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DISTRIBUTION AND DIFFERENTIATION OF ANIMALS ALONG THE COAST AND IN CONTINENTAL ISLANDS OF THE STATE OF SÃO PAULO, BRASIL. 2. LIZARDS OF THE GENUS *MABUYA* (SAURIA, SCINCIDAE)

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INTRODUCTION

This study is part of a series on evolutionary phenomena in a group of continental islands of approximately known age, as seen against the backdrop of the mainland. An introduction to the area and problems has already been published (Vanzolini, 1973) and this is the first case analyzed.

MATERIALS

General taxonomy

Lizards of the genus *Mabuya* are relatively common in southeastern Brasil. On the coastal range of São Paulo (Serra do Mar) and in the interior there occur the forms currently called *M. dorsivittata* Cope, 1862, and *M. frenata* (Cope, 1862). On the coast itself occur populations of the group of forms currently assembled under the name *M. m. mabouya.* The coastal and inland forms are nowhere sympatric, at least at these latitudes. Also nowhere along the coast sympatric species of this genus have been found, not even in those localities where relatively long stretches of coastline have been carefully searched with this possibility in mind.

The general taxonomic situation of South American *Mabuya* is far from satisfactory. The current arrangement originated with Dunn (1935), was added to but not modified by subsequent descriptions of new species (Hoge, 1946, *M. macrorhyncha,* Ilha da Queimada Grande; Schmidt & Inger, 1951, *M. heathi,* northeastern Brasil; *M. croizati* Horton, 1973, from Venezuela) and is adopted by the most recent catalog (Peters & Donoso-Barros, 1970). According to this scheme our coastal populations would be assigned to *Mabuya m. maboya,* characterized by "dorsolateral dark stripe two and one-half to three scale rows wide; usually sixth labial under eye, sometimes fifth on one side, sixth on other" (Peters & Donoso-Barros, 1970: 199), and "No auricular denticles; appressed legs overlapping or barely separated; no middorsal stripe; normally four supraoculars, the anterior small and not in contact with the frontal; no definite dorsolateral dark stripes; two frontopa-

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rietals; normally a single pair of nuchals; scales 28-34, sometimes with traces of three keels" (Dunn, 1935: 545).

Dunn recognized two subspecies of *Mabuya mabouya*: *mabouya*, occurring from the island of St. Vincent in the Lesser Antilles to approximately the latitude of 24 degrees South in South America, and *sloanii*, from St. Vincent to the Bahamas. This is a highly improbable type of geographic differentiation, unsupported by any biological or analogical rationale. That it is also unsupported by sufficient analysis is indicated by the low numbers of specimens seen by Dunn: from the whole of Brasil (8 million square kilometers) he had 24 specimens.

Actually, what can be provisionally called the *Mabuya mabouya* species group shows pronounced geographical differentiation in South America, and probably broad regional regularities will be found. Between the general Guiano-Amazonian area and the southeastern coast, for instance, some striking differences are found in morphology and ecology. The hylaean animals are much larger, thicker bodied, darker, more uniformly colored, have relatively longer limbs, and striated (instead of smooth) dorsals. They inhabit the forest, frequently climbing thick tree trunks (Vanzolini, 1972), while the coastal populations live in open formations.

It is obvious that South American *Mabuya* need to be studied comprehensively; it is also probable that the group will not be easily amenable to a single general treatment, but that numerous detailed regional studies, backed by genetical and biochemical methods will be needed before a broad understanding comes within reach.

Samples

We have studied 612 specimens, 316 males and 296 females, from the following localities (the abbreviations are those used in tables and graphs):

	Coast	Males	Females
Gb	Guanabara	7	11
Ut	Ubatuba	25	27
Ct	Caraguatatuba	21	14
Ss	São Sebastião	12	13
Bo	Praia de Boracéia	—	2
Be	Bertioga	22	21
En	Praia da Enseada	19	18
St	Santos	2	1
Mg	Mongaguá	14	8
It	Itanhaém	2	2
Pe	Peruíbe	49	31

	Islands		
Ib	São Sebastião (Ilhabela)	9	8
Vi	Vitória	13	45
Bz	Búzios	32	8
Al	Alcatrazes	8	7
Pd	Paredão	8	7
Sp	Sapata	1	1
Qg	Queimada Grande	72	73

Coastal localities

Vanzolini (1973) has described the most relevant features of the study area; here we shall present only the data necessary to the understanding of the immediate argument.

In the analysis of the coastal transect (see below) each locality was, of course, considered separately for each character. In the text, however, we frequently use the expressions "North Coast" and "South Coast". These correspond to a physiographical reality (Vanzolini, 1973).

The coastal range, Serra do Mar, is a fault escarpment, particularly abrupt in São Paulo. On the northern half of the coast of the state (Maps 1, 2, 4, aerophoto 1) it is very close to the sea, which it reaches from space to space with curved spurs that separate narrow, steep beaches ("praias de tombo") backed by short and narrow alluvial plains.

On the southern half, on the contrary (Maps 1, 3, aerophoto 2), the Serra runs parallel to the shore, some 20-40 km inland and sends few spurs to the shore. The alluvial plain is extensive, practically unbroken for tens of kilometers, and frequently marshy. There are some hills, geologically related to the Serra, but not in direct topographical connection with it ("disarticulated hills").

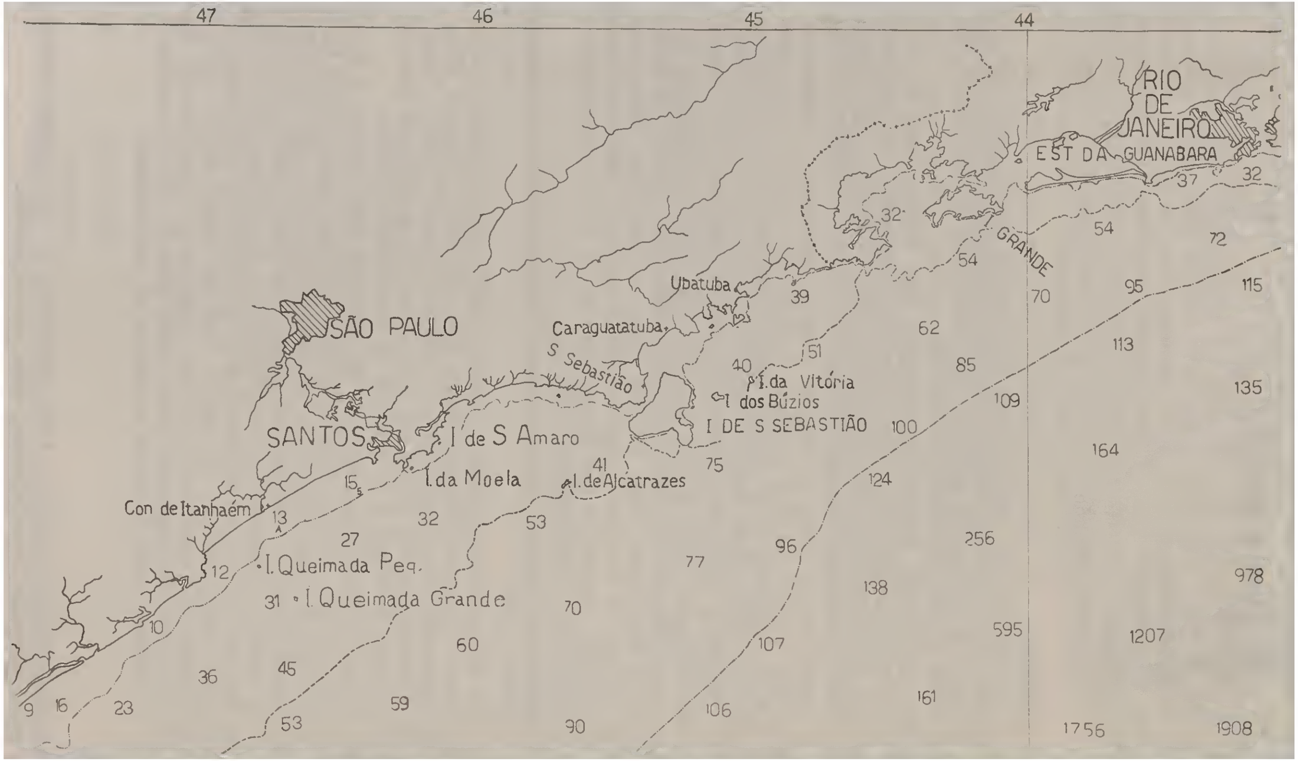
The transition between the two areas is rather abrupt and occurs in the Santos region.

In what follows, the expression "North Coast" (with capitals) means the localities of Ubatuba, Caraguatatuba, São Sebastião, Praia de Boracéia and Bertioga; the remainder are grouped under "South Coast". Praia da Enseada, in the island of Santo Amaro, is included here in the South Coast, although it is actually in the transition area.

The island of Santo Amaro is on its southern half separated from the continent by the narrow joint estuaries of some small rivers that run a short course from the Serra do Mar to the sea; the northern tip is separated from the continent by a narrow arm of sea, the Bertioga channel. It would be ideal to follow *Mabuya* on the inland side of the estuaries, but, due to the prevalence of mangrove swamps and industrial areas, we have not been able so far to find the lizard there. Taking into consideration the small width of the estuaries and channel and the fact that in almost all characters this sample agrees with the southern ones, it is included with them as a matter of convenience.

Islands

Vanzolini (1973) provides a brief description of the islands studied. For present purposes, the following data are sufficient.



Map. 1. Coast of southeastern Brasil, between Rio de Janeiro and Iguape (from Chart 80, "Brasil, Costa Sul, Do Rio de Janeiro à Ilha de Santa Catarina". 3rd. edition, 1966. Marinha do Brasil, Diretoria de Hidrografia e Navegação). (Published by permission of the Brasilian Navy. Not to be used for navigational purposes).

Map. 2. Coast of southeastern Brasil, between Ilha Grande and Ubatuba (from Chart 1600, "Brasil, Costa Sul, Do Rio de Janeiro à Ilha de S. Sebastião", 3rd. edition, 1948. Marinha do Brasil, Diretoria de Hidrografia e Navegação). (Published by permission of the Brasilian Navy. Not to be used for navigational purposes).

The island of São Sebastião (the sample is here called Ilhabela, from the town on the island, to avoid confusion with the coastal locality of São Sebastião) must be considered separately from the others. The latter are disarticulated spurs of the Serra do Mar, standing within but close to the 50 m isobath (Map 1). During glacial periods, when the lowered sea level caused the shore to lay some 100 km to the east, these islands had with the Serra do Mar about the same relationship as have today the disarticulated hills of the South Coast (Map 3) and similar ones in the State of Rio de Janeiro. Thus the age of these islands as such is determined by the rate of the marine ingression, a basic element in our reasoning (Vanzolini, 1973).

These are small islands, measuring from 400 to 750 thousand square meters. São Sebastião, on the contrary, is a complex horst, with an area of 336 square kilometers, separated from the coast by a channel 2 km wide at the narrowest, and with a maximum depth in places of only 20 m.

Búzios is close (7,5 km) to the island of São Sebastião. Vitoria is also close, some 7 km to the ENE (Map 4). The Alcatrazes group

Map 3. Coast of southeastern Brasil, from Santos to Peruíbe (from Chart 1700, "Brasil, Costa Sul, Da Ilha de S. Sebastião à Ilha de Bom Abrigo", 2nd edition, 1945. Marinha do Brasil, Diretoria de Hidrografia e Navegação). (Published by permission of the Brasilian Navy. Not to be used for navigational purposes).

(Alcatrazes, Paredão, Sapata) lays 36 km, Queimada 33 km from the nearest point on the coast. Paredão and Sapata are tiny islets, some 3 km from the major island of Alcatrazes.

Characters studied

Color pattern

All *Mabuya* on the southeastern coast have the ground color light to dark brown, with longitudinal stripes, one or two scales wide, lighter or darker than the background.

Map 4. Islands of S. Sebastião (Ilhabela), Búzios and Vitoria; coast of Caraguatatuba and S. Sebastião (from Chart 1600, see above Map 2). (Published by permission of the Brasilian Navy. Not to be used for navigational purposes).

In the most complex pattern there are two light stripes, one dorso--lateral and one lateral, bordered and separated by dark stripes. In the more simplified patterns the mid-dorsal dark stripe may be obsolete or absent, and the light latero-dorsal stripe may lack its upper dark border.

No sex differences were found in color pattern.

