Papéis Avulsos de Zoologia

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ON SOUTH AMERICAN *HEMIDACTYLUS* (SAURIA, GEKKONIDAE)

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ABSTRACT

Three forms of Hemidactylus are known to occur on continental South America (Kluge, 1969; Hoogmoed, 1973): (i) H. mabouia (Moreau dc Jonnès, 1818), widespread; (ii) H. brookii leightoni Boulenger, 1911, in Colombia from the Caribbean coast to the Amazonian slopes of the Andes; (iii) H. palaichthus Kluge, 1969, from the peninsula of Paria on the northwest, to coastal Surinam on the northeast, to the Brasil-Guyana border on the southeast, to the Duida region on the southwest. I hereby extend the distribution of palaichthus southwards on the Negro valley, describe H. agrius, sp. n., from the northeast of Brasil, discuss its origin and distribution and comment on the distribution and means of dispersal of H. mabouia.

INTRODUCTION

The Brasilian Academy of Sciences has under way a research program on the ecology of the semi-arid Northeast of Brasil. As part of the program the Museum has conducted four field trips to the area. In 1972 in Ceará and in 1975 in Piauí we obtained a number of lizards of the genus *Hemidactylus* that I think represent a hitherto undescribed species. The recognition of this form of course implied in a review of the other South American hemidactyls; the materials at hand permitted a re-assessment of certain problems of distribution and evolution, especially in terms of speciation patterns of non-forest lizards.

Hemidactylus agrius, sp. n.

Holotype: MZUSP 38391 3, Valença do Piauí, Piauí, 23-29.iii.1975, field number 75.0416.

Paratypes: MZUSP 38387-38390, 38392-38394, 38411-38431, same data as the type. Paratypes will be deposited in the Museum of Comparative Zoology.

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DIAGNOSIS

Close to *H. palaichthus* and *brookii leightoni* in having the basis of the fourth toe covered with lamellae, not granules. Dorsum with flat ribbed granules and trihedral tubercles, also ribbed; the tubercles irregularly arranged, 8-13 counted transversely at midbody, 12-24 on a paravertebral line between the level of the axilla and that of the groin. Male with an unbroken series of 26 to 34 pores, separated from the anus by one row of large and 3-4 rows of very small scales. Dorsal aspect of arm without tubercles.

DESCRIPTION

General habitus robust. Head with a shallow median depression from the frontal region to the supranasals.

Rostral high, with a median depression and a posterior cleft; hind margin transverse. Supranasals large, swollen, meeting on the midline or, in approximately one third of the specimens, separated by one granule or by two granules longitudinally arranged. Nostril large, surrounded by the rostral, by a small corner of the first labial, and by a large lower and a smaller upper postnasals. The largest granules of the head are on a straight patch between the eye and the supranasal, and decrease forwards; the smallest are on the median depression. On the parietal region the granules are very small, interspersed with small tubercles, keeled or not.

On the loreal region the granules are elongate and more or less arranged in longitudinal rows. There is a row of flat enlarged granules in contact with the upper labials. The mouth is curved around the posterior half of the eye. Eight to 11 upper labials, the posterior ones very small, separated from the eye by 2-3 rows of small granules. Superciliary edge with larger, flat granules in front, becoming smaller and erect posteriorly. Temporal region with very small granules interspersed with small conical smooth tubercles, irregularly distributed. Ear opening small, vertically elliptic, without differentiated auricular scales.

Symphysial large, triangular. Two pairs of post-symphysials, the median pair largest and meeting on the midline; the outer pair sometimes divided in two. Lower labials 8-10, decreasing, bordered by a row of small scales, also decreasing. Gular scales very small, smooth, flat, well imbricate, changing abruptly into the ventrals midway between the ear and the arm.

Dorsal lepidosis composed of a background of flat granules interspersed with tubercles. The granules have 3 coarse ribs or low keels. The tubercles are variable in size and shape, conical to trihedral, with 8 to 11 marked ribs on each face. They are not arranged in regular rows (not even the paravertebrals), and cover an area narrower at the level of arm and thigh, of variable extent down the flank, reaching the ventrals or stopping several rows of granules from them. Eight to 13 tubercles across midbody (where the number is maximum). Twelve to 22 tubercles on a paravertebral transect, in the males; 16 to 24 in the females. On the middle of the back there are one to three granules between two diagonally adjacent tubercles; rarely two tubercles meet. The lateral granules change gradually into the ventral scales, that are small, cycloid, smooth, well imbricate, arranged in diagonal rows. In the male, an unbroken series of femoral and preanal pores. The femoral pores are small and rounded, except for the innermost one, that may be a little larger; the preanal pores are large, transversely elongate, with the eventual exception of a median element, slightly displaced forwards, that may be rounded. The medial preanal pores are separated from the anus by 4-5 rows of scales, of which the first is large and the others minute. Sixteen (8 + 8) to 22 (11 + 11 or 10 + 12) femoral pores; 9-12 preanal pores; total number of pores 26-34. The smallest specimen with pores measures 47 mm shout to vent, and has 31 pores indistinguishable from those of the larger males.

Dorsal aspect of upper arm proximally with swollen but flat and imbricate scales, becoming towards the elbow more conical, erect, juxtaposed. Anterior edge of forearm and dorsal aspect of carpus with small, flat, smooth, imbricate scales. Forearm dorsally with granules and tubercles similar to those of the dorsal region. Remainder of fore limb granular. Fingers free, II-V subequal, I shorter; all ventral lamellae reaching the palm; distal phallanx of pollex shorter than the others, but clearly free and clawed.

Hind limb scaled dorsally as the dorsum, ventrally as the venter. Toes free, II-V subequal, I shorter; all lamellae reach the sole; 8-10 lamellae on the fourth toe; distal phallanx of pollex shorter than the others, but free and fully clawed. Dorsal aspect of tarsus with tubercles.

Tail with a marked constriction (preferential plane of autotomy) some 3 tubercles behind the posterior margin of the thighs. The tubercles of the first caudal annulus are placed immediately after the constriction. The two first annuli have 8 tubercles, regularly distributed on the dorsal half; the following annuli 6 tubercles. The complete tail (only 4 seen) has 22-24 annuli, and the number of tubercles per annulus decreases to 2 near the tip. The dorsal tubercles are conical, the lateral ones almost blade-like. The change from an 8- to a 6-tubercled annulus happens by the loss of two small and slightly out of line paramedian tubercles. The transverse rows of tubercles are separated by flat granules, those immediately adjacent to the tubercles larger and sub-imbricate. Between the second and third whorls of tubercles there are from 4 to 6 rows of granules. The scales of the median ventral row are as broad as their distance from the lateral tubercles, from which they are separated by 3 rows of scales, of which the paramedians are the largest. In the regenerated tail the dorsal and lateral aspects are covered by irregular flat small scales; the mid ventrals are short, broad, very irregular.

The dorsal parts vary from very heavily to very lightly patterned; this may be in part a matter of preservation rather than of actual phenotypes. At one end one has a network of heavy brown lines forming 5-6 grayish brown cells on each side of the back, from the shoulder to the root of the tail. At the opposite extreme the animal shows vague wavy transverse bands, varying in depth of brown, over an ashy background. Between these extremes there are many degrees of intermediacy. The color pattern of preserved animals is definitely not related to sex or age. The light zones, under magnification, show contracted, star-shaped melanocytes; the dark brown areas are smudged. This pattern cuts across the granules and tubercles. The dorsal surface of the limbs is more or less distinctly barred, in relation with the pattern of the back. The dorsal surface of the head shows poorly defined, longitudinally arcuate dark and light bands, again varying in degree of expression. The dorsal aspect of the tail shows more or less definite chevrons, not related to the caudal annuli.

The side of the head shows two more or less distinct streaks: an upper light one from the supranasal through the upper half of the eye to the scapular region; the lower one, dark, adjacent to the first, encompasses the upper half of the ear opening and ends at the root of the arm. The supralabials are irregularly spotted. On the sides of the neck and throat there is a condensation of dark points.

The lower parts appear white to the naked eye. Under magnification each ventral shows one to three, each gular usually one, at times two, contracted melanocytes. The midventral scales of the tail and the scales of the paramedian row are densely spotted along the edges; the other two rows of latero-ventrals are densely spotted all over.

The name, suggested by Ulpiano T. Bezerra de Meneses, is meant to stress that this form is not associated with forests, but with the middle north of Brasil.

GEOGRAPHICAL VARIATION

We have four additional specimens (MZUSP 27831, 28029-28031), all female, collected at Coluna, a crossroads near Justiniano Serpa in Ceará (Map 1). They agree closely with the type series except in the number of tubercles at midbody, that are 13-15 in Coluna, 8-13 in Valença (Table 3). Taking only Valença females (range 11-13) the difference is still highly significant (probability 0.01, median test). The differences in number of paravertebral tubercles (Table 4) are not significant (median test, probability 0.33, females only).

At present it is not possible to evaluate properly the meaning of the differences in number of tubercles, especially since there are no males available from Ceará. I am identifying these specimens as *agrius* for the time being, but of course they are not to be considered as paratypes.

DISCUSSION

Preliminary. I am inclined to believe that *palaichthus* and *agrius* represent a native stock (i.e., not a man-borne immigrant) and for this reason I shall keep my argument within South America; only three forms, *leightoni*, *palaichthus* and *mabouia*, will be compared with *agrius*. The African and West Indian forms are omitted.

