamellae on toe IV; tail longest in the genus. The new species is statistically compared to parapatric *G. geckoides*, widespread in the caatingas. Although only one meristic character (number of tubercle rows) is by itself diagnostic, the species are easily told apart. It is thought on provisional evidence that they are better considered for the time being as full species, not subspecies. A brief consideration is made of the speciation model that seems suitable, to wit, parapatric.

Key words: Speciation, Lizards, systematics.

INTRODUCTION

In a review of the genus *Gymnodactylus* (Vanzolini 1953) I once proposed that all specimens from the cerrados belonged to *G. amarali* Barbour, 1925 (then thought to be a subspecies of *G. geckoides* Spix, 1825), originally described from Engenheiro Dodt, Piauí, a town on the upper Rio Parnaíba, at the northeastern edge of the cerrados (Vanzolini 1976). Later (Vanzolini 1982) I felt dissatisfied with the scheme, and commented on the lack of critical materials. The main issue was thought to be the real nature of *G. amarali*. There being no authentic specimens of the form in Brasilian collections, I found it necessary to go to the type locality and try to obtain a sample capable of settling the problems of the group.

Engenheiro Dodt, founded in 1917 by a prospective agribusiness in Piauí (Iglesias 1951), is unobtrusively but explicitly present in current maps (including road maps) at 0848, 4556, on the right bank of the Rio Parnaíba, at the mouth of the tributary Riachão. Once one gets there, however, all that is seen is a derelict ruin, choked by vegetation, hard to reach, of which even the name has escaped regional memory. I tried there and got no specimens; however, at the town of Alto Parnaíba (some 35 km up river, to the south, on the opposite bank), one specimen was collected and, in spite of having torn dorsal skin, turned out to be sufficient to solve the problem.

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Description of *G. amaral* (MZUSP 93075, Alto Parnaíba, Maranhão), Fig. 3.

A juvenile (SVL 35 mm), tail broken. Snout, seen from above, triangular, plane; canthus rostralis not sharp but evident. Top of the snout, in front of the level of the eyes, with flat coarse granules; behind that level with very fine granules interspersed with button-like small tubercles. Loreal region with granules similar to those on top of the snout. Supralabials four, large, diminishing posteriorly, bordered above by enlarged flat granules. Infralabials three, moderate, decreasing posteriorly. Nostril indenting the rostral, placed between the upper corner of the first labial, two small postnasals, and one larger, slightly swollen supranasal. Ear opening low, slit-like, pointing forward and down. Symphysial broad, irregular, in direct contact with the gulars, that are small, uniform, flat, imbricate.

Dorsal granules very small. Tubercles small, variable in shape and size, poorly aligned, in 10 irregular longitudinal rows. The skin is damaged, preventing the counting of tubercles in a paramedian row. By counting the number of tubercles in a stretch of intact skin 5 mm long, I calculated a total of 66 (see below). Ventrals sub – cycloid, rather regular, in 20 transverse rows at midbody. A narrow transverse patch of very small preanals.

Upper and anterior aspects of arm with large, smooth, well imbricated scales; otherwise granular, including the elbow. Anterior half of forearm with large smooth scales, remainder granular. Palm of hand finely granular. Fingers, in increasing order of length, I, (IV – V), (II – III). Lamellae regular, slightly swollen.

Front half of thigh and leg with flat, smooth, imbricate scales, posterior half granular. Plantar surface granular, with one row of slightly enlarged granules on each margin. Toes I, II, (III – IV – V). Lamellae as those of hand.

Base of tail dorsally with enlarged tubercles, distinctly keeled, poorly aligned with the dorsal ones. Ventral caudal scales (those present), like those of the trunk.

Dorsal parts ashy brown, with a reddish tinge on the head. A light band, from the nostril through the upper half of the eye, curving into the parietal region. Dorsum with four irregular series of very vivid ocelli, with thick, irregular black borders and a stark white center, usually coinciding with a dorsal tubercle. Ventral parts cream – colored.

COMPARISON WITH CERRADO SAMPLES

The vegetation at Engenheiro Dodt (that was) and at Alto Parnaíba is cerrado. Biogeographically, both localities (Map 1) are on or near the edge of the domain, close to the transition to the caatingas. One must not forget (Ab'Sáber 1967, 2003) that transition between domains is never gradual, but a mosaic of fragments of the contrasting biomes. A first comparison of *G amarali* must be made with the form widespread in the cerrados, that I have in the past called *Gymnodactylus geckoides amarali* and describe below as *G. carvalhoi*, sp. n.

I started (Appendix, Map 1) with 76 specimens from 13 localities in the domain of the cerrados. The most striking difference is in color pattern. Ocelli are common in *Gymnodactylus* (Vanzolini 2004; below; Figs. 1, 3, 4) but never as conspicuous and vivid as those of *amarali,* which, furthermore, center on dorsal tubercles. I consider this character (of course combined with the locality), sufficient to uphold the identification of the Alto Parnaíba specimen as *amarali*. In fact, color pattern is the only strong point in Barbour's original description, which is very sketchy, specially considering the morphological homogeneity of *Gymnodactylus*.

The few pholidotic differences I notice are: (i) *amarali* has a better defined canthus rostralis, with smaller loreals; (ii) the dorsal tubercles of *amarali* are weaker and much less well organized; (iii) the ear opening of *carvalhoi* is round (iv) *carvalhoi* has no preanal patch.

Finally, with regard to meristic characters, there is of course variation in the cerrados, which I discuss below, but Table I shows that, in spite of the meager statistical basis, the differences are unquestionable.