Head scales

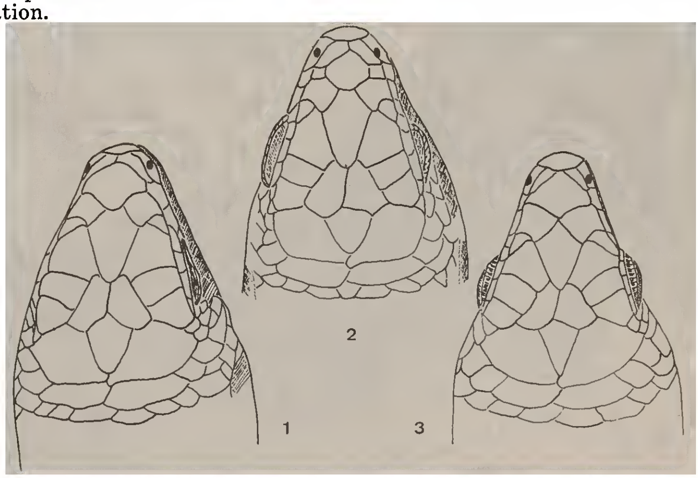
Given the great geographical variability shown by the head scales of South American *Mabuya*, we start with a detailed general description.

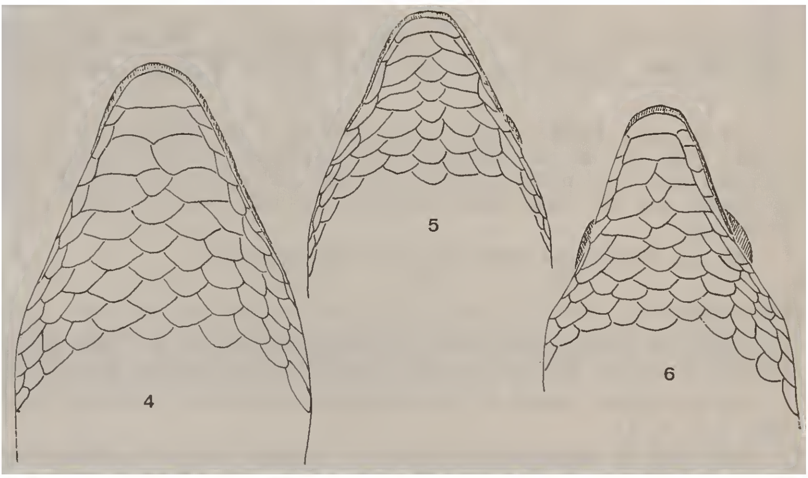
On the dorsal aspect of the head are found the following scales (figs. 1-3; pl. 1):

One pair of supranasals, usually in contact on the midline, but, in some populations, separated by the contact between the rostral and the frontonasal. In some insular populations the supranasals may be reduced, at times extremely so, but they are never absent in the samples at hand.

The frontonasal is a large scale, with convex front and hind margins; it has on each side a lateral process that reaches the loreals, mostly the anterior. These lateral processes are in many populations set off by sutures, forming separate scales, that we call "accessory frontonasals".

The prefrontals are polygonal, and meet the frontonasal, the frontal, the first (sometimes also the second) supraocular, and, depending on the extension of the lateral process of the frontonasal, one or both loreals. The relationship between the prefrontals varies from broad contact to wide separation, with some intra-sample, but also considerable geographic variation.





Dorsal aspect of head. 1, MZUSP 7312, Guanabara. 2, MZUSP 26790, S. Sebastião. 3, MZUSP 24031, Peruíbe. See plate 1. Ventral aspect of head. 4, MZUSP 7312, Guanabara. 5, MZUSP 26790, S. Sebastião. 6, MZUSP 24021, Peruíbe. See plate 3.

The frontal has postero-lateral margins converging into a blunt point, fitting between the fronto-parietals; the shape of the front edge varies depending on the degree of development of the prefrontals.

The frontoparietals form together a sort of butterfly figure, indented in front by the frontal and behind by the interparietal; the median suture is oblique.

The interparietal resembles the frontal, but is smaller. The parietals are large, irregular, and meet behind the interparietal. This character (presence or absence of contact) shows strong variation in other areas (Dunn, 1935: 540), but not in ours. There is only one pair of nuchals, short and broad, in contact.

The supraoculars are four. The first is small, triangular, and rests on the supraciliary series. The second is larger, polygonal, and reaches the prefrontal in front and the frontoparietal behind. The third is rectangular, and the fourth roughly triangular.

On the lateral aspect of the head (pl. 2) there are few features of interest. The nostril opens between two nasals, the posterior largest. The anterior loreal is smaller than the posterior, which is separated from the eye by several small scales of the infraocular series. There are five supraciliaries.

There are usually seven upper labials, of which the fifth or sixth (rarely the seventh) lies below the middle of the eye. There is variability within all samples, but no geographic differentiation was found.

On the ventral aspect of the head (figs. 4-6, pl. 3), the post--symphysial shows pronounced geographic variation. It may be broad, belt-like, occupying all the space between the lower labials, followed by two pairs of enlarged scales, the first of which partly or not in contact, the second always separated by the median row of gulars, or, in other localities, almost identical to the gulars.

No sexual differences were found in the cephalic scutellation.

Meristic characters

Ventral scales. We thus call the number of median ventral scales, counted between two imaginary lines: one tangent to the anterior margin of the arms kept perpendicular to the body, the other similarly related to the hind limb. Strong sexual dimorphism was found in this character.

Midbody scales. Counted transversely around the body, approximately midway between the insertion of the limbs. There being no sexual dimorphism, males and females are treated jointly.

Femoral scales. Counted along the middle of the ventral aspect of the thigh, between the inguinal and knee folds. No sexual dimorphism was found.

Fourth toe lamellae. The first lamella is taken as the most proximal one that spans the whole ventral surface of the toe, the last as the claw-bearing one. Again no sexual dimorphism was found.

Body proportions

Body length. This is the rostro-anal length, measured with a ruler, to the nearest millimeter, along the ventral surface of the animal.

Head length. Measured with calipers, to the nearest tenth of a millimeter, between the tip of the rostral and the anterior margin of the ear. The character studied is the regression of head length on trunk length, the latter being body length minus head length.

Strong sexual dimorphism was found in this character, and the regression lines show excellent fit (Appendix 1, tables 6 and 7). Rand (1967: 65) showed for Jamaican *Anolis lineatopus* that size differences between males and females are related to the avoidance of competition for food, since both sexes are territorial and the territories overlap. Schoener (1970 and previous papers) showed, for the same genus, that head size is related to prey size, and that specific and sexual differences can be interpreted as character displacement, tending to decrease competition between syntopic individuals. It is reasonable to expect that the sexual dimorphism in relative head length of *Mabuya* be due to the same causes, and perhaps the same explanation may be extended to other dimorphic morphometric characters (see below).

Head width. We were not able to obtain consistent measurements.

Snout length. Hoge (1946) emphasized this character by calling *macrorhyncha* the population from Ilha da Queimada Grande. We were not able to obtain consistent measurements, since one of the points of reference (the anterior angle of the eye) is not firm enough.

Limb length. Analysis of the regression of limb length on body length can provide much more information than the traditional system (still used by Dunn, 1935) of noting the degree of overlap of the adpressed limbs. Limb length was measured to the nearest millimeter, with a ruler adpressed to the ventral surface of the limb kept perpendicular to the body, the distal reference being the tip of the extended claw. This may seem a chancy measurement but, with some practice, it may be made quite precise (Vanzolini & Rebouças-Spieker, 1973). For both limbs marked sexual differences were found.

Statistical methods

The method used in the analysis of geographical differentiation was that of "transects" (Vanzolini, 1951; Vanzolini & Williams, 1970), in which statistical analysis (or, in favorable cases, simple inspection) is applied to the distribution of individual characters of samples linearly arranged. This method is particularly suitable to the coast of São Paulo, given the narrow width of the coastal plain.

It is of the essence of the method that each character be studied individually, common denominators being looked for in a subsequent synthesis. This procedure has the double advantage of making analysis easier and of permitting a better understanding of intergradation belts, as it should not be expected *a priori* that the several characters show the same type of intergradation (see Oliver, 1972, for an experimental approach).

Meristic characters. Initially it was checked whether each character was correlated with body size; such a correlation may be due to ontogenetic changes or to selection, certain values of the character appearing in the young and not, or less frequently, in the adult. In the first case one should have recourse to regression analyses; in the second, only samples of adults should be compared. No associations were found between meristic characters and body size.

Next it was checked whether correlations existed between pairs of characters, as it is obvious that characters strongly correlated intra-sample cannot be independently considered in the synthetic phase of the analysis. Again no correlations were found.

After these preliminary steps, the type of analysis adopted depended on the symmetry and range of the distribution. Distributions fairly symmetrical and with a reasonable range were submitted to analysis of variance (e.g., Steel & Torrie, 1960), and, when necessary, to Kramer's (1956) extension to samples of unequal size of Duncan's (1955) method of multiple comparisons. Distributions with only 2 or 3 classes, or very skew, were subjected to non-parametric methods, especially C^2 (chi square), even in cases where some cells had small or null frequencies (Lewontin & Felsenstein, 1965).

Body proportions. Scatter diagrams were plotted in all cases, and visually examined in order to assess the presence and probable form of the regression. In all cases good linear regressions were found. They were computed and the relevant data are shown in tables 6 to 11, Appendix 1, in which the following abbreviations are used:

- N number of individuals in the sample
- R_x range of the independent variable
- a regression constant, plus or minus its standard deviation
- b regression coefficient, plus or minus its standard deviation
- r^2 coefficient of determination
- y_x calculated value of the dependent variable for selected values of the independent variable.

Regressions were first compared graphically; when necessary, they were submitted to analysis of variance (Steel & Torrie, 1960). When found not homogeneous, they were analyzed by Duncan's (1970) extension to coefficients of regression of Kramer's (1956) method for means, and to an unpublished extension by Vanzolini of the same method to regression constants.

To lighten the text, results are throughout cited only as significant (at the 5% level) or not; the actual data are presented in Appendix 2.

Geographic differentiation

Color pattern

The North Coast samples (Ubatuba, Caraguatatuba, São Sebastião, Praia de Boracéia, Bertioga) show a middorsal light brown stripe, running along two half scales on the vertebral region (plate 4). Lateral to this the ground color occupies an area 2 to 2.5 scales wide. Next comes one stripe, darker than the middorsal, running from the supraciliary region to the tip of the tail. Next, one blackish stripe, one whole and two half scales wide, from the loreal region, through the eye, over the ear and along the flank to the inguinal region. Next a light stripe, two half scales wide, from the angle of the mouth, through the ear, over the insertion of the arm, along the flank to the inguinal region. Below this stripe the ground color changes into the belly color, a reticulate dirty gray with dense punctuation on the free edge of the scales. This color pattern is constant in all North Coast samples.

In the South Coast (Enseada, Santos, Mongaguá, Itanhaém, and Peruíbe) another pattern is found (plate 5). The ground color occupies the middorsal region, 2 whole scales on the middle, plus one half to one scale on each side. There is next a white, black-bordered stripe, running from the fourth supraocular to the root of the tail. The upper black border (usually a well defined stripe) joins its fellow on the proximal fourth of the tail; the lower black border, wider than the upper, vanishes above the insertion of the thigh. Next comes (plate 2) a narrow, irregular light stripe, that starts on the upper lip, crosses the lower half of the ear, passes over the insertion of the arm, and disappears on the flank.

Guanabara specimens (plate 6) have the middorsal stripe obsolete, at times hardly noticeable. The pattern on the sides of the body approaches that of the North Coast, but is much less vivid.

Among the insular samples, Ilhabela has the exact North Coast pattern. All other islands agree with the South Coast pattern, with a slight difference in the ground color (that tends to olive brown) and in the color of the lateral stripes (grayer than on the coast).

Dorsal head scales (figs. 1-3; pl. 1)

The contact between the supranasals is full, forming a short but distinct suture, in the North Coast and Guanabara; in the South Coast the supranasals are separate or barely touch each other.

The prefrontals are in contact in the South Coast, broadly separated in the other continental localities. This of course determines the shape of the anterior margin of the frontal, as can be seen in the figures.

Accessory frontonasals are found exclusively in the North Coast (not in Guanabara).

As to the islands, Ilhabela agrees exactly with the North Coast. All the other islands agree with the South Coast, with some minor peculiarities to be discussed below.