Seen alive, and, especially (as in the Negro) side by side, *H. mabouia* and *palaichthus* are very different animals; the former is a flatter lizard, with a slender neck and quick nervous movements; *palaichthus* is stockier and looks much more clumsy and deliberate. To the forewarned eye the differences in body shape are evident in preserved materials. As to *agrius*, I frankly do not remember having

seen it alive either in Valença or Coluna, not having paid any attention to town specimens when brought in; after preservation, it is hardly distinguishable from *palaichthus* and quite different from *mabouia*.

H. mabouia stands alone in that the infradigital lamellae of the fourth toe do not reach the sole; instead, the base of the digit is covered with minute scales. In *palaichthus* and *agrius* the lamellae go all the way from the sole of the foot to the tip of the digital dilation.

I attach importance to a character (Plate 1) that seems to have been so far overlooked: the toes of H. mabouia are slender, and toes IV and V form a right angle, very evident in Kluge's (1969) fig. 3A. On the contrary, the toes of *palaichthus* and *agrius* are stubby, and the angle formed by the hallux and the fourth toe is decidedly acute. To me, the anatomical design of the foot of a climbing lizard takes precedence over numbers of tubercles or femoral pores in estimating relationships. Convergence is of course always possible, but direct strong selective pressures result in more durable trends, an we are dealing here, as mentioned below, with a scale of a few thousands of years.

H. brookii leightoni has the complete row of infradigital lamellae, but its foot otherwise closely resembles that of *mabouia*, as does the general body build. Accessorily, it differs from *palaichthus* and *agrius* in having 2-4 poreless ventrals on the midline, separating the two series of pores, and, according to Kluge, may show differentiated auricular scales, which do not appear in the other species.

In what follows, I concentrate on a comparison between *palaichthus* and *agrius*, introducing *leightoni* for the sake of completeness, but no more than that.

Materials. Son after the publication of Kluge's paper we received from Colonel Moacyr Alvarenga three specimens of *palaichthus*, from Surumu, Roraima, an Air Force strip on the upper Rio Surumu, near the Venezuelan border.

In 1972 the Museum sent two herpetological parties to the Rio Negro, on board the "Lindolpho R. Guimarães" and "Garbe", che boats of the Expedição Permanente da Amazônia (EPA), then maintained by the Museum and by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP); both parties were led my myself. Six stations were worked and a good reptile collection assembled, among which was a reasonable series of *Hemidactylus*. In 1973 R. A. Mittermeier visited the middle Negro, using the EPA boats, and collected additional specimens at Barcelos. These materials are listed in the appendix and the localities shown on the maps.

We have one further specimen (MZUSP 4224) of H. palaichthus, received from the Instituto Butantan with the indication "Rio Purus", and no mention of collector, date or source. I had previously (Vanzolini, 1968) identified this animal as H. mabouia. Our collection has 248 Hemidactylus mabouia from the core of the hylaea (Iquitos to Belém), among which 19 from the Purus, and no palaichthus from outside the part of the Negro valley outlined above. I place the "Purus" specimen on record, but do not use it in this paper, as I am extremely doubtful of the locality.

Finally, two MCZ specimens, 53242 an 53243, both female, from San Felipe de Rio Negro, Venezuela, listed by Kluge as *leightoni*, turned out to be *palaichthus*. Kluge's mistake is understandable, as his diagnoses do not differentiate between females of *palaichthus* and *leightoni*. The matter, however, is easy. The number of paravertebral tubercles (Table 1) is diagnostic, as is the presence of tubercles on the upper arm and tarsus of *palaichthus*. Additionally, the scales adjacent to the anterior upper labials are enlarged, flat in *palaichthus*, and identical to the snout granules in *leightoni*.

		N	R	x	s- x	v
Pores						
leightoni		8	21-28	24.3	.63	8.5
palaichthus	Kluge	24	32-43	37.1	.73	8.3
	Negro	18	35-46	40.2	.71	7.5
agrius		10	26-34	30.8	.68	7.0
Tubercles (trai	nsverse)					
leightoni		27	14-23	18.3	.41	11.8
palaichthus	Kluge	40	17-25	21.5	.35	10.4
	Negro	49	11-17	13.6	.22	11.3
agrius		26	8-13	11.5	.20	9.0
Tubercles (para	avertebr	al)				
leightoni		27	16-22	18.9	.33	8.9
palaichthus	Kluge	42	17 - 28	22.0	.35	10.4
	Negro	46	23-35	27.8	.31	7.6
agrius		24	12-24	19.2	.63	15.7

TABLE 1 - Meristic data

Of H. b. leightoni we have 4 specimens from Honda and 3 from Barranquilla. Except for one adult female, they are not very well preserved, and do not afford adequate measurements, but permit an examination of all scale characters.

Meristic characters. I selected for analysis six meristic characters: number of upper and lower labials, of fourth toe lamellae, total number of pores, and number of dorsal tubercles, both counted transversely at midbody and longitudinally on the paravertebral region.

The distributions were tested for the presence of sexual differences, taking as females the specimens without pores that were as large as or larger than the smallest specimen with pores (adult male). No significant differences were found. The distributions were then completed by adding the specimens (juveniles) smaller than the

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smallest adult male. The data on the characters that afforded some degree of discrimination are shown in Tables 1 to 4. In Table 1, as usual, N stands for the number of individuals in the sample, R for the range of the variable, \bar{x} for its arithmetic mean, s_x for the standard deviation of the mean and V for the coefficient of variation. The data for *H. brookii leightoni* and for "*palaichthus* Kluge" were taken from Tables 19, 14 and 15 of Kluge (1969).

Checking my data against Kluge's I find perfect agreement in the number of labials and of lamellae. In the number of pores Kluge's mean is significantly smaller than mine (t = 5.45; probability less than 0.001). This is a character than can be determined without ambiguity and it is therefore possible to say that it shows geographical variation. Since Kluge lumped together all his samples of *palaichthus*, from St. Lucia, Trinidad, Venezuela, Colombia, and Brasil, nothing else can be said at present about the geographical pattern.

In both tubercle counts my values differ strikingly from Kluge's. In the case of the midbody counts, in which the two distributions barely overlap, this must be due in large part to the method of counting. In my specimens the arrangement of the tubercles is rather irregular, and I did not count tubercle rows, as did Kluge, but the tubercles that actually intersected a straight line at midbody. That the method of counting should explain at least a large part of the disagreement between my data and Kluge's is made more probable by the fact that the values I obtained for my Surumu lizards (11-14) are outside the range of Kluge's sample, that included 2 Roraima specimens, one of them from the lower Rio Surumu. As the main purpose of my scale counts is a comparison with the species described above, whose tubercles are still less well organized than those of Negro palaichthus, I adhered to my counting method. Checking its accuracy, I found that in 12 replicate counts 6 were identical to the first, 5 differed by one tubercle and one by two. I consider this a reliable scale count.

In the case of paravertebral tubercles there is overlap of the distributions but the difference is still highly significant (t = 12.396 for 86 degrees of freedom; probability less than 0.001). The reproducibility of this is not so good as that of the transverse count; in 11 independent replicates only two values coincided; there were 3 disagreements by one tubercle, 3 by two, and 3 by 3. There was no bias, however, and it can be safely expected that errors in counting may eventually modify the range by one unit or so, but certainly not the central tendency. On the other hand, although it is probable that part of the difference between my data and Kluge's may be attributed to the method of counting, the points of reference are well defined (level of the axilla and of the groin) and I think geographical differentiation will be found in this character. In agreement with this, the counts of the Surumu specimens are all at the lower extreme of the Negro distribution, right on the middle of the range of Kluge's counts.

Checking my scale counts for *H. b. leightoni* against Kluge's I find very good agreement, except again in the matter of tubercles at midbody. My range is 10-12, Kluge's 14-23; there is no doubt we

are counting different things. Of minor importance, I have one specimen with 29 pores, which is one above the previous highest value.

The practical import of the differences, in number of pores, of tubercles at midbody and of paravertebral tubercles, some differences being due to geographical variation, some to procedure in counting, is that H. agrius must be separately compared with Kluge's data and with my Negro materials. Their relevance to the problem of speciation will be discussed later.

As to the femoral pores, those of *agrius* tend to be small and round, and the preanal pores clearly oblong; in *palaichthus* there is practically no difference between the two series; in *leightoni* the pores vary from oblong to slit-like.

In agrius the preanal pores are separated from the vent by 4-5 rows of scales, those of the first row similar to the posterior abdominals, the others minute. In *palaichthus* and *leightoni* all scales of the 4-5 rows that separate the pores from the anus are large, similar to the abdominals.

As to the number of pores, the range of *agrius* narrowly overlaps Kluge's *palaichthus* distribution and fails to overlap my Negro data; *leightoni* overlaps *agrius* and no other (Table 1).

With regard to fourth toe lamellae, I can only compare my own *palaichthus* sample and *agrius;* the distributions of frequencies of number of lamellae are strikingly different, but the character is not diagnostic (Table 2).

As said, my data and Kluge's on the number of tubercles at midbody in *palaichthus* are not comparable; the comparison with *agrius* must be based on the Negro specimens, which were counted at the same time and in the same way. It can be seen in Tables 1 and 3 that the Valença sample differs markedly from Negro *palaichthus* and from *leightoni*.

Finally, Tables 1 and 4 show that the differences between all forms in the number of paravertebral tubercles are marked.