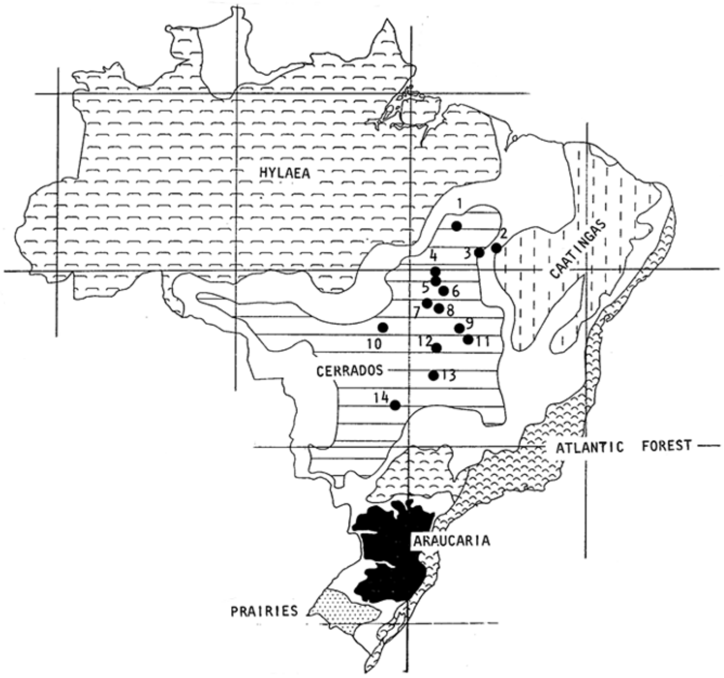
Estimation of number of tubercles in a para-

TABLE I

***Gymnodactylus amarali* and *carvalhoi*, statistics of the distributions of frequencies, meristic characters. See text for definitions of *carvalhoi* geographic samples.**

Sample		N	R	m	s	V
Tubercle rows						
amarali		1	10			
carvalhoi	A	2	14–16	15.0		
	B	7	14	14.0		
	C	20	13–15	14.0 ± 0.10	0.5	3.2
	D	19	13–15	13.9 ± 0.11	0.5	3.3
	E	5	14	14.0		
	F	2	13–16	14.5		
	B + C + D	69	13–15	13.9 ± 0.06	0.3	3.8
Tubercles in a paramedian row						
amarali		1	(66)	(66)		
carvalhoi	A	2	40	40.0		
	B	7	37–45	41.4 ± 1.00	2.6	6.4
	C	15	32–43	37.5 ± 0.80	3.1	8.3
	D	12	31–46	37.7 ± 1.36	4.7	12.5
	E	3	40–43	41.0		
	F	2	38–49	43.5		
	B + C + D	50	31–46	37.7 ± 0.53	3.7	9.9
Ventrals						
amarali		1	20	20		
carvalhoi	A	2	20	20.0		
	B	7	19–22	20.3 ± 0.42	1.1	5.5
	C	17	19–24	21.5 ± 0.30	1.2	5.7
	D	12	17–23	19.0 ± 0.48	1.9	9.8
	E	3	21–22	21.7		
	F	3	21–23	22.3		
	B + C + D	59	17–24	20.0 ± 0.22	1.7	8.4
Fourth toe lamellae						
amarali		1	14	14		
carvalhoi	A	2	18–21	19.5		
	B	7	13–15	14.0 ± 0.31	0.8	5.8
	C	21	14–18	15.6 ± 0.32	1.0	6.6
	D	25	13–16	14.4 ± 0.21	1.0	7.2
	E	3	13	13.0		
	F	5	13–17	15.0 ± 0.71	1.6	10.5
	B + C + D	76	13–18	14.7 ± 0.12	1.1	7.3

Conventions: N, individuals in sample. R, range. m, mean ± its standard deviation. s, sample standard deviation. V, coefficient of variation.



Map 1 – Localities of *Gymnodactylus amarali* and *G. carvalhoi* in the context of Ab'Saber's morphoclimatic domains of Brasil. Base map adapted from Ab'Saber (1967), with permission. (1) Carolina, Ma. (2) Engenheiro Dodt, Pi. (3) Alto Parnaíba, Ma. (4) Palmas, To. (5) Porto Nacional, To. (6) Ipueiras, To. (7) Gurupí, To. (8) Peixe, To. (9) Barra do São Domingos, To. (10) São Domingos, Rio das Mortes, Mt. (11) Posse, Go. (12) Serra da Mesa + Niquelândia, Go. (13) Pirenópolis, Go. (14) Rio Verde, Go.

median row in damaged specimens. I counted in 10 undamaged specimens the number of tubercles in 5 mm of skin, and multiplied the number of tubercles per millimeter by the length of the tubercle row.

There are in this procedure two irremovable sources of variance: the measurement of a 5 mm strip and, worse, the measurement of the length of the tubercle row, of which both end points involve considerable subjectivity (Vanzolini 2004). Thus, it is not surprising that the regression of the actual counts on the calculated values was not significant (F = 1.509). The means, however, closely agreed (t = 0.236, $p > 0.80$), so I propose that this method, though unsuitable for individual prediction, can be used for broad comparisons.

Gymnodactylus carvalhoi, sp.n.

Fig. 2

Holotype: MZUSP 91187, Ipueiras, Tocantins, 26-29.v.2002, ex MVA Planejamento e Consultoria Ambiental.

Paratypes: MZUSP 57017, Gurupí, Tocantins, 20.v.81, AMMRCosta. MZUSP 78244, Porto Nacional, Tocantins, 28.ix.90, ex Univ. Tocantins. MZUSP 87119 – 87121, Palmas, Tocantins, 11-27.iii.98, M.E.V. Calleffo, ex Instituto Butantan. MZUSP 91183 – 91186, same data as holotype. MZUSP 91509 – 91511, Peixe, Tocantins, 3-8.vii.52, C. M. Carvalho and C. Castro-Mello, ex MVA.