Ventral head scales (figs. 4-6; pl. 3)

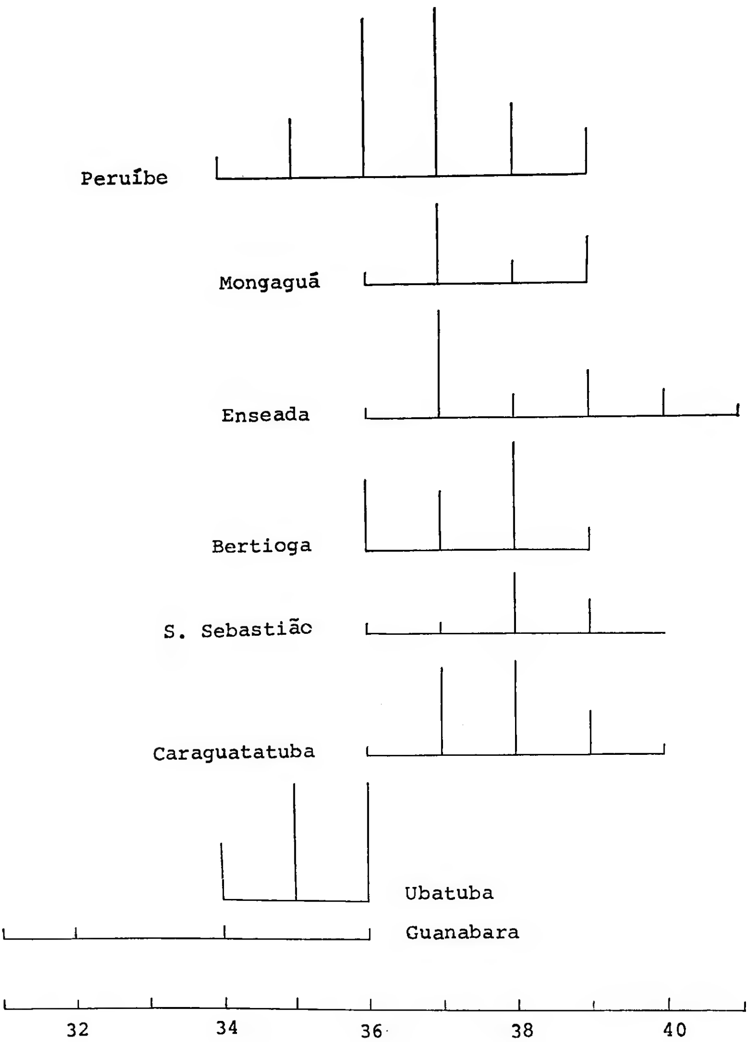
In the South Coast and Guanabara samples one finds a broad post-symphysial, occupying all the space between the lower labials. Behind this scale there is one pair of scales, also large, meeting on the midline but partly separated by the first median gular. In the North Coast samples there is no unpaired post-symphysial; in its place is found a pair of scales variously developed, sometimes meeting on the midline, sometimes not.

Among the islands, Ilhabela fully agrees with the North Coast, the remainder with the South Coast.

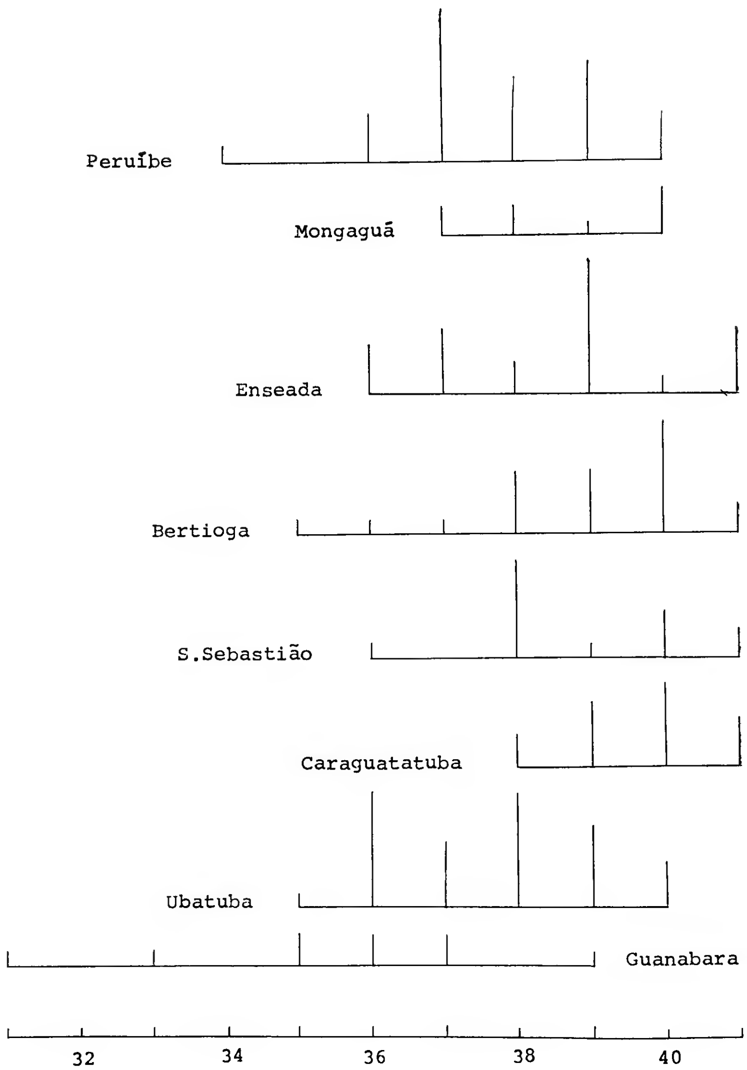
Ventral scales

Males. Table 1 (Appendix 1) and Graph 1 show that from Caraguatatuba to Mongaguá there is one unbroken series of localities with high values (Appendix 2, note 1). The Guanabara sample has very low values, and Ubatuba is intermediate. To the south, Peruíbe has low values, but not as low as Ubatuba. All the islands are decidedly on the side of higher counts; inter-island variation will be dealt with below.

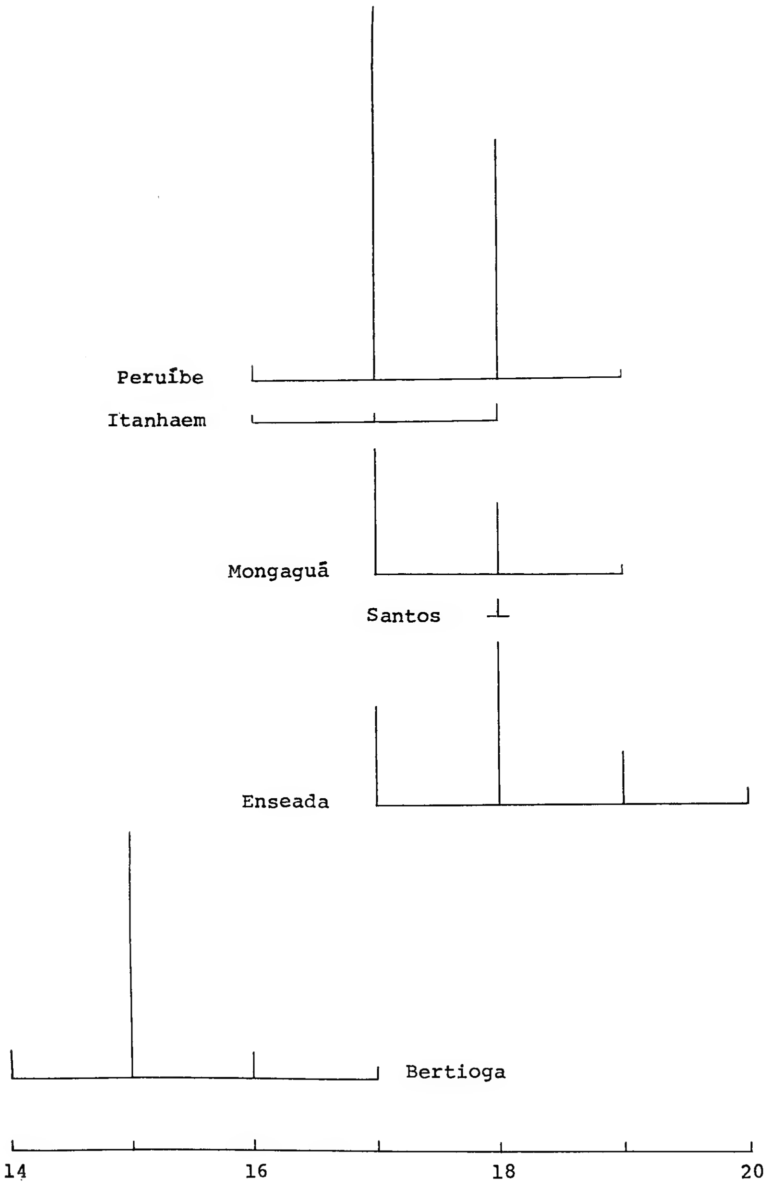
Females. Table 2 (Appendix 1) and Graph 2 show a pattern similar to that of the males (Appendix 2, note 2) with the difference that Ubatuba differs less from the remaining São Paulo samples. The islands in general agree with the high count samples, and will be discussed below.



Graph. 1. Ventral scales, males, frequency distributions on the continent (Table 1, Appendix 1).



Graph 2. Ventral scales, females, frequency distributions on the continent (Table 2, Appendix 1).



Graph 3. Fourth toe lamellae, both sexes, frequency distributions on the continent, from Bertioga south (Table 5, Appendix 1).

Midbody scales

It is seen from table 3 (Appendix 1) that there is no overlap between the North and the South Coast. Inside the North Coast there is significant diversification. Three groups may be discerned: (i) Bertioga; (ii) Ubatuba and Caraguatatuba; (iii) São Sebastião. The variation is thus not clinal. The Guanabara sample is intermediate between the North and the South Coast, but closer to the former.

Ilhabela falls between groups (ii) and (iii) of the North Coast. The remaining islands agree in general with the South Coast, but show considerable differentiation, to be discussed below.

Femoral scales

In this character again the North and the South Coast differ significantly, but each area presents an internal mosaic (Table 4, Appendix 1). In the islands we find a third mosaic, which will be separately discussed.

Fourth toe lamellae

Table 5 (Appendix 1) and Graph 3 show a clear difference between the North Coast (plus Guanabara) and the South Coast. Within the former there is significant variation: the Ubatuba sample differs from the others, having 90% of the specimens in the lowest class, 14 lamellae.

In the South Coast the lamellar counts are highest in Enseada, then progressively decrease towards the south.

Ilhabela is intermediate between the general North Coast range and the southern sample with lowest values, Peruíbe. The other islands are within the range of the South Coast, showing some diversification, to be discussed below.

Head length

Males. Table 6 (Appendix 1) shows that the regressions of head length on trunk length vary from good ($r^2 = 0.83$) to practically perfect ($r^2 = 0.99$), 8 out of the 14 lines showing coefficients of determination of 0.95 or better.

By tracing the lines on transparent paper and checking agreements and differences by superimposition, we see that there are 5 groups of samples (Table A), the lines within each group being practically identical. This conclusion is born by analysis of variance (Appendix 2, note 3). Graph 4 shows one sample from each group. It is easy to see that group V has a higher regression coefficient than the others, that is, the young have relatively shorter heads, and the adults relatively longer ones. The other lines are virtually parallel, but the differences among regression constants are significant, group I having the smallest and group V the largest heads (smaller, though, than those of group V). Plotting these data on Diagram 1, we find a mosaic.

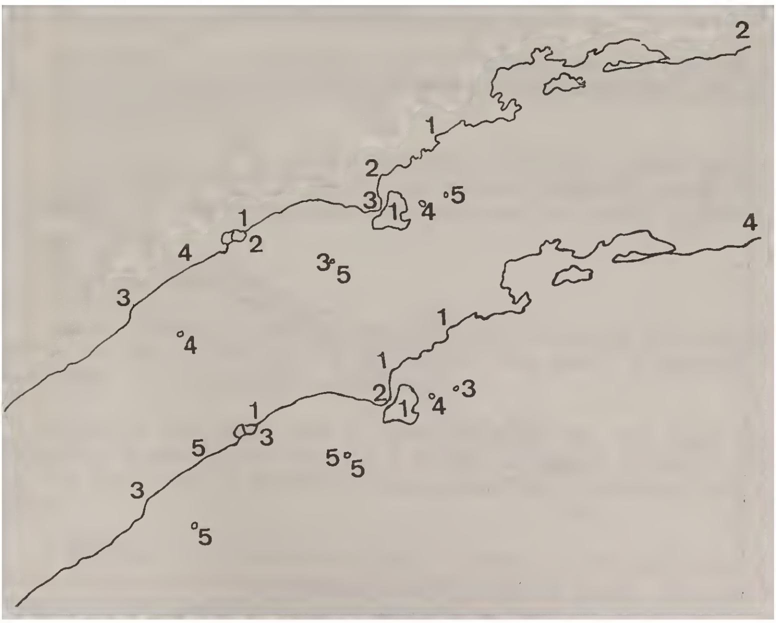
Table A

Regression of head length on trunk length, males, grouping of samples

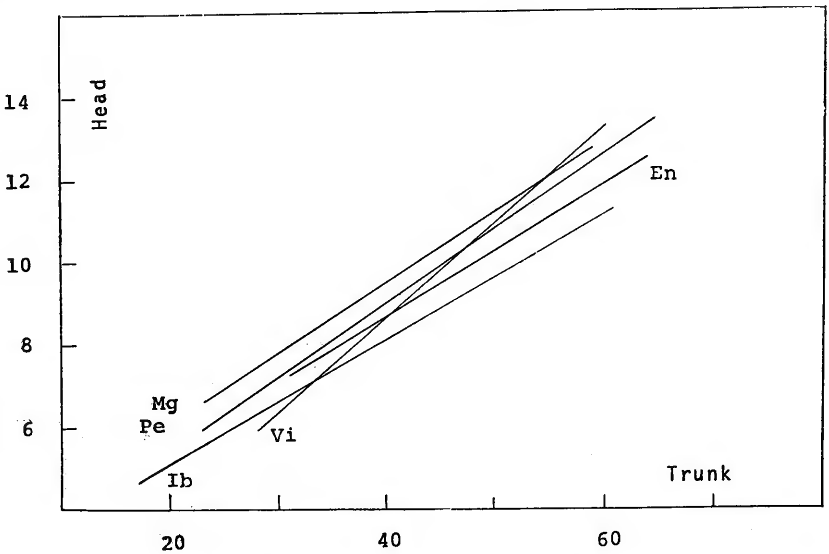
Group	*Mainland*	*Islands*
I	Ubatuba Bertioga	Ilhabela
II	Guanabara Caraguatatuba Enseada	
III	S. Sebastião Peruíbe	Paredão
IV	Mongaguá	Búzios Queimada Grande
V		Vitória Alcatrazes

Females. Also here the fit of the lines (Table 7, Appendix 1) is excellent. Repeating the type of analysis done for the males (Appendix 2, note 4), we also arrive at 5 groups of samples (Table B, Graph 5).