Other scale characters. As described, the supranasals of agrius are large, squarish; they either meet on the midline (69% of 29 specimens examined), are separated by one small granule (14%) or by two longitudinally arranged granules (17%). In *palaichthus* and *leightoni* there is always a polygonal scale broadly separating the supranasals, that are also polygonal, much smaller than those of agrius.

The dorsal surface of the upper arm in *agrius* is covered with scales thickened and a little raised, uniform in size and not keeled. In *palaichthus* the scales are irregular in size; usually there are actual tubercles, always at least large keeled subtubercular scales. In *leightoni* the brachial scales are flat, imbricate. *H. agrius* and *palaichthus* agree in having tubercles on the dorsal aspect of the tarsus; these are absent in *leightoni*.

Body proportions. I studied the regression of head length (tip of snout to anterior border of ear) and of snout length (to anterior border of orbit) on trunk length (snout to vent minus head) and of tail length on body length (snout to vent) in *agrius* and *palaichthus*; my *leightoni* specimens did not lend themselves well to measurement, and the results of the comparisons made did not justify further trouble. Linear regressions proved adequate in all cases. The respective data are shown on Table 5, in which N is the number of individuals, R_x is the range of the independent variable, b is the coefficient of regression, s_b its standard deviation, a the constant of regression, s_a its standard deviation and r^2 the coefficient of determination (square of the coefficient of correlation).

It will be noticed that the range of body lengths is broader in *palaichthus* than in *agrius*. This type of lack of homogeneity can lead to two kinds of distortion; (i) the error variance tends to diminish as the range of the independent variate increases; (ii) the coefficients of regression may differ even if the two distributions closely coincide in the region of overlap. Thus I have built a new distribution, "*palaichthus* truncated", by reducing the original distribution to the range of body sizes of *agrius*.

I have not been able to use Kluge's data because he presents them only as ratios. These are unadvisable in general (e.g. Atchley, Gaskins & Anderson, 1976) and specifically in this case, since the regression constants of the head and snout proportions differ significantly from zero (Table 5).

TABLE 2

		Fourth	toe	lamellae	
	8	9	10	11	N
palaichthus Negro		7	30	11	48
agrius	3	23	2		28

The regression of head length on trunk length (Table 5, Graph 1) in *H. palaichthus* has an excellent fit, both in the full and in the truncated distributions (r^2 respectively 0.97 and 0.92). The *agrius* fit (Graph 2) is inferior ($r^2 = 0.80$). Comparing the full samples, the difference between the coefficients of regression approaches but does not reach the 5% level of significance (t = 1.925 for 70 degrees of freedom, probability between 0.10 and 0.05); the difference between the constants of regression is significant at the 1% level (t = 2.8249). In the case of the truncated distribution the coefficients of regression differ at the 5% level (t = 2.550, 41 degrees of freedom). There is thus a real difference between the two forms, but it is too

	palaichthus	agr	ius
	Negro	Valença	Coluna
8		1	
9		-	
10		1	
11	6	10	
12	4	11	
13	13	3	2
14	13		1
15	8		1
16	3		
17	2		
	49	26	4

TABLE 3 - Tubercles at midbody

small to have diagnostic value or even to be noticed by the eye of the systematist.

The regression of snout length on trunk length (Table 5) is also better in *palaichthus*, both total and truncated, than in *agrius*. The regression coefficients differ at the 5% level in the case of the total samples; for the truncated sample, neither the coefficients nor the constants differ at the 5% level.

In tail length (only 10 specimens had intact tails) both forms agree very closely, and the fit of the regression line is excellent $(r^2 = 0.98)$, which I find remarkable in animals that excel in ease of autotomy and regeneration.

DISTRIBUTION AND EVOLUTION

NOTICE

No special mention will be made of localities shown on the 1:1,000,00 Map of the Americas of the American Geographical Society (AGS), which has a very good index. I have some comments on the 1:1,000,000 Map of Brasil published by the Instituto Brasileiro de Geografia e Estatística (IBGE), indexed in 1971.

	palaichthus	agr	ius
	Negro	Valença	Coluna
12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 33 33 33 33	1 4 6 7 12 8 5 - 1 - 1 - 1	1 - 3 2 4 2 - 3 6 1 1	1 - - - 1 1 1
	46	24	4

TABLE 4 - Paravertebral tubercles

H. palaichthus

I start (Map 1) with an analysis of the distribution of H. palaichthus, for which Kluge (1969) cites 19 mainland localities.

The Guyanan localities of Eartica (at the junction of the Mazaruni and Essequibo), Haiowa Fall and Kurupukari (on the middle Essequibo) are in forested areas (see GUYANA in the References). A less precise locality "lower Kuyuwini River" is also in a forested area. Kluge's Yapukarri is spelled Yupukarri in the AGS map and Yupukari in Guyanan maps; it is in the so-called "savannas" (more properly sub-types of cerrados) of the Brasil-Guyana border, near Karanambo and Lethem, Kluge localities not shown on the AGS map but easily found in other sources, such as the World Aeronautical

		N	Я	្ត 	ຜີ	đ	ນ ແ	∼́я
Head x trunk					2		3	
palaichthus		47	17-52	.31	.008	1.8	.33	.97
Ŧ	crunc.	18	26-44	.35	.026	.03	1.04	.92
agrius		27	25-44	.26	.026	3.3	.96	. 80
Snout x trunk								
palaichthus		47	17-52	.14	.004	• ت	.16	.97
Ŧ	trunc.	18	26-44	.15	.011	.2	.43	.92
agrius		27	25-44	.12	.014	1.4	.51	.74
Tail x body								
palaichthus		9	28-62	1.24	.197	-6.7	9.02	.991
agrius		4	35-54	1.28	.168	-9.7	6.53	.97
joint		10	28-62	1.26	.057	-7.9	2.58	.98

TABLE 5 - Data on linear regressions

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Chart. Isherton is a misspelling for Isheartun, a locality on the Upper Rupununi, at approximately $2^{\circ}5'N$, $59^{\circ}25'W$, some 30 km NW of Kuyuwini Landing (R. G. Zweifel, in litt.); it appears to be also in the "savannas".

In Brasil Kluge has two localities, Boa Vista, the capital of the Territory of Roraima, and Frechal, Rio Surumu. The former presents no difficulties; the latter (alternatively spelled Frexal and Flechal), is shown on the AGS map as Serra do Frechal. The locality is a cattle ranch on the right side of the Surumu, near its mouth on the Tacutu, and is named after the nearby hills. These two Roraima localities are also in open formations (Barbosa & Ramos, 1959).

Kluge's Venezuelan localities range from the peninsula of Paria to the upper Orinoco. Yucua is a misspelling for Yacua, on the south side of the peninsula, near its eastern tip; Puerto de Hierro is some 10 km to the west. Both localities are in an area of "espinares and cupizales" (Hueck, 1960), very xeric formations. Barrancas, Ciudad Bolivar, "nr mouth of Cinaruco River" (also spelled Sinaruco), and Puerto Ayacucho are well known localities on the Orinoco, all within the complex of the llanos. One MCZ specimen (83205) recorded as from "Loja Venade, Cerro Ayacucho", is actually from Laja Venado, near Puerto Ayacucho (J. A. Rivero, in litt.). Las Carmelitas (amusingly misspelled Las Caramelitas in Kluge) is on the Ventuari (Phelps & Phelps, 1950), in a region of mixed vegetation, including savannas (Hueck, 1960). Maroa, on the upper Guainia, and San Felipe de Rio Negro are in a similar area (*ibid.*), but apparently a more densely forested one. Finally Esmeralda, just south of Mount Duida, is said by Tate & Hitchcock (1930) to be in the middle of a savanna.

We have one specimen from Surumu, as said near the Venezuelan border, also in open formations (Barbosa & Ramos, 1959). All our other localities are on the Negro. Barcelos, Carvoeiro and Moura are to be found in any map. They all are reasonably old and populous villages (somewhat decadent nowadays), and sit in the middle of considerable clearings in the general forest of the Negro. At Carvoeiro *H. palaichthus* was common at night in its antropophilic niche, hunting insects on walls and posts. One single specimen was caught during the day, inside a house. At Moura the only *palaichthus* obtained was in second growth, in a patch where some 200 other lizards were collected, mostly *Anolis fuscoauratus* and *Gonatodes humeralis;* one single *H. mabouia* was brought in by children.

Paricatuba is a mission on the right bank of the Negro, opposite the eastern point of the Ilha Grande de Tapurucuara (ca 65° W). The area is densely forested, but all specimens were collected in open situations. They were frequent on the bases of leaves of two palms that grew in abundance in land cleared for pasture, *Maximiliana inajai* (Wall.) Spr. (inajá) and *Oenocarpus bacaba* Mart. (bacaba). They were also seen, but not caught, during the day, among dry palm fronds on the ground.

São João is a group of a few houses, on the right (south) bank of the Negro, a few kilometers above the mouth of the Aiuanã (misspelled Ajuana in the IBGE map), and so approximately 10 km east of Paricatuba. The settlement is small (6 dwellings in 1972), but is surrounded by much second growth, since it is one of a few places



Graph 1. Hemidactylus palaichthus, Rio Negro, regression of head length on trunk length.



Graph 2. Hemidactylus agrius, regression of head length on trunk length: H. palaichthus line added for comparison.

on the Negro where the inhabitants traditionally plant manioc not only for subsistence, but for sale of the flour (*farinha*); the amount of tilled land is larger than average for the area. All São João specimens were collected by women and children in scrubby second growth behind the settlement.