Fig. 1 – *Gymnodactylus geckoides,* MZUSP 92229, Salvador, BA. Fig. 2 – *Gymnodactylus carvalhoi*, sp.n., MZUSP 57017, Gurupí, TO. Fig. 3 – *Gymnodactylus amarali*, MZUSP 93075, Alto Parnaíba, MA.

ETYMOLOGY

Named after Celso Morato de Carvalho (Universidade Federal de Sergipe), old friend, colleague and field companion, who collected our specimen of *Gymnodactylus amarali.*

DIAGNOSIS

Color pattern plain or, more frequently, with moderately marked ocelli.

Meristic characters (Table I): Dorsal tubercles in 13 – 16 irregular rows (mode 14, 72%); 31 – 49 tubercles in a paramedian row; 17 – 24 transverse rows of ventral scales; 13 – 21 infradigital lamellae on the fourth toe.

Fig. 4 – *Gymnodactylus geckoides*, MZUSP 49763, Exu, Pe; ocelli degenerated into longitudinal stripes. Fig. 5 – MZUSP 47967, Exu, Pe; ocelli degenerated into short irregular transverse bars.

DESCRIPTION

Top of the snout moderately convex; in front of the level of the eyes covered with enlarged flat granules, behind that level with very fine granules interspersed with small button-like tubercles. Superciliary flap scaly, somewhat serrated. Rostral swollen, medianly incised. Nostril indenting the rostral, between the antero-superior tip of the first labial and two postnasals, not meeting the supranasal. Supralabials five, decreasing, reaching a little past the middle of the eye, followed by irregular granules. Ear opening small, round, approximately on the level of the rictus oris. Symphysial large, irregular, in contact with the gulars, which are small, flat, closely imbricate. Infralabials four, decreasing, the first separated from the symphysial by one triangular scale.

Dorsum with a background of very fine granules, and not very well-ordered longitudinal rows of keeled tubercles, with occasional gaps. Ventrals sub-cycloid. Ventral aspect of arm granular, otherwise with smooth imbricate scales. Forearm all scaly. Palm of hand granular. Infradigital lamellae slightly swollen, the rows on digits I and V prolonged on the margins of the hand. Thigh in front and below with smooth scales, otherwise granular. Leg ventrally with smooth imbricate scales, the remainder with small, irregular, sub-tubercular scales. Plantar surface granular; the rows of lamellae of toes I and V extending to the tarsus.

Intact tail dorsally with imbricate phylloid to triangular scales, in more or less regular transverse rows; ventral scales triangular, larger than the dorsals. Scales of the regenerated tail small, triangular, irregular, closely imbricate.

Color pattern variable from obsolete to, more frequently, ocellated. The ground color is ashy brown. Well-expressed ocelli have white centers and dark brown borders, often reduced to a half-moon on the front half. The white centers may be reduced to barely noticeable whitish smudges.

On an opposite trend, ocelli may approach the *amarali* pattern, the black and white elements, however, never so striking, and the ocelli not centered on tubercles. Head with at most faint dark markings. Limbs unpatterned or with faint transverse dark bars. Tail vividly patterned, with 9 – 12 transverse dorsal and ventral black bars, unconnected proximally, then coalesced into rings. The proximal black bars have overlaid stark white spots, extended into transverse bars after midlength of the tail. Tip of intact tail with a white spot. Regenerated portions of the tail uniform ashy brown. Belly light gray, often finely punctuated.

GEOGRAPHICAL DIFFERENTIATION

A statistical definition of *G. carvalhoi* has to take into account its obvious geographical variation.

MATERIALS AND METHODS

This work was started with 76 specimens from 13 localities in 4 Brasilian States, all in the morphoclimatic domain of the cerrados (Map 1; Appendix). The area covered by the sampling is on the order of 500,000 sq km.

There were at the beginning two very good one-locality samples, Barra do Rio S. Domingos, Tocantins, with 24 specimens, and Serra da Mesa, Goiás, with 23. All other samples were small, and not all specimens fully usable, so the assembling of geographical samples became necessary. The following scheme was adopted:

A Carolina, Maranhão (coordinates 0722, 4728), 2 specimens.

B Five localities on the middle Rio Tocantins, State of Tocantins, within a radius of ca. 150 km: Ipueiras, Palmas, Peixe, Porto Nacional and Gurupí (centroid 1055, 4835), 13 specimens.

C Barra do Rio S. Domingos, Tocantins (1243, 4718), 24 specimens.

D Serra da Mesa and Niquelândia, Goiás, localities ca. 15 km apart (centroid 1421, 4831), 27 specimens. After the preliminary phase of data collection and analysis, a large sample of uncatalogued specimens from Serra da Mesa became available. I extracted from it all 25 specimens with intact tails (also those with long regenerated tails, see below). I availed myself of the opportunity of checking my methods of scale counting by comparing the counts of these with samples from the same locality examined at different times. The respective values of t were

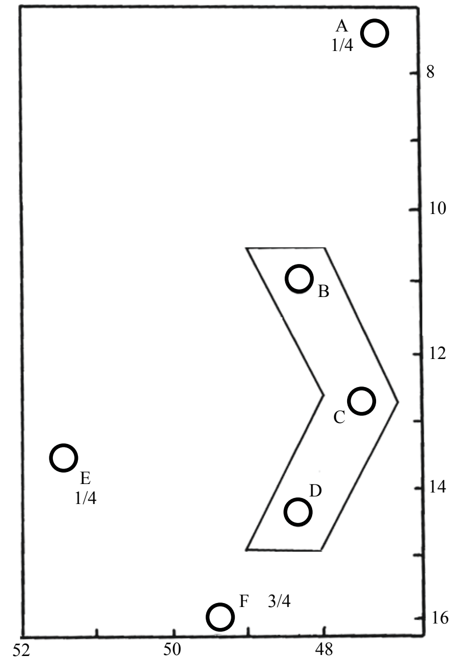
	t	df
Tubercle rows	0.752 ns	39
Tubercles in a paramedian row	0.416 ns	25
Ventrals	0.602 ns	33
Fourth toe lamellae	0.120 ns	46

The two counts, made independently, and well apart in time, agreed most comfortably, and were fused as sample D for all purposes.