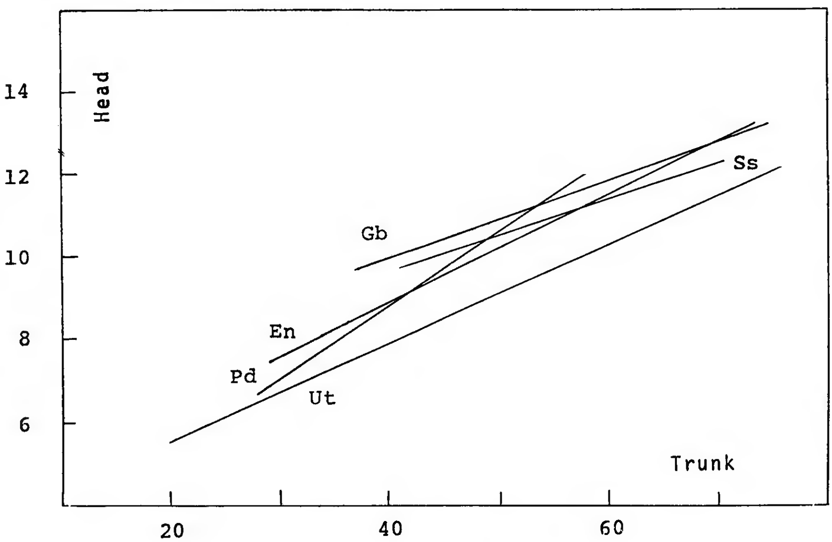
Group V again has a larger regression coefficient. The other lines, however, are not all parallel, but group I is parallel to III and II to IV. In general, group I has consistently smaller heads, but all other lines intersect each other at some point. Plotting the data on Diagram 2, we have again a mosaic. This, however, is not parallel to the male pattern (Appendix 2, note 5).



Diagrams 1 (top) and 2. Tracings of Map 1, showing the distribution of sample groups based on the regression of head length on trunk length, males (1) and females (2). (Tables A and B, the Roman numerals rendered into Arabic).



Graph 4. Regression of head length on trunk length, males, examples of the 5 groups of samples (Table A).



Graph 5. Regression of head length on trunk length, females, examples of the 5 groups of samples (Table B).

Table B

Regression of head length on trunk length, females, grouping of samples

Group	*Mainland*	*Islands*
I	Ubatuba Caraguatatuba Bertioga	Ilhabela
II	S. Sebastião	
III	Enseada Peruíbe	Vitória
IV	Guanabara	Búzios
V	Mongaguá	Alcatrazes Paredão Queimada Grande

As said above about the sexual differences in head length, this character is known to be related to prey size. If we correlate male and female head lengths on the continent, we obtain a coefficient (Spearman's coefficient of rank correlation) of 0.71, significant. However, this is a relatively low coefficient, since about 50% of the variance of one sex remains unexplained by the other.

Since there is a good spread in variability, we also applied rank correlation to the ranks of the coefficients of determination: the correlation is not significant.

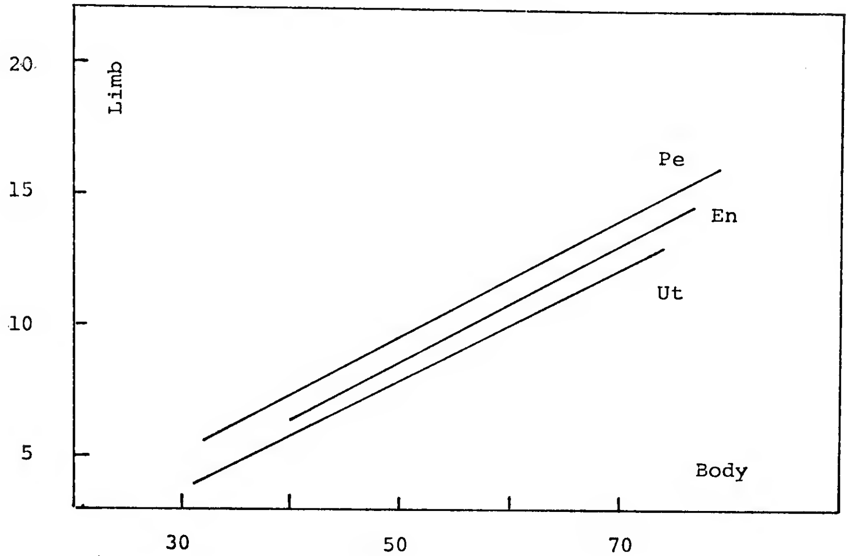
These data seem to indicate that this is a highly plastic character, responding readily to local selective pressures (probably related to the type of prey available) and that these pressures are partly different for the sexes.

Length of the fore limb

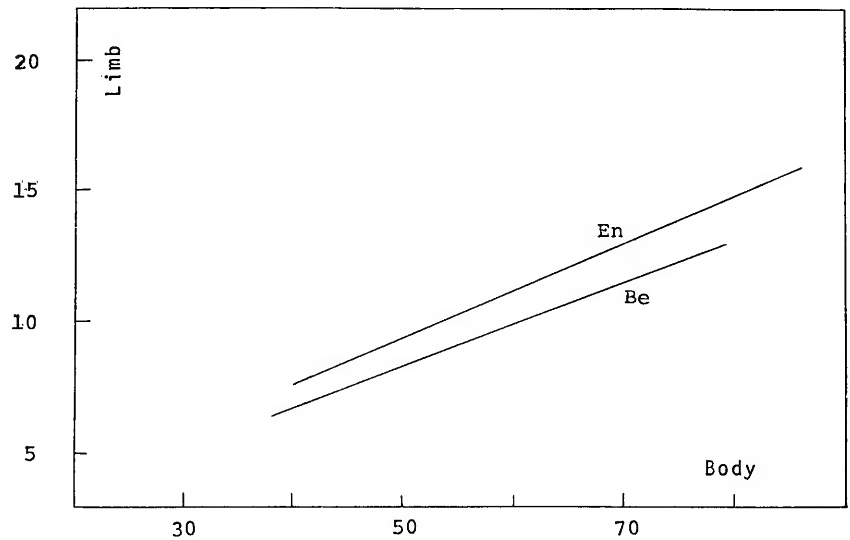
Males. Table 8 (Appendix 1) shows that, excepting the Guanabara sample, the fit of the lines is in general very good: 9 samples have coefficients of determination above 0.90.

Repeating the same type of analysis done for the head length (Appendix 2, note 6), we arrive at 3 groups of samples (Table C, Graph 6). All lines may be considered parallel, but the regression constants differ.

Analyzing the distribution of the 3 groups, we see that the North Coast samples all belong to group I, with shorter limbs. The southern samples belong in group III, and Enseada in group II, intermediate. As to the islands, Ilhabela agrees with the North Coast, Vitoria with Enseada, and the remainder with the South Coast.



Graph 6. Regression of fore limb length on body length, males, examples of the 3 groups of samples (Table C).



Graph 7. Regression of fore limb length on body length, females, examples of the 2 groups of samples (Table D).

Table C

Regression of fore limb length on body length, males, grouping of samples

Group	*Mainland*	*Islands*
I	Ubatuba Caraguatatuba S. Sebastião Bertioga	Ilhabela
II	Enseada	Vitória
III	Mongaguá Peruíbe	Búzios Paredão Alcatrazes Queimada Grande

The Guanabara sample shows such dispersion that is does not even afford any approximate indication of where it would belong.

Females. The fit of the lines is decidedly inferior to that of the males (Table 9, Appendix 1). Thus it becomes advisable not to test the data analytically, but to simply superimpose the scatter diagrams. It has been possible to perceive clearly the presence of 2 groups (Table D): (i) with shorter limbs the samples from the North Coast and Ilhabela; (ii) with longer limbs the remainder (Graph 7).

Table D

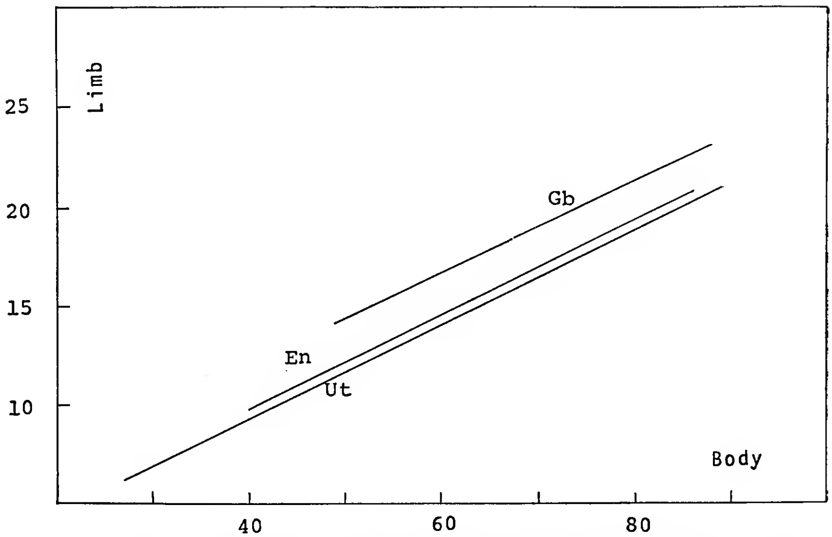
Regression of fore limb length on body length, females, grouping of samples

Group	*Mainland*	*Islands*
I	Ubatuba Caraguatatuba S. Sebastião Bertioga	Ilhabela
II	Guanabara Enseada Mongaguá	Vitória Búzios Paredão Alcatrazes Queimada Grande

Length of the hind limb

Males. In this character no geographic differentiation was noted (Table 10, Appendix 1).

Females. Table 11, Appendix 1, shows that all regressions but 2 (Búzios and Mongaguá) are very good, 8 of them having coefficients of determination above 0.90. Visual inspection of the graphs permits to separate the samples in 3 groups, within which agreement is so close that no further testing is necessary: Guanabara has very high values, the North Coast and Ilhabela have the lowest, and the South Coast and the remaining islands are intermediate (Table E, Graph 8).



Graph 8. Regression of hind limb length on body length, females, examples of the 3 groups of samples (Table E).

Table E

Regression of hind limb length on body length, females, grouping of samples

Group	*Mainland*	*Islands*
I	Ubatuba Caraguatatuba S. Sebastião Bertioga	Ilhabela
II	Enseada Mongaguá Peruíbe	Vitória Búzios Paredão Alcatrazes Queimada Grande

Differentiation on the continent: summary

We have studied the differentiation of 10 characters; as for 4 of them males and females have been separately considered, we have (Table F) 14 individual patterns of differentiation.

Of these 14 cases, 2 are mosaics: head length, males and females. One character showed no differentiation: hind limb length.

Among the 11 cases in which geographical regularities can be seen, two present a single area of stability within the area of study: ventral scales, males, Caraguatatuba to Mongaguá; ventral scales, females, Ubatuba to Peruíbe.

In the remaining 9 cases there is a distinct contrast between the North Coast and the South Coast.

In 6 of these characters (color pattern, dorsal and ventral head scales, femoral scales, fore limb length in females and hind limb length in females) the difference between the two groups is very clear and the transition sharp. The separation, in the samples available, occurs exactly between Bertioga and Praia da Enseada, and the constrasting areas are internally homogeneous.

Table F. Summary of character differentiation patterns on the continent.