Tapera (misspelled Papera on the IBGE map) is an estate on the left bank of the Negro, a little below the mouth of the Iahá (misspelled Jaú on the IBGE map). The longitude is approximately $64^{\circ}35$ 'W. Several specimens were brought in; the only one I caught personally was under the thick semidetached bark of a log in a pasture, near the forest edge.

Thus it seems that H. palaichthus is fundamentally an open formation animal, with good pre-adaptations for perianthropic life. In the Negro it inhabits parts of the juxta-fluvial network of open formations that is one of the facies of the hylaean complex; I should expect it to do the same in the forested areas of Guyana. Although primarily nocturnal, it seems to display some diurnal activity.



Graph 3. Hemidactylus palaichthus, Rio Negro, and H. agrius, joint regression of tail length on body length.

Additionally, one specimen from the Upper Orinoco (no further data) in the Brussels museum, reported upon by Parker (1936) as *mabouia*, turned out on examination to be *palaichthus*. It is also to be expected (on geographical grounds) that the specimens reported by Donoso-Barros (1968) as *mabouia*, before the description of *palaichthus*, from Macuro, Cumaná an Cumanacoa should be better assigned to *palaichthus*, but these assignements should be held in abeyance until the specimens are examined.

The distribution as known does not coincide with that of any plant formation or other eco-geographical unit; the open formations where H. *palaichthus* occurs (espinares of Paria, llanos of the Orinoco, "savannas" of the Roraima) are not continuous, and the distribution inside the forests seems so far haphazard. This type of distribution invites explanation by recourse to climatic cycles, but first let us consider H. *agrius*.



Map 1. Distribution of *Hemidactylus palaichthus, agrius* and *brookii leightoni* on continental South America.

1, Yacua; Puerto de Hierro; Macuro. 2, Barrancas. 3, Ciudad Bolivar. 4, Mouth of the Sinaruco. 5, Puerto Ayacucho. 6, Las Carmelitas. 7, Maroa. 8, Esmeralda. 9, Bartica. 10, Haiowa Fall. 11, Kurupukari. 12, Karanambo; Yupukari. 13, Lethem. 14, Isheartun. 15, Lower Kuyuwini. 16, Frechal. 17, Boa Vista. 18, Surumu. 19, Paricatuba; São João. 20, Tapera. 21, Barcelos. 22, Carvoeiro. 23, Moura. 24, Valença do Piauí. 25, Coluna. 26, Cartagena; Bocagrande. 27, Barranquilla. 28, Rio Frio. 29, Tolu. 30, Bodega Central. 31, Puerto Wilches. 32, Cúcuta. 33, San Vicente. 34, Honda; Mariquit.a 35, Cambao. 36, Girardot. 37, Villavicencio. 38, Barinitas. 39, Orocué. 40, Popayán. 41, San Felipe de Rio Negro. 42, Cumaná. 43, Cumanacoa. 44, La Guaira.



Map 2. Distribution of Hemidactylus mabouia on continental South America.

Map 2. Distribution of Hemidactylus mabouia on continental South America.
1, Georgetown. 2, Malali. 3, New Nickerie. 4, Encampment Wakay. 5, Marataka River. 6, Paramaribo. 7, Lower Marowijne. 8, Cayenne. 9, Barcelos. 10, Carvoeiro. 11, Moura. 12, Manaus: Paraná da Mucura. 13, Napo. 14, Iquitos: Rio Itaya; Moropón. 15, Centro Unión; Rio Maniti. 16, Nazareth. 17, Leticia. 18, Coarí. 19, Berurí. 20, Nova Olinda. 21, Maués. 22, Itapiranga. 23, Oriximiná. 24, óbidos. 25, Santarém; Alter do Chão; Taperinha. 26, Serra do Navio. 27, Carcovado. 28, Igarapé Taperebá. 29, Belém. 30, São Luis. 31, Requena; Cedro Isla. 32, Roaboya. 33, Pucallpa. 34, Posuso. 35, Féijó. 36, Bocca do Acre. 37, Canutama. 38, Tapauá. 39, Rio Mamoré. 40, Porto Velho. 41, Barra do Corda. 42, Valença do Piauí. 43, Fortaleza; Maranguape. 44, Guaraní; Coluna. 45, João Câmara; Ceará Mirim; Extremoz. 46, Natal. 47, Mamanguape. 48, Guarabira. 49, Junco do Seridó. 50, Itamaracá; Igaraçu; Cruz de Rebouças. 51, Recife. 52, Pesqueira. 53, Sítio dos Nunes. 54, Carnaubeira. 55, Macció. 56, Barra de Penedo. 57, Simão Dias. 58, Salvador; Ilha Madre de Deus. 59, Jaguaquara and Jequié. 60, Ilheus. 61, Chapada dos Guimarães. 62, Goiania. 63, Pirapora. 64, Santa Clara. 65, Belo Horizonte. 66, Sooretama. 67, Santa Teresa; Colatina. 63, Campo Grande. 69, São José do Rio Preto. 70, Ribeirão Preto; Bonfim Paulista. 71, Tuiutí. 72, Muriaé. 73, Guaraparí. 74, Manguinhos; Atafona; Campos. 75, Chavantes. 76, Casa Branca. 77, Porto Novo. 78, Botucatu. 79, Tanquinho; Amparo. 80, Engenheiro Passos. 81, Rio de Janeiro and Coraa Grande. 82, São Paulo, Santo André and Cotia. 83, Ubatuba. 84, Caraguatatuba; São Sebastião; Ilha de São Sebastião; Sinha do Toque-toque; As Ilhas; Ilha dos Búzios; JIha Vitoria. 85, Bertioga; Piassaguera; Cubatão, Santos; São Vicente. 86, Peruíbe. 87, Cananéa. 88, Florianopolis; Ilhas dos Moleques; Ilha Campeche; Ilha do Arvoredo. 89, Porto Alegre; Viamão. 90, La Guaira.

Valença do Piauí, the type locality of *agrius*, is in a complex cerrado-caatinga contact (Vanzolini, 1976); all specimens, however, were collected in houses and backyards of the town, that sits in a relatively wet valley.

Coluna is also in a transitional area. The Atlantic forest (Vanzolini, 1970, 1972) does not extend northward to the latitude of Ceará, but the coast (praia) there has a much milder climate than the harsh caatingas of the interior. The transitional belt is some 70 km wide, and Coluna sits on its middle, on the lower valley of the Rio Choró (Souza, 1975).

The disjunction between these two species morphologically so similar is enormous — about 2300 kilometers. The open formations of Brasil are in general poorly explored, but the area between the Negro and the eastern end of the hylaea is relatively well collected; it is to be expected that the disjunction is real.

A scenario of the evolution of this group and of the genesis of the present distribution must start with an ancestral species. The differences between *palaichthus* and *agrius* being very trivial, hypotheses about the morphology of the ancestor are not important. On the contrary, its inferred distribution is crucial to any argument.

Let us start with an analog, a very abundant and conspicuous species (or, more probably, tight species group) about whose distribution there can be no major doubt, Tropidurus torquatus sensu lato, i.e., including *hispidus* (Spix). It ranges from Venezuela to Argentina in open formations, but has not been capable of colonizing any areas cleared by man in Amazonia, except the city of Belém, where it is by far the commonest lizard. It is found, however (Vanzolini, 1972; Gasc, 1973) in isolated patches of open formations inside the hylaea. This pattern speaks forcibly in favor of a broad continuous distribution during the dry episode that preceded the present humid one (Fairbridge, 1976), when the rain forest was reduced to scattered refuges surrounded by open formations (Haffer, 1969; Brown, 1977); dissection of the range would follow the subsequent spread of the forest. This is the so-called "theory of refuges". Currently attention, in terms of plausible application, if not of critical examination, concentrates on the processes affecting forest faunas (for a review see Brown, 1977). This is understandable. As we have just gone by a peak of humidity and are embarking on the dry leg of the cycle, forest-bound phenomena (such as the patterns of spread following dissection, or the disjunctions without differentiation) are cleaner, clearer and more evident than the vicissitudes of the open-formation elements, some of which (as the present case, or that of the microteiids discussed by Vanzolini & Ramos, 1977) are just recovering or having trouble to recover from the recent maximum of moisture that conjoined the hylaea and the Atlantic forest.

It should not be forgotten that closed and open plant formations are strictly complementary, and that the respective core areas are polygonal: pulsations mean mutual interpenetrations. This is a fundamental feature of the model, and should not be forgotten even in applications such as to Anthropology; to stress, in the tradition of J. Stewart (as did, e.g., Meggers, 1977) Amazonia as the basic core, may reduce by much the efficiency of otherwise valuable insights. As models go, and hypotheses about evolutionary mechanisms should be no more than models, in need of hard testing rather than of amens or band-wagons, it can be accepted that during the last dry episode (Fairbridge's, 1976, Period V; Bombin's, 1977, Sub-Atlantic Period) that lasted from approximately 3400 to 2600 years ago, there was an enormously widespread species of *Hemidactylus* in northeastern South America, that subsequently became at least bisected by the spread of the rain forest, the severed populations developing the differences presently seen between *agrius* and *palaichthus*.