- E São Domingos, Mato Grosso (1330, 5124) on the Rio das Mortes, a tributary of the Rio Araguaia on its left bank, 5 specimens.
- F Three localities in southern Goiás, within a radius of ca. 300 km, Posse, Pirenópolis and Rio Verde (centroid 1555, 4924), 5 specimens.

All localities are in the domain of the cerrados. The variability of the composite samples is of the same order of magnitude as that of the single-locality ones (Table I).

The characters studied were: (i) number of tubercle rows; (ii) number of tubercles in a paramedian row; (iii) number of transverse rows of ventrals; (iv) number of fourth toe lamellae; (v) relative tail length. These characters are discussed in Vanzolini (2004).



Graph 1 – *Gymnodactylus carvalhoi.* Skeleton map, inter-sample differences in meristic characters.

In order to get a synoptic view of the pattern, a skeleton map (Graph 1) was drawn, in which the localities are shown on a scatter plot, so that topological relationships are preserved independently of geographical details. Such maps can be drawn for individual characters, or for the ensemble, and several devices can be used to indicate agreement or disagreement between samples.

As it is my belief and practice, the statistical methods used were elementary and directly related to the nature of the variables. They can be found in textbooks, e.g. Dixon and Massey (l983), Zar (1999), Vanzolini (1993). The abbreviations adopted are explained at the foot of the respective tables.

ANALYSIS

Only three of the six geographical samples are large enough to permit the choice method, analysis of variance followed by Tukey's test. Instead, in order to compare simultaneously all samples, χ^2 tests were performed, taking into consideration the contribution of each cell to the aggregate value of χ^2. The results, as exemplified in Table II, were as follows:

Character	χ^2	df	Discrepant samples
Tubercle rows	44.674**	15	A, F
Tubercles in a paramedian row	49.510**	30	F
Ventrals	65.974***	35	F
Lamellae	45.440**	25	E

We have thus (Graph 1) a core of homogeneous samples in the valley of the Rio Tocantins, from central Tocantins (state) to northern Goiás. From this area I selected the hypodigm. Sample F, from southern Goiás, is the most divergent, 3 characters out of 4. Sample E, on the other side of the Araguaia, and sample A, in the far north, differ by one character each. The species is thus best defined, statistically, by the combination of samples B, C and D (Table I, Graph 1).

I checked the potential presence of correlations between the meristic characters and latitude, mean annual rainfall and mean annual temperature, and found none.

In relative tail length no sign of geographical

TABLE II

***G. carvalhoi*, geographical differentiation, tubercle rows.**

	Samples						
Rows	A	B	C	D	E	F	sum
13	0	0	2	5	0	1	8
14	1	7	16	33	5	0	62
15	0	0	2	2	0	0	4
16	1	0	0	0	0	1	2
sum	2	7	20	40	5	2	76

Contributions to χ^2

A	B	C	D	E	F
0.2105	0.7368	0.0053	0.1480	0.5263	2.9605
0.2445	0.2912	0.0061	0.0042	0.2080	1.6316
0.1053	0.3684	0.8526	0.0053	0.2632	0.1053
17.0523	0.1842	0.5263	1.0526	0.1316	17.0526

$$\chi^2 = 44.674*** \qquad df = 15$$

differentiation was found. (see next section).

STATUS OF *G. carvalhoi*

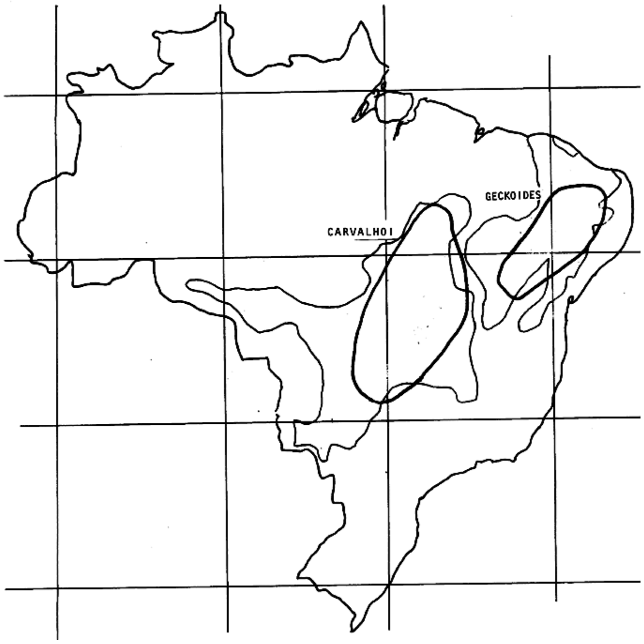
At this point it becomes necessary to consider whether we have before us a set of species or subspecies. The decision is not trivial: to me, the subspecific status implies many fundamental theoretical aspects.