Pattern and character	NC	SC	Gb
No differentiation			
Hind limb ♂	Uniform	Uniform	Uniform
Ventrals ♀	Uniform	Uniform	*
Mosaic			
Head lenght ♂	Mosaic	Mosaic	
Head length ♀	Mosaic	Mosaic	
Central area uniform			
Ventrals ♂	Ubatuba *	Peruíbe *	
North Coast x South Coast			
Color pattern	Homogeneous	Homogeneous	(N)
Dorsal head scales	Homogeneous	Homogeneous	(N)
Ventral head scales	Homogeneous	Homogeneous	(S)
Femorals	Homogeneous	Homogeneous	(N)
Fore limb length ♀	Homogeneous	Homogeneous	S
Hind limb length ♀	Homogeneous	Homogeneous	(S)
Fore limb length ♂	Homogeneous	2 groups	
Midbody scales	Mosaic	Homogeneous	(N)
Lamellae	Mosaic	Cline ?	(N)

NC	North Coast	SC	South Coast	Gb	Guanabara
N	agrees with NC	(N)	approaches NC	*	peculiar values
S	agrees with SC	(S)	approaches SC		

In the case of fore limb length, males, the North Coast is homogeneous, but there are two groups on the South Coast: one of them is formed by Enseada only, geographically and morphologically intermediate.

In the case of midbody scales the difference between the areas is sharp, but there is a mosaic on the North Coast.

Finally, in the case of the lamellae, there is also differentiation on the North Coast, and the distribution on the South Coast could perhaps be called clinal, if based on a larger number of localities.

Guanabara

This study started with emphasis on the insular patterns, and this is why the coastal collections were limited to the north by the latitude of the islands. To the south it seems at present that littoral *Mabuya* does not extend much beyond Peruíbe, if at all. However, the discovery of a sharp differentiation pattern on the coast made it necessary to introduce extra-limital materials. It was thought that one more sample, from an area to the north of Ubatuba, might afford an adequate estimate of the situation, without recourse to an extended geographical analysis. The area chosen was Guanabara, from which there were materials in the collections at hand.

It is seen in Table F that the Guanabara sample agrees or tends to agree with the North Coast in 5 characters, and with the South Coast in 3. We think it especially important that the head scalation is of the southern type.

In the two cases in which Guanabara sharply differs from both the North and the South Coast, Ubatuba is intermediate.

Table G

Relationships between the island and Guanabara patterns of differentiation with the continental patterns in the cases in which there is a difference between the North Coast and the South Coast.

Character	*Ilhabela*	*Other islands*	*Guanabara*
Color pattern	N	S	(N)
Dorsal head scales	N	S	(N)
Ventral head scales	N	S	(S)
Midbody scales	N	S	(N)
Femorals	*	Mosaic	(N)
Lamellae	*	S	N
Fore limb length ♂	N	S	—
Fore limb length ♀	N	S	S
Hind limb length ♀	N	S	(S)

N agrees with North Coast
S agrees with South Coast
(N) approaches North Coast
(S) approaches South Coast
* peculiar values

General insular pattern

With respect to the characters in which there is a contrast between the North Coast and the South Coast, it is seen (Table G) that Ilhabela differs markedly from the other islands.

In 7 out of the 9 characters, Ilhabela agrees with the North Coast; in the other 2 it has peculiar values, failing to agree with either continental area. The other islands agree with the South Coast in 8 out of the 9 characters, showing a mosaic in the remaining character.

Ecological differences

We have personal observations on the following mainland localities: Ubatuba, Caraguatatuba, São Sebastião, Bertioga, Enseada, Mongaguá and Peruíbe. From Ubatuba to Bertioga *Mabuya* was only seen and collected in grass clumps. From Enseada to Peruíbe it was found only in ground bromeliads.

There are some observations on the islands that tend to confirm these data: (i) the 1963 expedition of this Museum (then Departamento de Zoologia, Secretaria da Agricultura) to Búzios obtained a good sample in ground bromeliads; (ii) in the Alcatrazes group, Luederwaldt & Fonseca (1923) make it clear that *Mabuya* is also bromelicolous.

It is perfectly safe to say that these ecological preferences cannot be explained by present availability of environments: grassy areas are frequent to the south and north of the North Coast; within the latter, ground bromeliads are extremely abundant. In fact, based on experience in the south and in the islands, we wasted much time looking for *Mabuya* in extensive bromeliad patches around Caraguatatuba before local children told us that the lizards were in the grass.

Insular differentiation

It is possible to further investigate the relationships among islands (and eventually between the islands and the continent) in the case of the following characters; (i) supranasals; (ii) ventral scales, males (iii) midbody scales; (iv) femoral scales; (v) fourth toe lamellae; (vi-vii) head length, males and females; (viii) hind limb length, females.

Character analysis

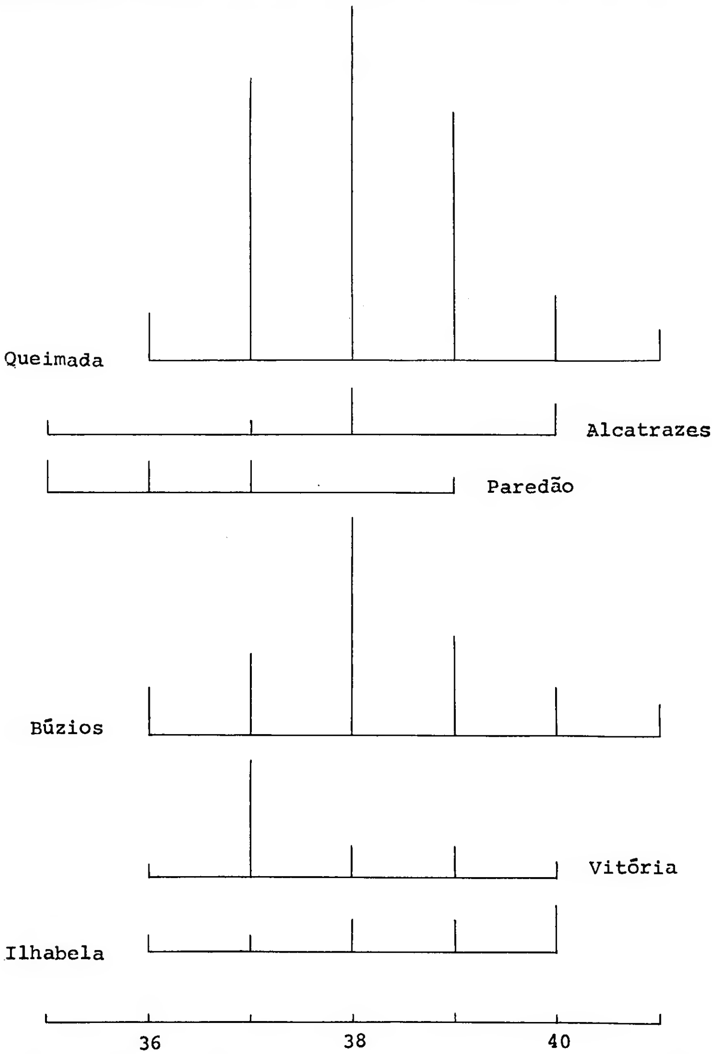
Supranasals. The Vitoria sample has almost all specimens with extremely reduced supranasals. In Queimada Grande we find the same type of reduction, less extreme, however.

Ventrals, males (Table 1, Appendix 1; Graph 9). Analysis of variance (Appendix 2, note 7) shows that the Paredão values are significantly lower than those of other islands, excepted Vitoria, that is intermediate.

Midbody scales (Table 3, Graph 10). Ilhabela is excluded from the analysis, as it agrees with the North Coast and sharply contrasts with the other islands.

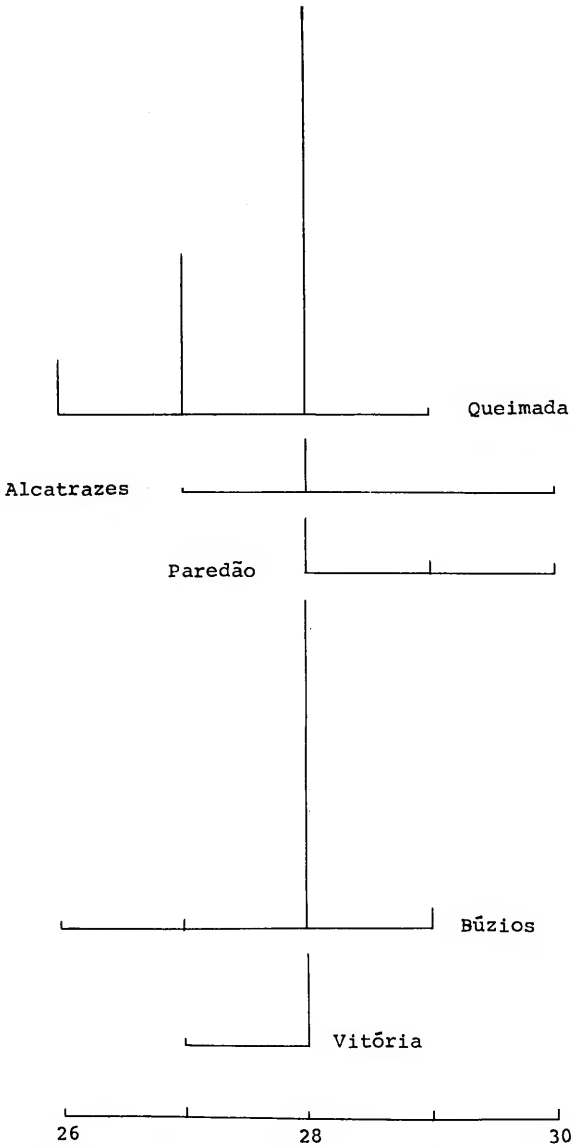
Vitoria and Paredão have such asymmetrical distributions that analysis of variance cannot be applied. Thus we initially tested by C^2 the agreement, on one side between Vitoria and Búzios, on the other within the Alcatrazes archipelago. It was possible to join the respective samples and do an analysis of variance with 3 groups: Vitoria plus Búzios, Alcatrazes group, Queimada Grande.

The three groups differ significantly among themselves (Appendix 2, note 8), but no geographical regularity is seen, or obvious relationships with island size or position, since the highest values are in the Alcatrazes, the intermediate ones in Vitoria and Búzios and the lowest ones in Queimada. This corresponds exactly to what is found on the mainland,

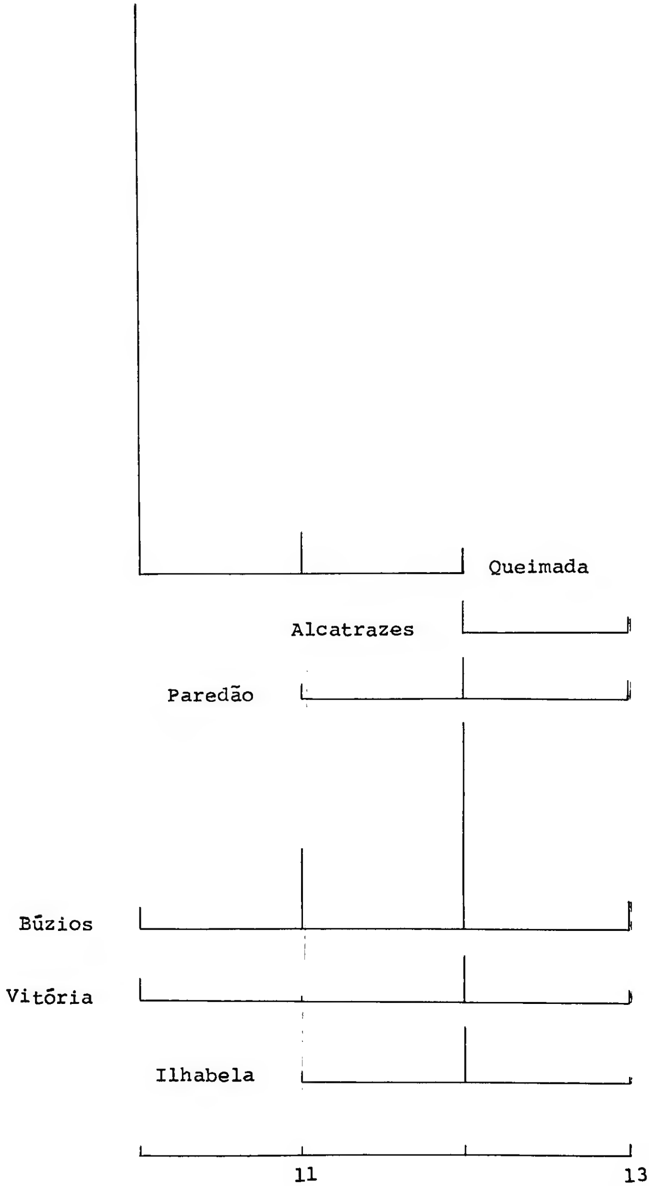


Graph 9. Ventral scales, males, frequency distributions of the insular samples (Table 1, Appendix 1).

where there are also some strongly skew samples and local variation within the ranges (respectively higher and lower) characteristic of the North and of the South Coast.