This simple model, however, does not explain satisfactorily all the major aspects of the case. First we have to consider *palaichthus* in the Negro. Are these populations relictual, maintaining a toehold on the network of juxtafluvial open formations, or do they represent a new cycle of expansion, possibly along man-made habitats?

		date		palaichthus	mabouia
Paricatuba	nov	9-15		36	0
São João	jan	30-feb	l	5	0
Tapera	oct	31-nov	6	7	0
Barcelos	aug	22-25		5	1
Carvoeiro	feb	3-6		1	19
Moura	jan	30-feb	1	1	1

TABLE 6 - Hemidactylus collected on the Negro, 1972/73

We lack at least two elements indispensable to the solution of this question. Present data indicate that there is geographical differentiation in *palaichthus*. It will be important to elucidate the features of this differentiation, to find out whether we have on the continent a mosaic, a North-South cline, definite subspecies, or even full species. It may even be the case that the difference between Kluge's data and mine is determined by the insular samples he had and I did not — which would make the case trivial. The second missing element is a thorough exploration of the natural juxta-fluvial open habitats peculiar to the Negro Valley, the "campinas", characterized by a special type of vegetation growing on very poor sandy soils (Lisboa, 1975). It is conceivable that these play a role in the spread of open formation forms independently from human activity, but their vertebrate fauna has not been systematically sampled.

But even in the absence of such vital information the data at hand permit a preliminary approach. In Table 6 are shown the numbers of *palaichthus* and *mabouia* collected by EPA on the Negro. The collections may be said to have been random, since we had many people collecting for us and not even mangled lizards were ever turned down.

The localities are arranged on the table in downstream sequence. The first three are close together (ca. 60 km from Paricatuba to Tapera) and at roughly the same latitude; 48 palaichthus and no mabouia were obtained. Barcelos is some 220 km downstream and one half a degree of latitude South: palaichthus predominates but one mabouia was collected. Carvoeiro and Moura are again close to each other, respectively 120 and 150 km from Barcelos down the river, another half degree of latitude South, and can be assembled: here we have 2 palaichthus against 20 mabouia. These data are compatible both with the hypothesis that *palaichthus* is making its way down the Negro from the north, or that mabouia is spreading from the south. Either way the two species would be competing. There is very little hard evidence for interspecific competition among lizard species in the Amazon. Further exploration of the Negro and Branco and especially a study of the interactions between the two species should be rewarding.

Returning to the general picture, another difficult fact to explain is the presence of H. agrius, so far, in only two localities. It is true that, H. mabouia being usually shunned by collectores as "an African house gecko", opportunities of collecting agrius have very probably been passed by. Even so, the available samples of mabouia (see below) indicate that agrius is at least not evenly distributed in northeastern Brasil — in fact, the differences noted between the type series and the Coluna sample would be hard to understand in an abundant, uniformly distributed open-formation lizard.

The distribution of agrius brings to mind a possible analog: Tretioscincus agilis, not common in collections, is seasonally very abundant in one locality, the city of Oriximiná, Pará. This local population shows some striking peculiarities (Vanzolini & Rebouças-Spieker, 1969). This pattern allows us to think that, very possibly, H. agrius is a scarce or shy animal, if not both, in natural environments, but in some contexts urban populations may become very vigorous. Several examples, such the "Belém Park Effect" (Williams), the urban populations of Anolis aeneus in Trinidad (Holt), and the abundance of various anoles in plantations in Ecuador (Miyata) are to be found in Williams (ed., 1977). On the other hand, the fact that the only two known populations are urban tends to make it improbable, in spite of the disjunctions, that the present distribution is relictual.

I would suggest that the ancestral form that evolved into *palaichthus* and *agrius* (i) was widespread northeastern South America during the last dry-cool phase (Fairbridge's period V, Bombin's Sub-Atlantic, 11.cc.); (ii) became bisected, differentiated and went through a period of extremely low density during the succeeding maximum spread of the rain forest (i.e., during the maximum of humidity from which we are climbing down) and (iii) the two derived forms are presently recovering and expanding, due to the desiccation of the climate after the recent wet maximum (Vanzolini, 1974:86).

Hemidactylus brookii leightoni

Kluge (1969) lists 10 definite Colombian localities, and one state record (Cundinamarca). One of the localities has been eliminated from the list. In addition (Map 1) we have the type locality (Honda, Boulenger, 1911) and the following records that may be confidently assigned to the species: Bodega Central (Steindachner, 1902, as *H. mabouia*); Mariquita and San Vicente (Dunn, 1944, as *haitianus*); Girardot and Tolu (Mechler, 1968, as *haitianus*); Barinitas (Donoso-Barros, 1968, as *brookii*). The following records seem better left in abeyance: Popayan (Berthold, 1846, *mabouia*); Orocué (Werner, 1900, *mabouia*).

The 15 localities where it is certain the *H. b. leightoni* occurs may be divided in 3 groups: (i) coastal or near-coastal localities around the mouth of the Magdalena: Tolu, Cartagena, Bocagrande, Barranquilla, Rio Frio; (ii) localities on the Magdalena or near it: Bodega Central, Puerto Wilches, San Vicente, Honda, Mariquita, Cambao, Girardot; (iii) localities to the east of the Cordillera Oriental: Cúcuta, Barinitas and Villavicencio.

It would seem that H. b. leightoni is expanding its territory, having the Magdalena as the main highway, but crossing the Andes in favorable spots. Kluge's state record "Cundinamarca" documents the passage from the Magdalena (e.g., Girardot) to the hylaea (Villavicencio). Werner's (1900) Orocué record may represent a further expansion of leightoni down the Meta, or of mabouia from Amazonia, or of palaichthus from the Orinoco. Donoso's Barinas record probably represents a further extension of leightoni to the east along the Cúcuta route. Farther east we have a record of H. mabouia for the São Carlos fort, near La Guaira (Ernst, 1889), which must also remain in abeyance for the time being.

I think that, at least with regard to the last two climatic episodes, the history of *leightoni* has been independent from that of *palaichthus* and *agrius*. Otherwise, the geography of the coastal area from which it is presently known tends to preclude immigration by natural means, favoring instead human agency; it is, however, too soon to make this type of inference, as much collecting of *Hemidactylus* remains to be done.

F'INAL COMMENT

Kluge (1969, fig. 10) derives *H. palaichthus* from the *brookii* group through a series of Antillean intermediates: intermediate 6 giving rise to Hispaniolan *brookii* and to intermediate 7; the later originating *leightoni* and intermediate 8; this envolving into *brookii* in Cuba and into intermediate 9, the last one, differentiating on its turn into Puerto Rican *brookii* and *palaichthus*.

I find faults with this scheme. As a matter of method, I see no a priori reason to postulate so many strict dichotomies in an area where geography ensures that many things are happening simultaneously, indeed an area where simultaneity is a key element (Williams, 1969). Straight Hennigian dichotomy or hedging of bets, never the best strategy in general, is particularly lame here. I find it also improbable for a mainland form to be derived from Greater Antillean forebears. The opposite route or independent arrivals are much more probable. If the original stock came from Africa through human agency, landing in South America is just as probable as in any part of the west Indies. On the other hand, if the trip occurred by natural rafting, the probability of a South American landing is even larger (Kluge, 1969: 50).

It must be also remembered that Kluge's analysis starts from the postulate that all Neotropical hemidactyls are directly related; he tests the degree of relatedness by the arithmetical comparison of scale characters among members of the New World set only. It is not impossible that the relationship between agrius-palaichthus and brookii is not so close as postulated by Kluge; the algorithm has no provision to estimate that. Possibly the original stock from which the former arose belongs in an older South American gekkonine group. The shape of the foot of *leightoni* and its distribution lead me to prefer this hypothesis. It should be also remembered that two specialized (by loss of claw or digit) genera related to Hemidactylus are known in South America: Briba and Bogertia. The latter is known from sand dunes on the coast of Bahia and Pernambuco (Vanzolini, 1974, 1976) and might (or may) represent the beachhead of a moderately successful invasion, but the former is a bona-fide inhabitant of the northeastern open formations (Vanzolini, 1974, 1976). Another gekkonine genus, formerly referred to as *Lygodactylus* (e.g. Vanzolini, 1974), is now thought to be endemic; it is *Vanzoia* Smith, Martin & Swain, 1977, with one species on the northeastern end and another on the southwestern end of the great South American diagonal of open formations (Vanzolini, 1974), a distribution that, in spite of the African relationships (which to me are indeed very close), speaks in favor of a history on the continent lasting at least for one complete climatic cycle (one wet and one dry episodes).

Hemidactylus mabouia

It was thought until recently that, being a contemporary introduction restricted to edificarian environments, H. mabouia would not interact with native faunas to the point of deserving to be considered a bona fide member. It is now clear that such is not the case, and an assessment is needed of its distribution, both from the ecological and the zoogeographical viewpoints. Based on these data it will be possible also to further the understanding of the problem of the transatlantic dispersal of the gecko, traditionally thought to have arrived in the New World stowed away in slave ships, but believed by Kluge (1969) to have availed itself of natural rafts.