The differences between *G. amarali* and *G. carvalhoi* are important and, at least until better geographical coverage is available, I think it is advisable to consider them two good species. This is not so immediately clear in the case of *G. geckoides*. This form and *G. carvalhoi* are allopatric, but, at the nearest, no more than some 250 km apart (Map 2), not very far on the scale of South American geographical distributions. There are no decisive qualitative pholidotic differences between them: *Gymnodactylus* is, in this respect, a very homogeneous genus. Among the other three species of the genus there are pronounced differences in color pattern. *G. amarali* has been discussed above. *G. darwinii* has dark crossbars on the back and a characteristic nuchal band. *G. guttulatus* has a unique pattern of white round spots, sometimes with a faint outline of a brown border. *G. geckoides* and *G. carvalhoi* are very similar in color pattern (Figs. 2, 4, 5).

A medium-intensity pattern consists, in both *G. geckoides* and *G. carvalhoi*, of an ashy-brown background with ocelli. These have a white center, not quite as contrasting as that of *G. amarali*, and a darker or lighter border, often reduced to a half-moon in front. Variation in the direction of inconspicuousness is more frequent in *G. carvalhoi*, whose ocelli may be reduced to indistinct round white spots; more rarely one finds strongly expressed ocelli. In *G. geckoides* one may also find reduction of the brown border, with fine punctuations in the residual white spots. Frequent are specimens of *G. geckoides* with disorganized ocelli, resulting in short interrupted transverse dark brown bars (Fig. 5), more rarely in irregular longitudinal dark stripes, with no white left (Fig. 4).

In both forms there are occasional specimens with strongly marked ocelli, approaching the *G. amarali* condition, which stresses the essential homogeneity of the genus.

The main differences between the two forms lie in the meristic characters (Table III). In all three cases the differences are highly significant, but only



Map 2 – Distribution of *Gymnodactylus geckoides* and *G. carvalhoi* in the context of the cerrado and caatinga morphoclimatic domains. Base map adapted from Ab'Sáber (1967), with permission.

one character is by itself diagnostic: in fact my first clue to the identity of *G. carvalhoi,* the number of tubercle rows, 12 in all *G. geckoides,* 13 or more in *G. carvalhoi.*

RELATIVE TAIL LENGTH

A further comparison can be made, in spite of the scarcity of materials – that of relative tail length. Gekkonids are bad subjects for this type of study: their tails are fragile, frequently broken in collection specimens (over 80% in this case; see Appendix); breaks near the tip are impossible to detect, and add both bias and variance to the measurement. The only sample large enough for regression analysis is the improved (for the purpose) sample from Serra da Mesa. I started the analysis by looking for sexual or ontogenetic variation in it (Table IV). Analysis of covariance showed perfect homogeneity among (unsexed) juveniles, adult males and adult females; a joint regression was computed (Table IV, Graph 2).

No other sample of *carvalhoi* being suitable for comparison, all available tail lengths were plotted against the Serra da Mesa line (Graph 3). The differences observed are all within the range of the single-sample distribution, so I conclude that the presently available data do not indicate the presence of (at least) marked geographical differentiation in relative tail length of *G. carvalhoi.* A further joint regression (Table IV) was computed, comprising all specimens, and used to represent the species in interspecific comparisons.

G. carvalhoi was compared (Table III, Graph 4) with *G. darwinii*, represented by a good topotypical sample from Salvador, Bahia, and with *G. geckoides*, represented by a composite sample from Exu, Catinga do Moura and Paraíba, statistically very homogenous and covering well the geographical distribution of the form (Vanzolini 2004). Of *G. guttulatus* there were not enough materials.

Analysis of covariance shows that the lines of

TABLE III

***Gymnodactylus carvalhoi* and *G. geckoides*, comparison of meristic characters.**

Species	N	R	m	s	V	t
Tubercle rows						
geckoides	192	12	12			
						64.584***
carvalhoi	76	13 – 16	14.0 ± 0.06	0.4	3.0	
Tubercles in a paramedian row						
geckoides	192	37 – 52	44.7 ± 0.19	2.7	5.9	
						14.434***
carvalhoi	57	31 – 49	38.2 ± 0.52	3.9	10.2	
Ventrals						
geckoides	203	18 – 24	20.8 ± 0.09	1.2	5.8	
						3.170**
carvalhoi	68	17 – 24	20.2 ± 0.21	1.7	8.4	
Lamellae						
geckoides	214	13 – 19	15.7 ± 0.08	1.3	8.0	
						7.155***
carvalhoi	86	13 – 18	14.6 ± 0.16	1.1	7.6	

Conventions as in Table I, plus *t*, Student's, significance of the difference between means.

TABLE IV

***Gymnodactylus*, statistics of the regression of tail length on body length.**

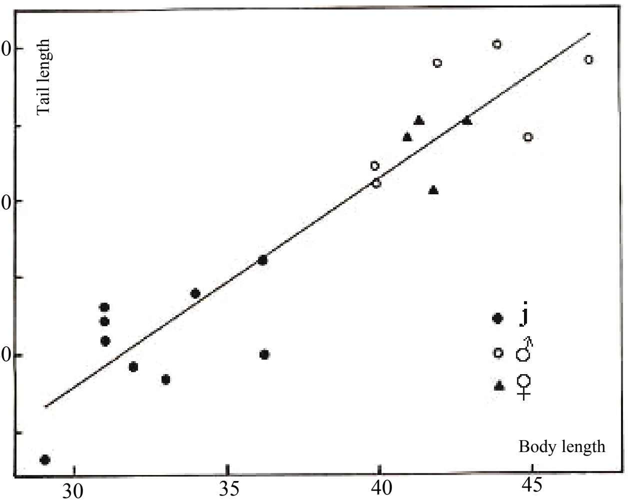
Sample	N	R(x)	R(y)	b	a	F	r^2
carvalhoi							
Serra da Mesa II j	9	29 – 37	33 – 48	1.17 ± 0.470	2.7 ± 3.02 ns	6.227*	0.4708
♂ ♀	8	40 – 47	51 – 60	1.14 ± 0.370	7.4 ± 2.68*	9.574*	0.6147
j ♂ ♀	17	29 – 47	33 – 60	1.44 ± 0.124	–5.7 ± 2.18**	135.433***	0.9003
all	27	29 – 49	33 – 60	1.28 ± 0.077	0.9 ± 2.00 ns	266.457***	0.9142
darwinii Salvador	35	23 – 52	24 – 66	1.42 ± 0.053	–7.1 ± 2.09***	721.832***	0.9562
geckoides all	73	20 – 42	23 – 53	1.26 ± 0.058	–0.7 ± 1.12 ns	474.915***	0.8699