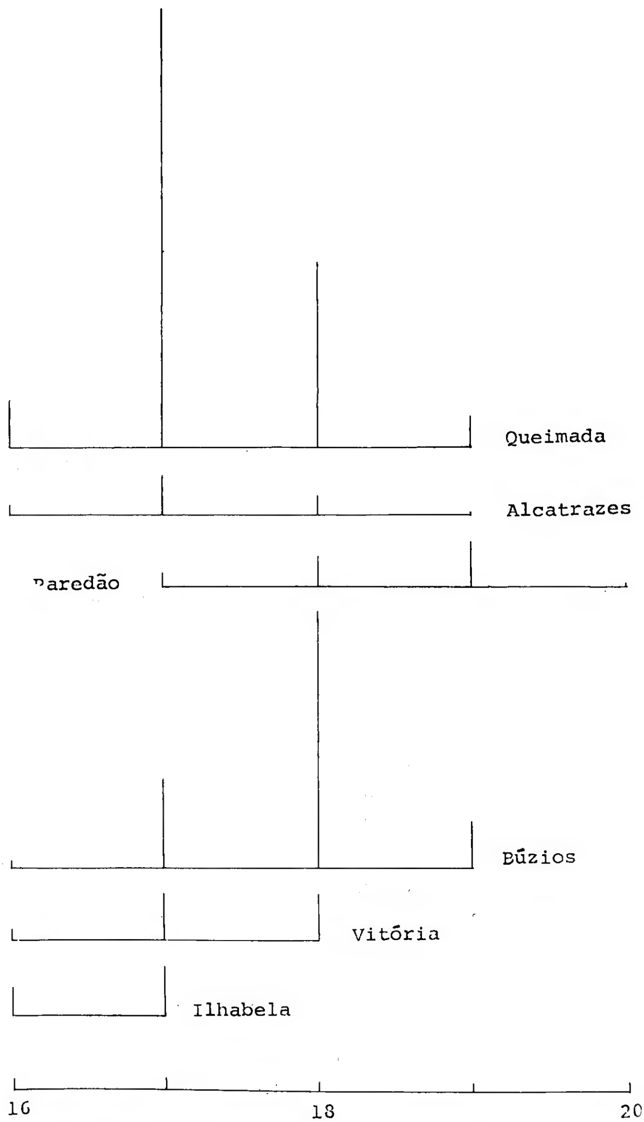


Graph 10. Midbody scales, both sexes, frequency distributions of the insular samples (Table 3, Appendix 1).



Graph 11. Femoral scales, both sexes, frequency distributions of the insular samples (Table 4, Appendix 1).

Femorals (Table 3, Appendix 1; Graph 11). Queimada Grande is outstanding both for its skewness and low values; it is unnecessary to include it in further analysis.



Graph 12. Fourth toe lamellae, both sexes, frequency distributions of the insular samples (Table 5, Appendix 1).

Vitoria also shows an excess of specimens in the lowest class. Its distribution (Appendix 2, note 9) differs from that of Búzios, but the means do not. It is again necessary to group the Alcatrazes in a single sample.

After these manipulations it is possible to do an analysis of variance, that shows that the 4 groups differ significantly. The general pattern would be (averages in decreasing order): (i) Alcatrazes group; (ii) Ilhabela; (iii) Búzios (plus Vitoria); (iv) Queimada Grande. Ilhabela is intermediate between Alcatrazes and Búzios.

Lamellae (Table 5, Appendix 1; Graph 12). Ilhabela is not amenable to analysis of variance. This method (Appendix 2, note 10), applied to the other samples, reveals 3 groups: (i) Paredão; (ii) Búzios; (iii) Vitoria, Queimada Grande and Alcatrazes. Thus the inter-island pattern is the same as the continental one, and shows no special regularities.

Head length. The insular mosaics are as disorderly as the continental ones, and there is no correlation between the male and the female patterns.

Summary

Assembling previous results and those of the present chapter, it can be said that: (i) Ilhabela behaves entirely as part of the North Coast; (ii) the remaining islands, independently of latitude, area and accessibility from the mainland, follow the South Coast; (iii) the inter-insular variation and the relationships with the continent, in those characters in which there is no agreement with the South Coast, show no particular geographical patterns.

Discussion

It is clear that the samples from the North and South Coasts differ markedly, and to prove this it would not have been necessary to analyze as many characters as we did, or to present the data on non-discriminating characters. In fact, the differences in color pattern and head scalation are such as, in current herpetological practice, warrant species status to the forms involved. Our analysis, however, intends to permit the consideration of some evolutionary problems.

One first fact is that there is concordance of many important characters within each of the contrasting areas. A second one is that the transition between them is rather abrupt, occurring (according to present materials) between two localities (Bertioga and Praia da Enseada) separated by a channel less than 1 km wide. The first hypothesis to be examined then is that we have here two parapatric species. The testing of such a hypothesis is a task beyond simple morphological analysis. At the present stage of inquiry two counter-arguments might be cited: (i) the differentiation of the ventral scales, both in males and females, presents a geographical regularity independent of the North-South dichotomy; (ii) the Enseada sample is intermediate between North and South in forelimb length of males.

These facts may indicate that the abruptness of the transition between the two forms is not due to the meeting of two parapatric species, without or with extremely limited gene flow, but instead to the existence of very strong selective pressures. The fact that in some characters of low variability one finds mosaic patterns of differentiation would also favor the idea of strong selective forces.

In favor of the interpretation as parapatric species we may mention here the information (to be published elsewhere) that preliminary karyotypic and electrophoretic comparisons between the adjacent populations of Bertioga and Enseada show that very probably they do not interbreed or, at least, that genetic compatibility is low.

We have much less information on the northern populations, but what exists tends to confirm the picture found in the South: Guanabara broadly agrees with or at least approaches the South Coast. This would make the North Coast of S. Paulo a pocket of marked differentiation. But we must remember that Ubatuba, our northernmost S. Paulo locality, in some features approaches Guanabara. The possibility of introgression cannot be dismissed offhand; the intervening area must be closely studied.

What seems to us very strong evidence in favor of the hypothesis of the differentiation of a North Coast form from a formerly (relatively at least) homogeneous ensemble is the situation in the islands. Excepting on the horst of S. Sebastião (Ilhabela), discussed below, all the populations of the islands, even the northernmost ones as Búzios and Vitoria, close to the mainland and to Ilhabela (Map 4), are in strong agreement both in morphology and ecology, with the South Coast type, from which they are broadly separated (Map 1).

This favors the hypothesis that the North Coast populations have recently differentiated from an ancestral homogeneous population that occupied a continuous coastal plain in the last glacial.

The situation on the Ilhabela horst seems to be explainable on three counts: (i) recency of isolation (a shallow channel); (ii) easy gene flow even after isolation; (iii) physiographical similarity to the continent, implying similar selective pressures.

A model

Thus a general explanation of the pattern found would involve:

1. During the latest glacial the coast, from Rio de Janeiro to southern S. Paulo (at least) was a continuous gently sloping plain, with disarticulated hills, supporting populations of *Mabuya* living in ground bromeliads, and characterized by: (i) absence of a middorsal light stripe; (ii) absence of accessory frontonasals; (iii) one large post-symphysial, followed by a pair of enlarged scales; (iv-vi) high counts of midbody and femoral scales, and of fourth toe lamellae; (vii-viii) relatively long fore limb, in males and females; (ix) relatively long hind limb in females.

2. With the subsequent marine ingression the North Coast became broken up in bays containing small steep shores, backed up by narrow alluvial plains. The disarticulated hills became islands. In the South Coast and in the State of Rio de Janeiro the effects of the introgression were much less conspicuous, long beaches and unbroken alluvial plains remaining.

3. On the North Coast and in the island of S. Sebastião (Ilhabela) *Mabuya* changed its habitat to grass clumps, and underwent morphological modifications.

Problems

According to this model, we have in the continental area investigated 3 units linearly arranged: South Coast, North Coast and Guanabara.

South Coast and Guanabara are much closer morphologically to each other than either to North Coast, but, given the practically certain absence of *Mabuya* of this group on slopes of the Serra do Mar and inland, they may be taken as effectively separated. Gener flow along the chain of small islands is theoretically possible, but at best it would be extremely tenuous.

The breaks between the 3 units still need to the better defined. With regard to North Coast and South Coast we have the good Bertioga and Enseada samples. It will be necessary now to go inland in the flood plain behind Santos and to explore the northern tip of the South Coast. We expect this will turn out as an exercise in prudence, and that the pattern here presented will be confirmed.

Things are a little different on the northern side. It will be necessary first to ascertain what our "Guanabara" sample really represents, by collecting intensively in the state of Rio de Janeiro. At the same time a good transect has to be run between Ubatuba and Guanabara. Simultaneously, intensive work has to be done on the karyotypic and electrophoretic aspects of the problem, and on the biology of the lizards in the different areas.

We face here a clear case of parapatric speciation. It matters very little whether gene flow between the 3 areas is impeded totally or partially: the relevant fact is that stark differentiation has occurred in the absence of geographical or ecological barriers. Establishing this fact is important, and is the point made by the present paper. A main task remaining, however, is to use these coastal populations of *Mabuya* for further investigation of this little understood phenomenon.

NOMENCLATURE

The nomenclatural situation here is fortunately quite easy.

Guanabara (Rio de Janeiro) is the type locality of an old and undisputed name: *Scincus agilis* Raddi, 1820.

If one accepts, as we do, that the insular populations are cospecific with the South Coast populations, *Mabuya macrorhyncha* Hoge, 1946, type locality Ilha da Queimada Grande, is unchallenged.

We propose to call the North Coast form *Mabuya caissara,* sp. n., maintaining for the time being all forms at the species level.

Mabuya caissara, sp. n.

Holotype: MZUSP 17565, male, Praia de Massaguassu, Caraguatatuba, S. Paulo, 27.ix.1969, R. Rebouças-Spieker & W. Spieker coll.

Paratypes: MZUSP 17548-17571, males and females, same data as the holotype. MZUSP 17535-17540, same locality as holotype, collected on 14.ix.1969 by R. Rebouças-Spieker & W. Spieker.

Paratypes will be deposited in the Museum of Comparative Zoology, Harvard University.

Diagnosis

Color pattern as in plate 1. Accessory frontonasals present. No unpaired differentiated post-symphysial. Ventral scales, males 34-40, females 35-41. Midbody scales 30-34. Femoral scales 10-12. Fourth toe lamellae 14-17.

The name derives from the Brasilian "caiçara", the cognomen of the native inhabitants of the area.

Distribution: Coast of the state of S. Paulo north of Santos (Ubatuba, Caraguatatuba, S. Sebastião, Praia de Boracéia, Bertioga) and island of São Sebastião.

Mabuya macrorhyncha Hoge, 1946

Distribution: Coast of the State of S. Paulo from Guarujá south (Praia da Enseada, Santos, Mongaguá, Itanhaém, Peruíbe) and islands of Vitória, Búzios, Queimada Grande and the Alcatrazes group.

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Discussion between my advisor and Dr. E. E. Williams (Museum of Comparative Zoology) has extended the scope of this work beyond what I would have been able to do by myself, although Dr. Williams should not be held responsible for the final version.