MATERIALS

Kluge's (1969) South American sample was moderately good: 115 specimens from 39 nominal localities — 37 actual ones, since Corcovado, Manguinhos and Recreio dos Bandeirantes are in the city of Rio de Janeiro. (There are other Corcovado and Manguinhos in our sample). There are some misspellings in his list: (i) Rio Momore is Mamoré; (ii) Fazenda São Sebastio, Vazonas, is Fazenda São Sebastião, Vassouras (E. E. Williams, in litt.); (iii) Porte Alegre is Porto Alegre; (iv) Toco de Onca is Toca da Onça, presently Jaguaquara, in Bahia; (v) Malai, in Guyana, is Malali (A. G. Kluge, in litt.). Otherwise Baixa Verde has been changed to João Câmara and Anápolis, not the well-known locality in Goiás, but in Sergipe (Kluge, in litt.) to Simão Dias. Varnhagen and Rio Mamoré are not shown in Kluge's map. None of these mistakes is really important.

In 1968 I published a list of *H. mabouia* localities, which Kluge (1969) disregarded because I had not distinguished *palaichthus* from *mabouia*. In fact, I had one *palaichthus* (the Purus example metioned above) and three *H. brookii leightoni* (from Barranquilla) personally misidentified as *mabouia*; additionally I had accepted uncritically some mistaken museum identifications. My revised materials now comprise 1256 specimens in the MZUSP collection, from 109 localities, 10 of wich are also on Kluge's list.

TABLE 7 - H. mabouia,

distribution by morphoclimatic domains

	Localities	Specimens
Hylaea	36	327
Atlantic forest	50	403
Cerrado	б	13
Caatinga	4	11
NE transitional	11	136
SE transitional	22	37
São Paulo islands	7	685
Santa Catarina islands	3	5
Other	10	29
	149	1646

Some records in the literature may be used with confidence. They are (1) in Peru: Posuso (Peters, 1971) and Moropon (Dixon & Soini, 1975); (2) in Brasil: Natal and Independencia, now Guarabira (Schmidt & Inger, 1951); Barra de Penedo (Griffin, 1917); Barreira (L. Müller, 1927); Ilha do Toque-toque, Ilha do Arvoredo (or Alvorada), Ilha Campeche, Ilhas dos Moleques, Florianópolis (P. Müller, 1969, 1969); Viamão (Ribeiro, 1976); (3) in Surinam: Paramaribo, Nieuw Nickerie, Maratakka River, Encampment Wakay and Lower Marowijne (Hoogmoed, 1973); (4) in French Guiana: Cayenne (Hoogmoed & Lescure, 1975).

GENERAL DISTRIBUTION

An examination of Map 2 shows that *H. mabouia* is not restricted to a narrow margin along the eastern coast, but has reached far inland: the upper Amazon, the upper Madeira, the edges of the Mato Grosso pantanal. There is no doubt that much of this expansion has been on the tracks of man; in my experience an overwhelming proportion of the specimens are collected in edificarian situations. However, in many places, from the Amazons to the caatingas, *H. mabouia* has also been found in environments very little disturbed, showing at least some colonizing ability.

A preliminary quantitative approach to the major ecological aspects of the distribution is made possible by the reasonable number of specimens assembled by Kluge and by myself. In addition, some of the papers mentioned above as extending the list of localities contain information on the number of specimens obtained, and furthermore Beçak, Beçak & Denaro (1971, 1972) and Lema (1962) mention specimens, respectively from São Paulo (city), Ilha da Queimada Grande and Porto Alegre. Adding all these data we have Table 7, in which the localities are grouped according to Ab'Saber's (1977) scheme of morphoclimatic domains (see also Vanzolini, 1970, 1972).

Table 7 of course cannot be submitted to statistical analysis; not even the relatively large number of localities can ensure a reasonable degree of randomness. However, simple inspection, as it should, shows several interesting features.

H. mabouia occurs in the core areas of all four intertropical morphoclimatic domains of Brasil, hylaea, Atlantic forest, cerrado and caatinga. It is enormously more abundant, however, in the forested domains. Since the actual collecting sites in most cases (and especially in the much-decimated Atlantic forest) are urban or agricultural, the association should not be attributed to the presence of forest proper, but rather to wetter climates. This seems to me to explain why the species has travelled much farther inland in the hylaea, along the rivers, than, for instance, at 20 degrees of latitude South: the cerrados must have impeded the march westward.

The categories "NE transitional" and "SE transitional" in Table 7, i.e., localities in intermediate belts between cores, at different latitudes, are not comparable: in the former case we have a few intensive collections made by expeditions, in the latter a slow accumulation of small samples (usually 1-2 specimens) sent along several years to Instituto Butantan and to the Museum. Even so, it can be seen that the lizard is especially abundant in the open areas peripheral to the caatingas, and in the cultural steppe of São Paulo east of the cerrado, which strongly indicates that it is well adapted to open formations, but not a xerophil. This is probably relevant to the matter of its physiological ability to withstand the rigors of natural rafting.

Since H. mabouia is a tropical lizard, the matter of its southern limit, especially in a recently adopted home, is of interest. Kluge (1969) cites one specimen from Montevideo, which would be the southernmost locality of mabouia. Since neither Vaz-Ferreira & Sierra de Soriano (1960), Lema & Fabian-Beurmann (1977) or Federico Achával (in litt.) refer the presence of the lizard in Uruguay, I checked with Dr. Kluge, who kindly informed me that his record was based on a Michigan specimen obtained from the British Museum. Dr. Alice G. C. Grandison, of the latter, informed that they have a further Montevideo specimen, a juvenile, received from Alan Insole in 1923. She thoughtfully added a list of other lizards in the Insole collection. As, among other species, there are Tropidurus torquatus and Enyalius b. brasiliensis, which do not occur in Montevideo, I think these records are better omitted. The next southernmost locality is Porto Alegre, well documented; two specimens in the Field Museum (Kluge, 1969), two in our collection, and two notes in the literature (Lema, 1962; Ribeiro, 1976). There is one further citation of the species for Viamão (Ribeiro, 1976), a few kilometers east of Porto Alegre. Thus, an understanding of the limiting factors of the distribution of H. mabouia depends on the analysis of zonal climatic patterns around ca. 30 degrees of latitude South and 58 degrees of longitude West.

Examining the available climatic maps of Rio Grande do Sul (Reis, 1972), that contain routine meteorological data (temperatures, rainfall, insolation), and searching for patterns of coincidence with the distribution of H. mabouia, one sees that average yearly temperature (mean of means) shows the only reasonable fit. Porto Alegre is located within the 18°-20°C belt, temperatures to the South being lower than 19.°; H. mabouia seems to prefer averages 18°C and higher. Contrary to expectation, the isotherms of the means of minimum temperatures do not fit the distribution data very well. Of course it has to be kept in mind that the present data are weak to the extent that there are no extensive collections of lizards from Rio Grande do Sul, and thus the actual distribution of H. mabouia, when known, may lead to different conclusions. On the other hand, the climatic data at hand are very summary, and it is known that other indexes, not customarily available in South America, may afford better explanations of distributional phenomena, as suggested by Vanzolini & Rebouças-Spieker (1976) for Mabuya on the São Paulo coast.

BRASILIAN SHELF ISLANDS

At the heart of the problem of the distribution of H. mabouia, as posed by Kluge, are its ability to be rafted naturally and to colonize new "natural" environments, besides, of course, the overall logic of its distribution. The shelf islands of southern Brasil afford some information. Vanzolini (1968) and P. Müller (1969) have shown that H. mabouia occurs on all the shelf islands investigated (for reasons discussed elsewhere — Vanzolini, 1973 — I do not include the island of São Sebastião among the shelf islands, prefering to include it in the Atlantic forest; the same applies, in the present context, to the island of Santa Catarina).

TABLE	3
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H. mabouia on the shelf islands

Specimens

São Paulo	
Vitória	353
Búzios	207
Toque-toque	1
Alcatrazes	38
Farol	14
As Ilhas	14
Queimada Grande	5 8
Santa Catarina	
Arvoredo	1
Campeche	2
Moleques	2

Some of the islands where H. mabouia occurs are inhabited, e.g. Vitoria and Búzios; it is abundant there both around houses and in habitats disturbed but not in current use by man. Other islands, such as Queimada Grande, were very briefly inhabited by lighthouse keepers, but have been deserted for a long time, 50 years or more. Toque-toque and the Alcatrazes group have never been inhabited. This shows that H. habouia is not entirely dependent on man and can establish itself on small islands. It also tends to indicate that, at least on the scale of the short distances involved (up to 35 km), it can be rafted by natural means.

OCEANIC ISLANDS

On the other hand, the evidence from oceanic islands is equivocal, favoring neither the hypothesis of natural rafting along oceanic currents nor that of human agency. *H. mabouia* exists in Ascension, in the middle of the South Atlantic Ocean (ca. 3000 km from Africa and 2000 km from Brasil) and Fernando de Noronha (360 km from Brasil) (Boulenger, 1890; also one specimen in our collection). These islands are favorably placed with regard to currents, and belong to linear systems of volcanic islands quite recently reduced to sea-level or less by erosion (Almeida, 1965); on the other hand, they have sizable human populations and maintain steady contacts with the continents. Fernando de Noronha has two endemic lizards, one *Mabuya* of African affinities, and one *Amphisbaena*, possibly of South American origin; these I take to be the descendants of old waifs. But, again on the other hand we have from the island, in our Museum, one specimen of the amphisbaenian *Leposternon microcephalum*, surely imported, and probably from Rio de Janeiro.

Farther south $(20^{\circ}30'S, 29^{\circ}20'W)$ is the uninhabited island of Trindade. *H. mabouia* was not there in 1916 (Miranda-Ribeiro, 1919) nor in 1950 (Dalcy Oliveira Albuquerque, pers. comm.). The island is not on the way of the major oceanic currents, and no land reptiles are known from it.