Conventions: N – specimens in sample. R(x), R(y) – ranges of the variables. b – coefficient of regression ± its standard deviation. a – intercept ± its standard deviation. F – Fisher's quotient of variances (significance of the regression). r^2 – coefficient of determination. ns – not significant at the 5% level. * – significant at the 5% level. ** – significant at the 1% level. *** – significant at the 0.1% level.

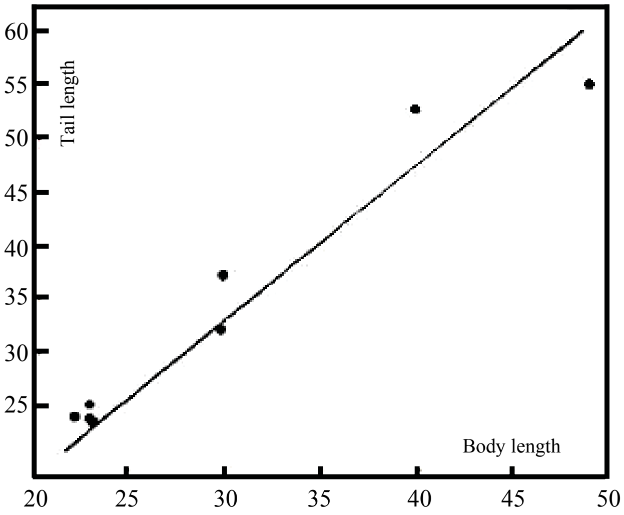
the three species may be considered parallel (F = 1.962, 2/130 df), but that there is a barely significant difference in the intercepts (F = 3.267, 2/130 df). Tukey's test shows that *G. carvalhoi,* with longer tails, is the discrepant species, but the differences are very small.

COMMENT

As can be seen in Map 2, the presently known areas of distribution of the two forms do not overlap, do not even meet: they are separated by a gap some 250 km wide. This gap has not been explored for *Gymnodactylus.* Otherwise, given their extensive



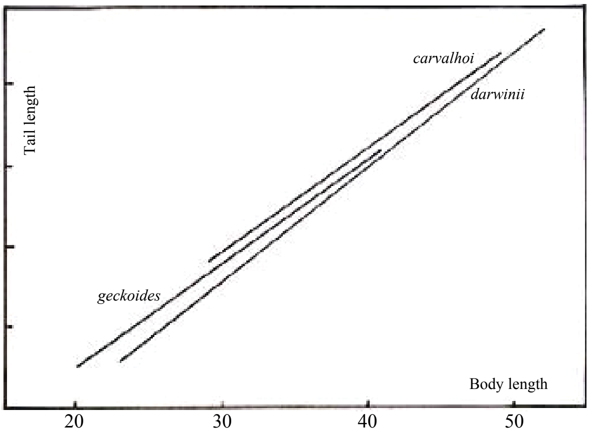
Graph 2 – *Gymnodactylus carvalhoi.* Regression of tail length on body length, Serra da Mesa, Go.



Graph 3 – *Gymnodactylus carvalhoi.* Regression of tail length on body length. Specimens from other samples plotted against the Serra da Mesa regression.

distribution in the caatingas and in the eastern cerrados, there is every reason to expect that the gap will be ultimately closed by further collecting. For practical purposes the two forms may be considered parapatric.

This geographical setting and the nature of the differences between *G. carvalhoi* and *G. geckoides* make it impossible to reject *prima facie* the hypothesis of two subspecies. This is the hypothesis I embraced in 1953, impressed by allopatry and by resemblance. These still impress me very much, but I now prefer to rely on intergradation. However, we



Graph 4 – *Gymnodactylus,* Regression of tail length on body length. Interspecific comparisons.

GAZETTEER

All latitudes South, all longitudes West.

Alto Parnaíba, Ma. 0906, 4557.
Barra do São Domingos, To.
A tributary of the Rio Paranã on its right bank, at 1324, 4712.
Carolina, Ma. 0722, 4726,
Catinga do Moura, Ba. 1058, 4045.
Engenheiro Dodt, Pi. 0848, 4556.
Exu, Pe. 0731, 3943.
Gurupí, To. 1143, 4904.
Ipueiras, To. 1114, 4828.
Mesa, Serra da, Go. 1415, 4835.
Niquelândia, Go. 1427, 4827.
Palmas, To. 1002, 4820.
Peixe, To. 1202, 4821.
Pirenópolis, Go. 1551, 4857.
Porto Nacional, To. 1042, 4825.
Posse, Go. 1405, 4620.
Rio Verde (locality), Go. 1748, 5056.
Salvador, Ba. 1300, 3830.
São Domingos, Rio das Mortes, Mt. 1330, 5124.
Xingó, Al. 0924, 3758.

have no transect between the two areas, and it will not be easy to arrange for one. There are no roads, of whatever description, crossing from the western caatingas into the eastern cerrados.