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Appendix 1

Statistical tables

Table 1. Ventral scales, males, frequency distributions

	Mainland										Islands							
	Gb	Ut	Ct	Ss	Be	En	St	Mg	It	Pe	Ib	Vi	Bz	Pd	Sp	Al	Qg	
31	1																	31
32	1																	32
33	-																	33
34	1	5								2								34
35	-	10								5				2		1		35
36	1	10	1	1	6	1	1	1		13	1	1	3	2		-		36
37			7	1	5	9	1	7	1	14	1	7	5	2		1	17	37
38			8	5	9	2		2	1	6	2	2	13	-		3	21	38
39			4	3	2	4		4		4	2	2	6	1	1		15	39
40			1	2		2					3	1	3			2	4	40
41						1							2				2	41
	4	25	21	12	22	19	2	14	2	44	9	13	32	7	1	7	62	

Table 2. Ventral scales, females, frequency distributions

	Mainland										Islands							
	Gb	Ut	Ct	Ss	Bo	Be	En	Mg	It	Pe	Ib	Vi	Bz	Pd	Sp	Al	Qg	
31	1																	31
32	-																	32
33	1																	33
34	-									1								34
35	2	1				1				-			1				1	35
36	2	7		1		1	3			3			1	1			3	36
37	2	4		-		1	4	2	2	9		2	12	4		1	10	37
38		7	2	6		4	2	2		5		-	10	3		2	19	38
39	1	5	4	1	1	4	8	1		6		3	10	2	1	1	20	39
40		3	5	3	1	7	1	3		3	2	-	6			-	11	40
41			3	2		4	4				4	3	4			2	4	41
	9	27	14	13	2	22	22	8	2	27	6	8	44	10	1	6	78	

Table 3. Scales around midbody, both sexes, frequency distributions

	Mainland											Islands						
	Gb	Ut	Ct	Ss	Bo	Be	En	St	Mg	It	Pe	Ib	Vi	Bz	Pd	Sp	Al	Qg	
26							4		1		7			1				12	26
27	1						4		2		19		2	3			1	34	27
28	1						29	2	19	4	63		19	68	12	2	11	85	28
29	1										1			5	3		-	2	29
30	10	8	11		2	34									3		1		30
31		9	4			7						2							31
32	1	40	19	20		2						14							32
33			1	1								1							33
34				4															34
	14	57	35	25	2	43	37	2	22	4	90	17	21	77	18	2	13	133	

Table 4. Femoral scales, both sexes, frequency distributions

	Mainland											Islands						
	Gb	Ut	Ct	Ss	Bo	Be	En	St	Mg	It	Pe	Ib	Vi	Bz	Pd	Sp	Al	Qg	
10	2	4	2	14	1	5							6	5				131	10
11	14	12	19	11		37	18		22	3	63	3	1	19	4			10	11
12		36	14		1	8	19	2			18	13	11	47	10	1	8	3	12
13											1	1	3	7	5	1	4		13
	16	52	35	25	2	44	37	2	22	3	82	17	21	77	19	2	12	144	

Table 5. Fourth toe lamellae, both sexes, frequency distributions

	Mainland											Islands						
	Gb	Ut	Ct	Ss	Bo	Be	En	St	Mg	It	Pe	Ib	Vi	Bz	Pd	Sp	Al	Qg	
14		51	3			3													14
15	6	4	29	21	2	27													15
16	7	1		3		3				1	2	6	2	1			2	9	16
17	5		2			1	11		14	1	41	10	9	17	3		8	82	17
18							18	2	8	2	26		9	48	6	2	4	35	18
19							6		1		1			9	9		1	6	19
20							2								1				20
	18	56	34	24	2	44	37	2	23	4	80	16	20	75	19	2	15	131	

Table 6. Regression of head length on trunk length, males

	N	R_x		b		a		r^2	y_{20}	y_{65}
Guanabara	6	42,6 -	58,6	0,17 ±	0,018	3,7 ±	0,85	0,96	7,10	14,7
Ubatuba	20	24,5	59,0	0,16	0,0092	3,4	0,47	0,95	6,60	13,8
Caraguatatuba	20	46,1	62,0	0,14	0,011	5,3	0,58	0,89	8,10	14,4
São Sebastião	12	44,0	56,6	0,18	0,014	3,4	0,71	0,94	7,00	15,1
Bertioga	23	28,9	59,5	0,17	0,0051	2,9	0,25	0,98	6,30	14,0
Enseada	19	33,0	61,6	0,16	0,0081	3,9	0,39	0,96	7,10	14,3
Mongaguá	14	25,3	57,2	0,17	0,010	4,4	0,52	0,96	7,80	15,5
Peruibe	45	25,6	62,0	0,18	0,0036	3,6	0,18	0,98	7,20	15,3
Ilhabela	9	19,8	68,4	0,15	0,020	3,5	1,04	0,89	6,60	13,4
Vitória	13	30,0	54,7	0,23	0,0092	1,8	0,41	0,98	6,40	16,8
Búzios	32	43,4	57,4	0,16	0,011	4,8	0,56	0,88	8,00	15,2
Paredão	8	30,2	60,2	0,16	0,021	4,2	0,87	0,90	7,40	14,6
Alcatrazes	8	26,7	54,2	0,21	0,0071	2,6	0,27	0,99	6,80	16,3
Queimada Grande	71	33,4	58,9	0,18	0,0098	4,2	0,49	0,83	7,80	15,9

Table 7. Regression of head length on trunk length, females

	N	R_x		b		a		r^2	y_{20}	y_{65}
Guanabara	11	39,8 -	72,0	0,095 ±	0,0095	7,1 ±	0,56	0,92	9,0	14,2
Ubatuba	27	22,1	73,5	0,12	0,0037	4,3	0,22	0,98	6,7	13,3
Caraguatatuba	14	54,0	71,0	0,11	0,011	5,1	0,65	0,90	7,3	13,4
São Sebastião	13	43,5	68,4	0,090	0,013	6,9	0,72	0,81	8,7	13,7
Bertioga	22	31,7	64,5	0,13	0,0046	4,0	0,22	0,98	6,6	13,8
Enseada	18	32,9	70,0	0,13	0,0056	5,0	0,33	0,97	7,6	14,8
Mongaguá	8	50,5	60,5	0,095	0,0265	7,7	1,49	0,68	9,6	14,8
Peruibe	27	31,0	70,5	0,13	0,0097	5,3	0,58	0,88	7,9	15,1
Ilhabela	8	26,9	76,7	0,13	0,0099	3,8	0,59	0,97	6,4	13,6
Vitória	8	33,7	62,9	0,14	0,010	4,5	0,54	0,97	7,3	15,0
Búzios	44	42,8	66,8	0,10	0,0080	7,1	0,46	0,80	9,1	14,6
Paredão	11	30,1	53,9	0,18	0,0053	3,4	0,24	0,99	7,0	16,9
Alcatrazes	7	43,2	60,5	0,16	0,011	3,9	0,60	0,98	7,1	15,9
Queimada Grande	73	38,0	61,2	0,15	0,0074	4,8	0,39	0,86	7,8	16,1

Table 8. Regression of fore limb length on body length, males

	N	R_x		a		b		r^2	y_{30}	y_{80}
Guanabara	6	53	68			0,087 ±	0,045	0,49		
Ubatuba	19	32	72	1,6 ±	0,8	0,21	0,014	0,93	7,9	18,4
Caraguatatuba	18	58	76	3,3	1,5	0,19	0,024	0,80	9,0	18,5
São Sebastião	11	55	70	3,7	1,4	0,19	0,023	0,88	9,4	18,9
Bertioga	23	37	73	2,5	0,6	0,19	0,0098	0,95	8,2	17,7
Enseada	19	42	75	2,0	0,4	0,22	0,0064	0,99	8,6	19,6
Mongaguá	14	34	71	0,6	0,9	0,25	0,015	0,96	8,1	20,6
Peruibe	45	34	77	2,9	0,6	0,22	0,0090	0,93	9,5	20,5
Ilhabela	8	26	71	1,9	1,1	0,21	0,019	0,95	8,2	18,7
Vitória	13	39	69	2,0	0,8	0,22	0,015	0,95	8,6	19,6
Búzios	32	54	71	4,5	1,0	0,19	0,015	0,85	10,2	19,7
Paredão	7	39	60	1,0	0,6	0,25	0,013	0,99	8,5	21,0
Alcatrazes	8	35	68	0,4	0,6	0,26	0,012	0,99	8,2	21,2
Queimada Grande	71	43	72	3,2	0,9	0,21	0,015	0,82	9,5	20,0

Table 9. Regression of fore limb length on body length, females

	N	R_x		a		b		r^2	y_{30}	y_{80}
Guanabara	11	51 -	86	10,2 ±	1,5	0,086 ±	0,022	0,64	12,8	17,1
Ubatuba	27	29	87	4,2	0,7	0,15	0,0093	0,92	8,7	16,2
Caraguatatuba	14	65	84	5,3	1,5	0,14	0,021	0,78	9,5	16,5
São Sebastião	13	55	81	9,6	0,9	0,079	0,013	0,77	12,0	15,9
Bertioga	21	40	77	3,5	0,4	0,16	0,0071	0,96	8,3	16,3
Enseada	18	42	84	4,0	0,7	0,18	0,010	0,95	9,4	18,4
Mongaguá	8	63	74	8,2	2,4	0,12	0,035	0,68	11,8	17,8
Peruibe	27	40	85	6,5	1,1	0,15	0,015	0,79	11,0	18,5
Ilhabela	8	34	90	3,7	0,7	0,16	0,010	0,98	8,5	16,5
Vitória	8	43	76	2,7	1,2	0,20	0,018	0,95	8,7	18,7
Búzios	45	54	81	6,9	1,2	0,14	0,017	0,62	11,1	18,1
Paredão	11	39	67	2,2	0,8	0,22	0,015	0,96	8,8	19,8
Alcatrazes	7	54	74	5,1	2,1	0,17	0,033	0,83	10,2	18,7
Queimada Grande	71	49	72	4,8	1,0	0,17	0,015	0,66	9,9	18,4

Table 10. Regression of hind limb length on body length, males

	N	R_x		a		b		r^2	y_{30}	y_{80}
Guanabara	6	52	68	0,8 ±	3,4	0,37 ±	0,058	0,91	10,3	28,8
Ubatuba	19	32	72	1,5	1,6	0,31	0,025	0,90	10,8	26,3
Caraguatatuba	19	54	75	7,8	2,1	0,22	0,033	0,72	14,4	25,4
São Sebastião	11	55	70	-1,1	2,9	0,36	0,046	0,87	9,7	27,7
Bertioga	23	37	73	1,3	0,8	0,31	0,014	0,96	10,6	26,1
Enseada	19	42	75	1,2	1,2	0,32	0,020	0,94	10,8	26,8
Mongaguá	14	34	71	3,2	1,4	0,30	0,022	0,94	12,2	27,2
Peruibe	45	34	75	1,5	0,8	0,32	0,013	0,94	11,1	27,1
Ilhabela	6	26	67	0	1,9	0,33	0,033	0,96	9,9	26,4
Vitória	13	39	69	0,4	0,8	0,33	0,015	0,98	10,3	26,8
Búzios	32	58	71	4,6	1,5	0,28	0,023	0,83	13,0	27,0
Paredão	8	39	63	-1,3	1,2	0,38	0,024	0,98	10,1	29,1
Alcatrazes	8	35	68	-1,0	0,9	0,38	0,018	0,99	10,4	29,4
Queimada Grande	69	43	72	3,8	1,2	0,28	0,019	0,77	12,2	26,2

Table 11. Regression of hind limb length on body length, females

	N	R_x		a		b		r^2	y_{30}	y_{80}
Guanabara	11	51 -	86	7,5 ±	1,7	0,23 ±	0,025	0,91	14,4	25,9
Ubatuba	27	29	87	4,5	1,0	0,24	0,014	0,92	11,7	23,7
Caraguatatuba	15	65	84	6,8	1,8	0,20	0,025	0,84	12,8	22,8
São Sebastião	13	55	81	10,5	1,7	0,16	0,026	0,76	15,3	23,3
Bertioga	20	40	77	1,7	0,8	0,28	0,014	0,96	10,1	24,1
Enseada	18	42	84	5,0	1,2	0,24	0,016	0,93	12,2	24,2
Mongaguá	8	63	74	8,6	4,5	0,20	0,066	0,60	14,6	24,6
Peruibe	27	40	85	7,3	1,4	0,22	0,019	0,85	13,9	24,9
Ilhabela	8	34	90	5,3	1,2	0,23	0,018	0,97	12,2	23,7
Vitória	7	43	76	2,9	1,1	0,27	0,017	0,98	11,0	24,5
Búzios	45	54	81	9,4	1,7	0,18	0,024	0,59	14,8	23,8
Paredão	11	39	67	2,2	0,7	0,29	0,013	0,98	10,9	25,4
Alcatrazes	7	54	74	0	1,4	0,33	0,021	0,98	9,9	26,4
Queimada Grande	71	49	72	4,9	1,1	0,25	0,017	0,76	12,4	24,9

Appendix 2

Data on statistical analyses

Abreviations

Ms	mean square
df	degrees of freedom
*	significant at the 5% level
**	1% "
***	0,1% "
NS	not significant

In Kramer's tests, coefficients or constants underlined by the same line do not differ significantly.

Notes

1. Ventral scales, males, variation between Caraguatatuba and Mongaguá.

Analysis of variance

	Ms	df	F
Between samples	2.42	4	1.98 (NS)
Error	1.22	83	

2. Ventral scales, females, variation between Caraguatatuba and Mongaguá.

Analysis of variance

	Ms	df	F
Between samples	2.94	4	1.32 (NS)
Error	2.22	74	

3. Regression of head length on trunk length, males.

   a) Coefficient of regression, analysis of variance, Ubatuba, Enseada, Mongaguá, Peruíbe and Vitória, representing 5 groups formed by inspection.

	Ms	df	F
Between samples	0.92	4	9.66 ***
Error	0.096	101	

b) Regression coefficients, Kramer's test, same samples.

Sample	Vi	Pe	Mg	En	Ut
b	0.228	0.184	0.171	0.165	0.164

c) Regression constants, Kramer's test for the samples homogeneous for the test above.

Sample	Mg	Pe	En	Ut
a	4.15	3.90	3.39	2.77

(all differences significant)

4. Regression of head length on trunk length, females.

a) Coefficients of regression, analysis of variance, Ubatuba, Enseada, S. Sebastião, Guanabara, Peruíbe and Paredão, representing 6 groups of samples formed by inspection.