COMMENT

It is quite possible that H. mabouia is capable of extended rafting and of colonizing foreign shores, in spite of seeming to be not very well pre-adapted to dry conditions. It certainly has had enough time in which to make the trip from Africa to South America unaided by man. However, this same characteristic of being a good natural sailor leads to believe that it has also travelled with man, and probably much more frequently than it did on its own. If a lizard is a good traveller and feels at home with man, there is no reason why it should not avail itself of the constant opportunities, not only of embarking, but of arriving (well-fed to boot) at safe ports instead of at wave-beaten shores.

This facility in travelling, as I see it, further voids one of Kluge's main arguments against human transport. He says (1969:46): "One of the most difficult single pieces of negative evidence against the thesis of an introduction of *mabouia* and *brookii* with the slave trade is their absence from islands known to be major clearing houses for slaves coming directly from Africa. It seems impossible to resolve the fact that hemidactyls do not occur in Jamaica...".

Even if it is accepted that hemidactyls did not come in slave ships and did not make a primary landing in Jamaica, they certainly must have visited the island and indeed the whole area. I quote Williams (1969: 364), writing on a sucessful colonizer: "Given its distant sucessful voyages, the *carolinensis* group has surely more than once tested *all* the closer islands. If it has failed to colonize these closer islands, that is a very impressive and instructive failure". Williams has brought to my attention the paper by Levins & Heatwole (1963) in which exactly this point is made with regard to *Hemidactylus brookii* and *mabouia*.

It would seem that the uneven distribution of the hemidactyls in the New World is more a matter of ecological interactions in situ than of mechanisms of dispersal. In the specific case of H. mabouia, the lizard probably availed itself repeatedly both of natural and human means of transportation to reach the present distribution, and I think it is beyond hope to try to reconstruct with available data a detailed history of its movements and vicissitudes.

THE GENERAL DISTRIBUTION OF THE HEMIDACTYLS IN SOUTH AMERICA

Map 3 and Table 6 show that there is very little real overlap between the South American forms of *Hemidactylus*.

H. agrius is encircled by *mabouia*, but in an area where the density of the latter is very low. *H. palaichthus* and *brookii leightoni* do not overlap. *H. palaichthus* and *mabcuia* do overlap, very briefly, on the Negro and northern Guyana. The situation in coastal Venezuela is not clear. They are actually syntopic in three Negro localities.



Map 3. General distribution of Hemidactylus on continental South America.

Thus it would seem that, to explain this pattern, and remembering that, of the four forms involved, two are thought to be autochtonous (agrius and palaichthus) and two introduced from Africa (mabouia and brookii, to this point without any hypotheses as to when) we should have recourse to exclusion by competition. This is a rare indeed pattern in South American lizards, and it should not be a matter of chance that two protagonists are recent immigrants. It should be very rewarding to study the mechanisms and nuances of coexistence among these forms.

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APPENDIX 1

Specimens examined

All specimens, unless otherwise noted, belong to the lizard collection of the Museu de Zoologia. Localities marked with an asterisk are not shown on Map 3, to avoid overcrowding.

Hemidactylus brookii leightoni

COLOMBIA. Atlantico: Barranquilla (11°00'N, 74°49'W): 2365-2367. Tolima: Honda (05°12'N, 74°45'W): 44734-44737.

Hemidactylus mabouia

PERU. Loreto: Centro Unión (03°49'S, 73°04'W): 39223. Iquitos (03°47'S, 73°13'W).

BRASIL. Amazonas: Barcelos, Rio Negro (00°58'S, 62°56'W): 35379-35386. Berurí, Rio Purus (03°54'S, 61°22'W): 38097-38100. Boca do Acre, Rio Purus (08°45'S, 67°24'W): 36976, 36977. Canutama, Rio Purus (06°33'S, 64°21'W): 37445-37450. Carvoeiro, Rio Negro (01°26'S, 62°01'W): 25968-25983, 25985-25987. Coarí, Rio Solimões (04°06'S, 63°09'W): 17321, 17322, 17354, 32910-32923. Itapiranga, furo de Silves (02°44'S, 58°01'W): 33024-33049. Manaus, Rio Negro (03°07'S, 60°00'W): 603, 2779, 2780, 2782. Moura, Rio Negro (01°30'S, 61°40'W): 25988. Nova Olinda, Rio Madeira; 26159-26183, 26186-26200, 26465-26485, 26532-26551. Paraná da Mucura, Rio Negro (03°00'S, 60°20'W): 29347. Tapauá (05°46'S, 63°02'W): 37754-37760. Pará: Alter do Chão, Rio Tapajós (02°32'S, 54°57'W): 19311. Belém (01°26'S, 48°29'W): 4237, 4238, 7128-7130, 7142. Corcovado, furo de Breves (01°39'S, 50°32'W): 12079-12081. Oriximiná, Rio Trombetas (01°46'S, 55°51'W): 16336, 16337, 31462, 35354-35374, 36036-36040. Santarém, Rio Tapajós (02°25'S, 54°48'W): 512, 2774, 2775, 35728, 36330-36335. Igarapé Taperebá, Ilha de Marajó (00°12'S, 48°51'W): 7131, 7132. Taperinha (02°32'S, 54°18'W): 19564. Acre: Feijó (08°16'S, 70°46'W): 5385. Rondônia: Porto Velho, Bio Madeira (08°46'S, 63°55'W). Maranhão: Barra do Corda (05°32'S, 45°16'W): 3176-3182. São Luis (02°32'S, 44°18'W): 3508. Piauí: Valenca (06°24'S. 41°45'W): 38395-38410, 38433-38446. Ceará: Açude Amanarí, Maranguape (04°01'S, 38°52'W): 3116. Coluna, near Justiniano Serpa (04°02'S, 38°29'W): 27805-27813, 27824-27830. Fortaleza (03°45'S, 38°33'W): 3115. Guaraní, Pacajus (04°13'S, 38°27'W): 27229-27231, 27334-27349, 27685-27691. Morro Branco, near Beberibe (04°10'S, 38°06'W): 28124-28169. Rio Grande do Norte: Natal (05°48'S, 35°12'W): 8100. Paraiba: Junco do Seridó (07°00'S, 36°43'W): 44201. Mamanguape (06°50'S, 35°07'W): 5401. Pernambuco: Carnaubeira