One (admittedly weaker) alternative is to check the pattern of geographical differentiation of

G. carvalhoi for suggestions of distributional structure compatible with intergradation. I can find none; anyway, the density of coverage is not promising. On this provisional, and acknowledgedly precarious basis, I keep (in the interest of caution and parsimony) the two forms for the time being as separate species.

PROCESS

Whether full species or subspecies, *G. geckoides* and *G. carvalhoi* are obviously closely related, sharing recent common ancestry, and we should inquire on the mechanism of differentiation. The study of speciation based on plain systematics involves advantages and disadvantages. Among the former are the ability to explore vast geographical and ecological spaces; among the latter are the usual unavailability of genetic information and, in many cases, the lack of natural history data. In the present case, the sampling is excellent, covering ca. 700,000 sq km, representing much of the morphoclimatic domain of the caatingas and of the eastern half of the cerrados. There is conclusive evidence (Vanzolini 2003) that, in the species core area, in Tocantins, it has a decided preference for interfluvial cerrado, rather than for the other elements of the domains' landscape, gallery forest and backswamp.

In the circumstances, the preeminent fact is that two adjacent morphoclimatic domains are involved. When differentiation occurs within a domain, one is naturally led to a model of refuges, i.e., of past discontinuities in presently continuous ecologies, either of open or forested biomes (Vanzolini 1997, 2002). On the contrary, in the case of two adjacent domains, one has to have recourse to parapatric speciation.

There is a traditional distinction between sympatric and parapatric speciation (e.g., Via 2001, Gavrilets et al. 2000). The concepts are in fact different, as sympatry implies overlap of ranges, and parapatry specifically adjacency. From the viewpoint of speciation theory, however, the two concepts do not necessarily differ. The relevant feature for sympatric speciation (Mayr 1963) is "the origin of isolating mechanisms within the dispersal area of the offspring of a single deme". Since one of the populations has managed to colonize an adjacent area, the criterion is obviously fulfilled. This is especially true in the case of the Brasilian morphoclimatic domains, separated not by clinally arranged intermediate belts, but by mosaics of interdigitations, often amputated, resulting into minor enclaves of the contrasting biomes (Ab'Sáber 1967, 2003, Vanzolini 1974, 1976, 2002) and facilitating transit between them.

The theoretical basis of parapatric (sympatric) speciation is well established (e.g., Via 2001, Turelli et al. 2001, Church and Taylor 2002), but cannot be automatically extended to purely systematic studies, which must rest on the analysis of spatial and statistical patterns. I think in this regard the present study is well founded, and may be considered as evidence of the presence of the process in South America – a thing still to be desired (Turelli et al. 2001).

The novel feature of the case, from the South American viewpoint, is the presence of closely related forms specialized respectively to caatinga and to cerrado, in contradiction with the general pattern of absence of such specializations and prevalence of a common lizard fauna in the " diagonal of open formations" that aggregates caatingas and cerrados, southwest to the Chaco (Vanzolini 1976).

POSTSCRIPT REGENERATED TAILS

The Serra da Mesa sample afforded an opportunity of investigating a subject seldom dealt with, the potential of regeneration of the gekkonid tail. There are in the sample six adult specimens with relatively long but (inferring from the morphology of the scales) clearly regenerated tails. Their length varies from 75 to 83% of the length calculated by the regression equation for specimens of their body length. This is a considerable power of recuperation, but they all fall below the 5% confidence interval of the regression.

APPENDIX

***Gymnodactylus carvalhoi*, raw data.**

MZUSP	Locality	Sex	Length	Tubercles		Ventr.	Lam.
				trv.	lgt.		
4006	Barra do Rio S. Domingos, To	j	38 + x	13	–	23	14
4007	”	j	37 + x	14	38	24	14
4008	”	♀	40 + x	14	43	–	17
4009	”	j	36 + x	14	–	21	15
4010	”	j	29 + x	14	32	20	16
4011	”	j	30 + 42	15	38	22	15
4012	”	j	36 + x	14	–	22	15
4013	”	j	33 + x	14	–	–	-
4014	”	j	28 + x	13	36	22	15
4015	”	♂	36 + x	–	–	–	16
4016	”	j	23 + x	14	40	20	17
4018	”	j	30 + 37	14	38	22	–
4019	”	j	33 + 35	14	22	21	17
4020	”	j	21 + 36	14	38	22	16
4021	”	j	26 + x	14	–	22	16
4022	”	j	38 + x	–	–	–	15
4023	”	j	27 + x	14	37	–	15
4026	”	j	23 + x	14	42	20	15
4027	”	j	22 + x	14	37	21	15
4029	”	j	23 + 29	–	–	22	16
4030	”	j	22 + 29	14	36	19	15
4031	”	j	24 + x	15	33	22	15
4032	”	♀	42 + x	14	39	–	18
4033	”	j	23 + 30	–	–	–	–
4052	S. Domingos (Rio das Mortes), Mt	♀	42 + x	14	40	21	13
4053	”	♂	42 + x	14	40	21	13
4053	”	j	35 + x	14	43	22	13
4054	”	♂	43 + x	14	–	22	13
4854	”	j	22 + x	14	–	–	–
7115	Carolina, Ma	♂	41 + x	16	40	20	14
7116	”	j	36 + x	14	40	20	15
29617	Rio Verde, Go	♂	42 + x	16	49	23	17
56572	Pirenópolis, Go	♀	46 + x	13	38	23	16
57017	Gurupí, To	♀	45 + x	14	41	21	14
69394	Posse, Go	♂	40 + 58	–	–	–	15
69395	”	♂	–	–	–	21	14
69396	”	♀	–	–	–	–	13
77824	Niquelândia, Go	j	33 + x	14	–	17	–
78244	Porto Nacional, To	♂	46 + x	14	44	22	15

APPENDIX (continuation)

MZUSP	Locality	Sex	Length	Tubercles		Ventr.	Lam.
				trv.	lgt.		
87119	Palmas, To	♂	49 + 60	14	40	20	13
87120	”	j	39 + x	14	41	21	13
87121	”	♀	41 + x	14	–	22	14
90093	Niquelândia, Go	♂	45 + 54	–	38	23	16
90094	”	♀	47 + x	13	37	19	15
90095	”	♀	45 + x	13	–	–	16
91183	Ipueiras, To	♂	41 + x	14	41	21	14
91184	”	j	33 + x	14	37	20	13
91185	”	j	23 + 29	14	41	22	14
91186	”	♂	43 + x	14	42	23	16
91187	”	♀	48 + x	13	19	21	16
91288	Serra da Mesa, Go	♂	43 + x	–	–	14	
91289	”	♂	43 + x	–	32	–	14
91290	”	♂	46 + x	14	31	18	13
91292	”	♀	42 + x	–	43	–	–
91293	”	♂	45 + x	14	42	–	16
91294	”	♂	42 + x	14	–	18	14
91295	”	♂	43 + x	14	–	–	15
91296	”	♀	48 + x	13	–	–	15
91297	Serra da Mesa, Go	♀	40 + x	14	–	17	14
91298	”	♀	45 + x	–	–	–	13
91299	”	♀	48 + x	14	–	18	15
91300	”	♀	47 + x	14	41	17	14
91301	”	♂	41 + x	–	34	18	14
91302	”	♂	40 + x	14	–	–	13
91303	”	♀	48 + x	14	46	20	16
91304	”	♀	42 + x	–	–	–	16
91305	”	♀	41 + x	14	–	18	13
91307	”	♀	–	14	–	20	14
91308	”	♀	49 + x	14	34	–	14
91309	”	♀	49 + x	15	36	19	14
91310	”	♂	46 + x	–	–	21	14
91311	”	j	33 + x	14	–	–	13
91313	”	♀	42 + 50	14	–	22	14
91509	Peixe, To	♀	45 + x	14	42	19	14
91510	”	♂	42 + x	14	45	19	14
91511	”	♂	45 + x	14	37	20	15

APPENDIX (continuation)

MZUSP	Locality	Sex	Length	Tubercles		Ventr.	Lam.
				trv.	lgt.		
Uncatalogued sample							
Field number							
33594	Serra da Mesa, Go	j	38 + 40	14	–	–	14
33870	”	j	37 + 48	13	40	21	14
34022	”	j	29 + 33	13	36	19	13
34066	”	♀	41 + 54	15	–	22	14
35062	”	♂	44 + 60	14	–	19	14
35082	”	♂	40 + 52	15	39	19	14
35145	”	♂	46 + 49*	14	35	20	14
35584	”	j	31 + 42	–	–	–	–
35824	”	j	31 + 43	14	33	21	14
36514	”	♂	47 + 59	14	37	19	14
36528	”	♂	44 + 45*	14	34	18	14
36562	”	J	39 + 39	–	–	–	–
36939	”	J	34 + 44	15	36	29	14
38217	”	♂	42 + 54	14	34	19	14
39192	”	♂	40 + 51	14	33	20	14
39817	”	j	35 + 40	14	–	19	15
40026	”	j	31 + 41	15	35	21	14
40283	”	♀	42 + 41*	15	44	18	14
40921	”	j	35 + 46	13	–	19	15
43983	”	♀	42 + 55*	13	34	19	14
44308	”	♀	42 + 43*	15	–	18	14
44388	”	j	33 + 38	14	37	18	13
46627	”	♀	43 + 55	15	43	21	14
46635	”	♂	42 + 48	–	–	–	16
47922	”	♂	43 + 44*	14	38	18	14

Abbreviations. Length, body + tail. Tubercles, trv., transversely counted at midbody; lgt., in a paramedian row. Ventr., ventral scales, transversely counted at midbody. Lam., fourth toe lamellae. *Tail regenerated.

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RESUMO

Gymnodactylus amarali vem sendo considerada uma subespécie de *G. geckoides* amplamente distribuida nos cerrados brasileiros. Exame de um exemplar de Alto Parnaíba, Maranhão, localidade próxima da localidade tipo, Engenheiro Dodt, Piauí, indica que se trata de uma espécie válida, aparentemente limitada ao Alto Parnaíba. A forma anteriormente identificada como *Gymnodactylus geckoides amarali* é aqui descrita como *Gymnodactylus carvalhoi,* sp. n., assim diagnosticada: padrão de colorido dorsal obsoleto ou, mais frequentemente, com ocelos de expressão moderada; 13 – 16 (moda 14, 72%) fileiras longitudinais, pouco regulares, de tubérculos dorsais; 31 – 49 tubérculos em uma fileira para – mediana; 17 – 22 fileiras transversais de escamas ventrais; 13 – 18 lamelas infradigitais no 4° artelho; cauda (pouca coisa) mais longa do gênero. A nova espécie é estatisticamente comparada a *G. geckoides*, extensivamente distribuída nas caatingas; há acentuadas diferenças em todos os caracteres merísticos, mas apenas um deles (número de fileiras de tubérculos) é por si mesmo diagnóstico. Propõe-se, em caráter provisório, por questão de cautela e parcimônia, considerar as duas formas como boas espécies. Breve consideração é feita do modelo de especiação julgado mais provável, o parapátrico.

Palavras-chave: Especiação, Lagartos: sistemática.

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