(08°18'S, 38°45'W): 22245-22247, 22618. Cruz de Reboucas (07°52'S, 34°54'W): 8781, 8782. Igaraçu (07°50'S, 34°54'W): 8783. Itamaracá (07°45'S, 34°50'W): 21476, 21477. Pesqueira (08°21'S, 36°43'W): 8548. Recife (08°02'S, 34°35'W): 7086, 10901, 45959. Sitio dos Nunes (08°02'S, 37°51'W): 23063-23066. Alagoas: Maceió (09°39'S, 35°43'W): 604. Mato Grosso: Campo Grande (20°27'S, 54°38'W): 10415, 10416. Chapada dos Guimarães (15°26'S, 55°45'W): 45690. Goiás: Goiania (16°41'S, 49°16'W): 12966. Bahia: Ilheus (14°48'S, 39°03'W): 741. Jequié (13°52'S, 40°06'W): 8928. Salvador (13°00'S, 38°30'W): 503, 504. Minas Gerais: Muriaé (21º08'S, 42º22'W): 4225, 4226. Pirapora, Rio São Francisco (17°21'S, 44°57'W): 450. Porto Novo (21°53'S, 42°42'W): 4212, 4213. Tuiutí (21°19'S, 47°16'W): 4220. Espírito Santo: Colatina, Rio Doce (19°32'S, 40°28'W): 8973. Guaraparí (12°40'S, 40°30'W): 8834. 8835. Santa Teresa (19°46'S, 40°37'W): 17442. Refugio Sooretama (19°00'S, 40°00'W): 10286. Rio de Janeiro: Areal* (22º14'S, 43º07'W): 4239, 4240. Atafona, Rio Paraiba (21°37'S, 41°01'W): 13899-13902. 30 km SW Campos (21°50'S, 41°22'W): 10165. Casa Grande, Vila Geni* (22°55'S, 43°52'W): 7077-7084. Engenheiro Passos (22°30'S, 44°41'W): 45697. Ilha Grande * (23°09'S, 44°15'W): 13310-13319. Manguinhos, São João da Barra (21°35'S, 41°04'W): 10253, 10254. Maricá * (22°57'S, 42°49'W): 8974-8976. Rio de Janeiro (22°55'S, 43°15'W): 607, 3096, 7085, 7301-7308, 8441-8466. São Paulo: Ilha dos Alcatrazes * (24,05'S, 45,42'W): 375, 2744-2746, 4156-4187, 4242. Amparo (22°42'S, 46°47'W): 4214. Artemis * (22°40'S, 47°45'W): 4218. Artur Nogueira * (22°34'S, 47°09'W): 4210, 4222. As Ilhas (23°47'S, 45°42'W): 29701-29714. Barra do Icapara* (24°41'S, 47°26'W): 13298-13300. Bertioga (23°51'S, 46°09'W): 770, 2761, 3585-3591, 44732. Bonfim Paulista (21°16'S, 47°39'W): 4221. Botucatu (22°54'S, 48°27'W): 1970. Ilha dos Búzios (23°47'S, 45°09'W): 294, 295, 10980-11138, 11314-11359. Cananeia (25°02'S, 47°56'W): 3114. Candido Rodrigues * (21°19'S, 48°38'W): 4219. Caraguatatuba (23°37'S, 45°25'W): 2660, 7731. Casa Branca (21°47'S, 47°05'W): 4216. Chavantes (23°01'S, 49°45'W): 6848, 6849, Cocuera * (23°34'S, 46°07'W): 44697, 44959, 45057, Cubatão (23°53'S, 46°26'W): 3118. Ilha do Farol, arquipélago dos Alcatrazes * (24°06'S, 45°45'W): 4194-4207. Iguape * (24°42'S, 47°34'W): 13301-13307, 40761. Itanhaém * (24°12'S, 46°48'W): 515, 3119. Itapira * (22°26'S, 46°49'W): 4233. Fazenda Itaquerê, Nova Odessa * (21°44'S, 48°35'W): 10361, 10390. Jundiaí (23°10'S, 46°55'W): 4232. Jurumirim * (23°13'S, 49°13'W): 4227. Mogi das Cruzes * (23°31'S, 46°11'W): 45920. Peruíbe (24°20'S, 47°00'W): 8255. Piassaguera (23°50'S, 46°22'W): 514, 2772, 2773. Pindamonhangaba* (22°56'S, 45°28'W): 4236. Piracicaba (22°42'S, 47°38'W): 37-41. Pongaí* (21°45'S, 49°23'W): 4228. Ilha da Quemada Grande* (24°29'S, 46°41'W): 4112-4136, 4138-4155, 4188-4193, 4208, 4209, 4241, 28204-28206. Km 25 Via Raposo Tavares * (23°36'S, 46°52'W): 29609. Ribeirão Bonito * (22°05'S, 48°10'W): 4231. Ribeirão Preto (21º11'S, 47º47'W): 19511-19518. Santo André (23º41'S, 46°26'W): 8263. Santos (23°57'S, 46°20'W): 600, 2743. São José do Rio Preto (20°48'S, 49°23'W): 11901. São Paulo (23°27'S, 46°38'W): 45, 510, 781, 1968, 1973, 1974, 2657, 2658, 2661. 2732-2735, 3092-3095, 4211. 36925, 42691, 42702. São Sebastião (23°49'S, 45°26'W): 2747-2760, 3097-3105, 7070, 7071, 8432, 8433, 10896-10898, 10902, 27097-27099, 29560, Ilha de São Sebastião (23°49'S, 45°20'W): 44, 517, 601, 2762-2771, 3106-3113, 8267-8274, 42696. São Vicente (23°58'S, 46°23'W): 2651-2656, 2736-2742. Tanquinho (22°46'S, 47°00'W): 4230. Tietê * (23°07'S, 47°43'W): 4229. Ubatuba (23°27'S, 45°05'W): 554, 13308. 17090-17105. Ilha Vitória * (23°45'S, 45°00'W): 10442-10492, 10512-10526, 10582-10819, 10823-10842, 10845-10882. Rio Grande do Sul: Porto Alegre (30°00'S, 51º10'W): 3173, 3257.

Hemidactylus palaichthus

COLOMBIA. Guainia: San Felipe de Rio Negro (01°55'N, 67°04'W): MCZ 53242-53243.

BRASIL. Roraima: Surumu (04°17'N, 61°31'W): 13295-13297. Amazonas: Barcelos (00°58'S, 62°56'W): 31811-31815. Carvoeiro (01°26'S, 62°01'W): 25963. Moura (01°30'S, 61°40'W): 25931. Paricatuba (00°31'S, 65°01'W): 29079-29090, 29412-29435. São João, near Tapurucuara (00°33'S, 64°57'W): 28478-28482. Tapera (00°25'S, 64°35'W): 29344-29346, 29348-29350.

Appendix 2

Gazetteer of localities from the literature

In the first appendix are given the coordinates of the localities of our specimens. In this appendix are cited the localities from the literature. It must be kept in mind that the coordinates are given as an aid in finding the localities, rather than for plotting purposes. Maps and other sources of geographical information are not always in perfect agreement, among themselves and with base maps. Plotting a locality based exclusively on published coordinates may result in moving it away from some significant landmark.

In the case of rivers, the coordinaes cited are those of the mouth.

COLOMBIA. Bolivar: Boca Grande, 10°24'N, 75°33'W. Bodega Central, 08°09'N, 73°46'W. Cartagena, 10°25'N, 75°32'W. Tolu, 09°31'N, 75°35'W. Magdalena: Riofrio, 10°54'N, 74°11'W. Norte de Santander: Cúcuta, 07°55'N, 72°31'W. Santander: Puerto Wilches, 07°21'N, 73°55'W. San Vicente, 06°54'N, 73°25'W. Cundinamarca: Cambao, 04°54'N, 74°44'W. Girardot, 04°18'N, 74°50'W. Boyacá: Orocué, 04°48'N, 71°21'W. Tolima: Mariquita, 05°12'N, 74°54'W. Meta: Villavicencio, 04°09'N, 73°37'W. Cauca: Popayan, 02°25'N, 76°36'W. Amazonas: Leticia, 03°50'S, 69°55'W.

VENEZUELA. Distrito Federal: La Guaira, 10°36'N, 66°56'W. Sucre: Cumaná, 10°28'N, 64°11'W. Cumanacoa, 10°15'N, 63°55'W. Macuro, 10°39'N, 61°56'W. Puerto de Hierro, 10°38'N, 62°05'W. Yacua, 10°39'N, 61°59'W. Monagas: Barrancas, 08°42'N, 62°11'W. Barinas: Barinitas, 08°45'N, 70°25'W. Apure: Rio Sinaruco, 06°39'N, 67°08'W. Bolivar: Ciudad Bolivar, 08°08'N, 63°33'W. Amazonas: Esmeralda, 03°10'N, 65°33'W. Las Carmelitas, 04°09'N, 66°33'W. Maroa, 02°43'N, 67°33'W. Puerto Ayacucho, 05°40'N, 67°35'W.

GUYANA. Bartica, 06°24'N, 58°37'W. Georgetown, 06°47'N, 58°11'W. Haiowa Fall, 05°08'N, 58°49'W. Isheartun, 02°05'N, 59°25'W. Karanambo, 03°45'N, 59°16'W. Kurupukari, 04°40'N, 58°38'W. Kuyuwini River, 02°21'N, 58°21'W. Lethem, 03°24'N, 59°49'W. Malali, 05°38'N, 58°22'W. Yupukari, 03°40'N, 59°21'W.

SURINAM. Maratakka River, 05°15'N, 56°50'W. Marowijne (or Maroni) River, 05°45'N, 53°38'W. New Nickerie, 05°57'N, 56°58'W. Paramaribo, 05°20'N, 55°10'W. Encampment Wakai, 05°18'N, 57°16'W.

FRENCH GUIANA. Cayenne, 04°56'N, 52°20'W.

PERU. Loreto: Cedro Isla, 04°53'S, 73°46'W. Centro Unión, 03°49'S, 73°04'W. Iquitos, 03°47'S, 73°13'W. Rio Itaya, 03°45'S, 73°06'W. Rio Maniti, 03°27'S, 72°48'W. Moropón, 03°46'S, 73°25'W. Nazareth, 04°21'S, 70°57'W.

Pucallpa, 08°23'S, 74°33'W. Requena, 05°04'S, 73°53'W. Roaboya, 07°48'S, 74°46'W. *Huánaco*: Posuso, 10°03'S, 75°33'W.

BRASIL. Roraima: Boa Vista, 01°18'N, 48°00'W. Frechal, 03°27'N, 68°18'W. Amazonas: Manaus, 03°07'S, 60°00'W. Maués 03°23'S, 57°43'W. Pará: Óbidos, 01°55'S, 55°31'W. Amapá: Serra do Navio, 00°59'N, 52°05'W. Maranhão: São Luis, 02°32'S, 44°18'W. Rio Grande do Norte: Ceará-Mirim, 05°38'S, 35°24'W. Extremoz, 05°42'S, 35°19'W. João Câmara, 05°32'S, 35°48'W. Paraiba: Guarabira, 06°52'S, 35°30'W. Alagoas: Barra de Penedo, 10°30'S, 36°25'W. Sergipe: Simão Dias, 10°43'S, 37°48'W. Mato Grosso: Campo Grande, 20°27'S, 54°38'W. Goiás: Goiania, 16°41'S, 49°16'W. Bahia: Ilheus, 14°48'S, 39°03'W. Jaguaquara, 13°32'S, 39°58'W. Jequié, 13°52'S, 40°06'W. Ilha Madre de Deus, 12°47'S, 38°39'W. Minas Gerais: Belo Horizonte, 19°55'S, 43°55W. Rio de Janeiro: Coroa Grande, 22°56'S, 43°55'W. Santa Clara, 20°49'S, 41°55'W. Santa Catarina: Ilha do Arvoredo, 27°18'S, 48°23'W. Ilha Campeche, 27°42'S, 48°23'W. Florianópolis, 27°34'S, 48°33'W. Ilhas dos Moleques, 27°50'S, 48°26'W. Rio Grande do Sul: Viamão, 30°04'S, 51°00'W.



 Left hind foot of Hemidactylus palaichthus, MZUSP 29413, Paricatuba, Rio Negro, Am. 2. Right hind foot of Hemidactylus mabouia, MZUSP 45950. Recife. Pe.