	Ms	df	F
Between samples	1.14	5	5.72 ***
Error	0.099	95	

b) Coefficients of regression, Kramer's test, same samples.

Sample	Pd	En	Pe	Ut	Gb	Ss
b	0.178	0.133	0.130	0.124	0.0948	0.0896

c) Regression constants, Kramer's test, Enseada, Peruíbe and Ubatuba.

Sample	Pe	En	Ut
a	5.30	5.14	3.91

d) Regression constants, difference between S. Sebastião and Guanabara: t = 2.86, 21 degrees of freedom (**).

5. Regression of head length on trunk length. Spearman's coefficient of rank correlation between male and female differentiation patterns.

Coefficients of determination, mainland, all samples, $r_s = 0.179$ (NS).

Coefficients of determination, mainland, Mongaguá excluded, $r_s = 0.302$ (NS).

Adult head length, mainland, $r_s = 0.707$ *.

6. Regression of fore limb length on body length, males.

a) Coefficients of regression, analysis of variance, Ubatuba, Enseada and Mongaguá, representing 3 groups formed by inspection.

	Ms	df	F
Between samples	0.65	2	2.83 (NS)
Error	0.23	46	

b) Regression constants, analysis of variance, same samples.

	Ms	df	F
Between samples	9.67	2	42:39 ***
Error	0.23	46	

c) Regression constants, Kramer's test, same samples.

Samples	Mg	En	Ut
a	2.28	1.59	0.75

(all differences significant)

7. Ventral scales, males, variation in the islands.
a) Analysis of variance

	Ms	df	F
Between samples	4.81	5	3.14 *
Error	1.53	124	

b) Means, Kramer's test

Samples	Ib	Bz	Qg	Al	Vi	Pd
Mean	38.6	38.2	38.1	38.0	37.6	36.4

8. Midbody scales, insular variation
a) Paredão and Alcatrazes, $C^2 = 4.35$, 3 df (NS)
b) Vitória and Búzios, $C^2 = 2.67$, 3 df (NS)
c) Analysis of variance

	Ms	df	F
Between samples	8.96	2	25.60 ***
Error	0.35	261	

d) Means, Kramer's test

Sample	Group Al	Vi + Bz	Qg
Mean	28.3	28.0	27.6

(all differences significant)

9. Femoral scales, insular variation
a) Paredão and Alcatrazes, $C^2 = 2.90$, 2 df (NS)
b) Búzios and Vitória, $C^2 = 10.96$, 3 df, (*)
c) Analysis of variance

	Ms	df	F
Between samples	2.53	2	5.56 **
Error	0.45	124	

d) Means, Kramer's test

Sample	Group Al	Ib	Bz
Mean	12.2	11.9	11.7

10. Fourth toe lamellae, insular variation
a) Analysis of variance

	Ms	df	F
Between samples	8.25	4	18.22 ***
Error	0.45	256	

b) Means, Kramer's test

Sample	Pd	Bz	Vi	Qg	Al
Mean	18.4	17.9	17.4	17.3	17.3

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Aerophoto 1 (above), Caraguatatuba, SP; aerophoto 2 (below), Peruíbe, SP.

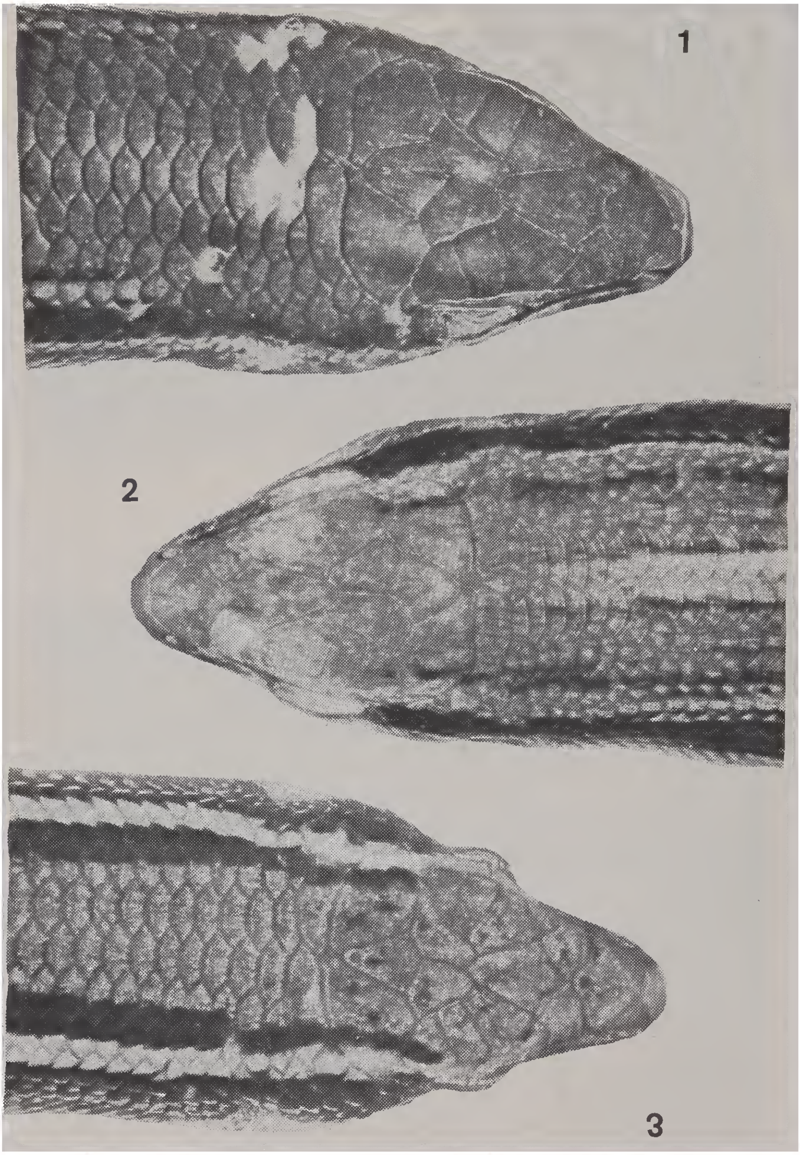

Plate 1. Dorsal aspect of head. 1, MZUSP 7312, Guanabara. 2, MZUSP 26790, S. Sebastião. 3, MZUSP 24031, Peruíbe.

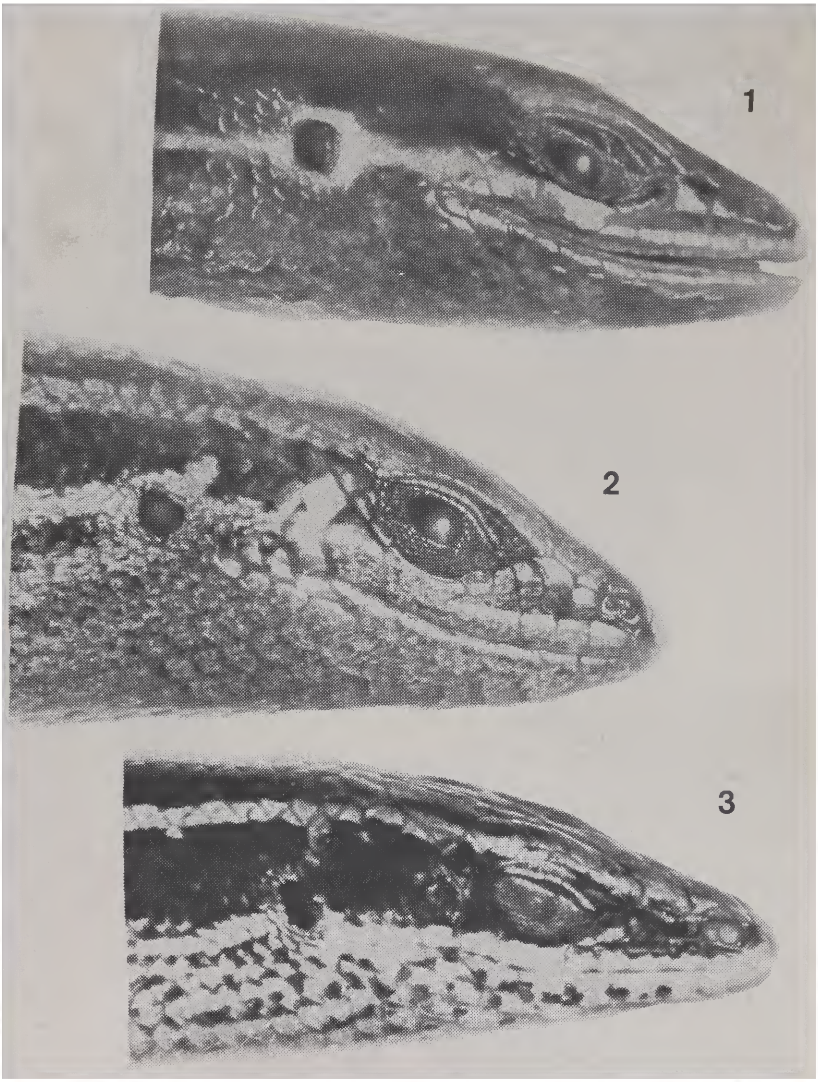

Plate 2. Lateral aspect of head. 1, MZUSP 7312, Guanabara. 2, MZUSP 26790, S. Sebastião. 3, MZUSP 23968, Peruíbe.

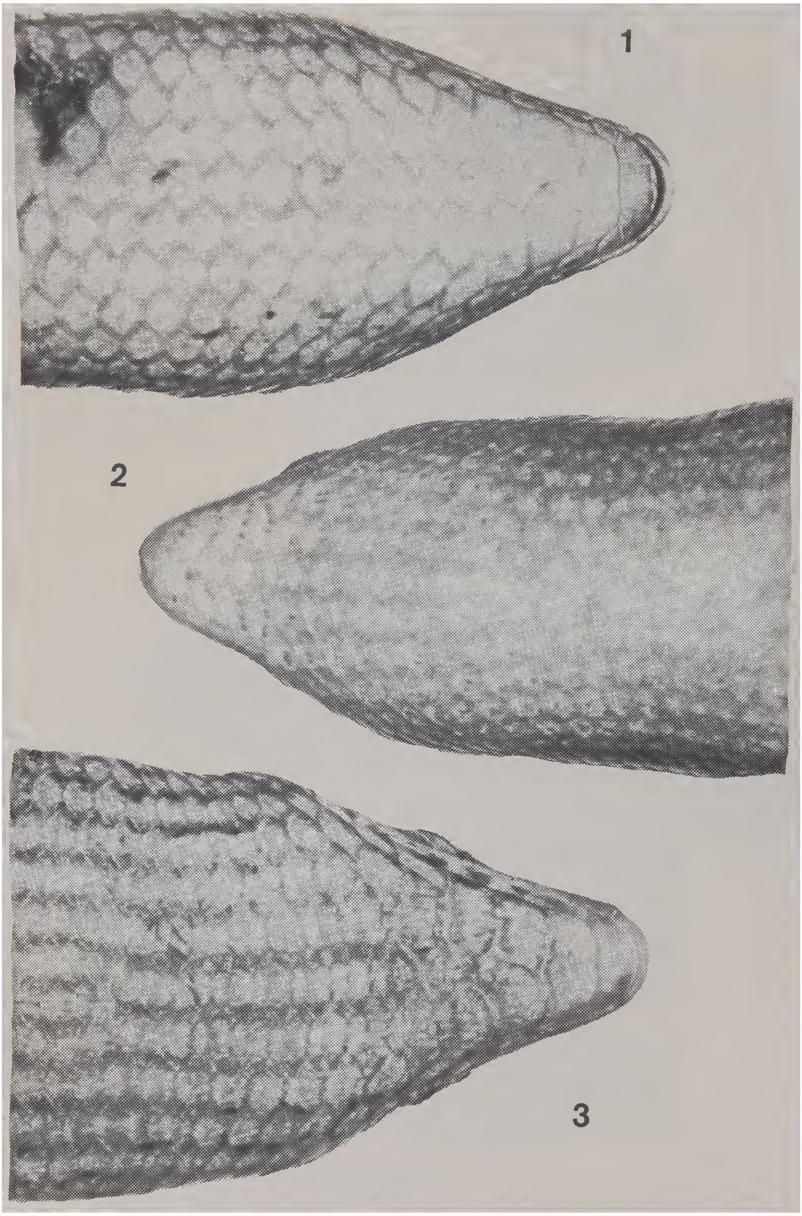

Plate 3. Ventral aspect of head. 1, MZUSP 7312, Guanabara. 2, MZUSP 26790, S. Sebastião. 3, MZUSP 24031, Peruíbe.

Plate 4. North Coast color pattern. MZUSP 26790, S. Sebastião.

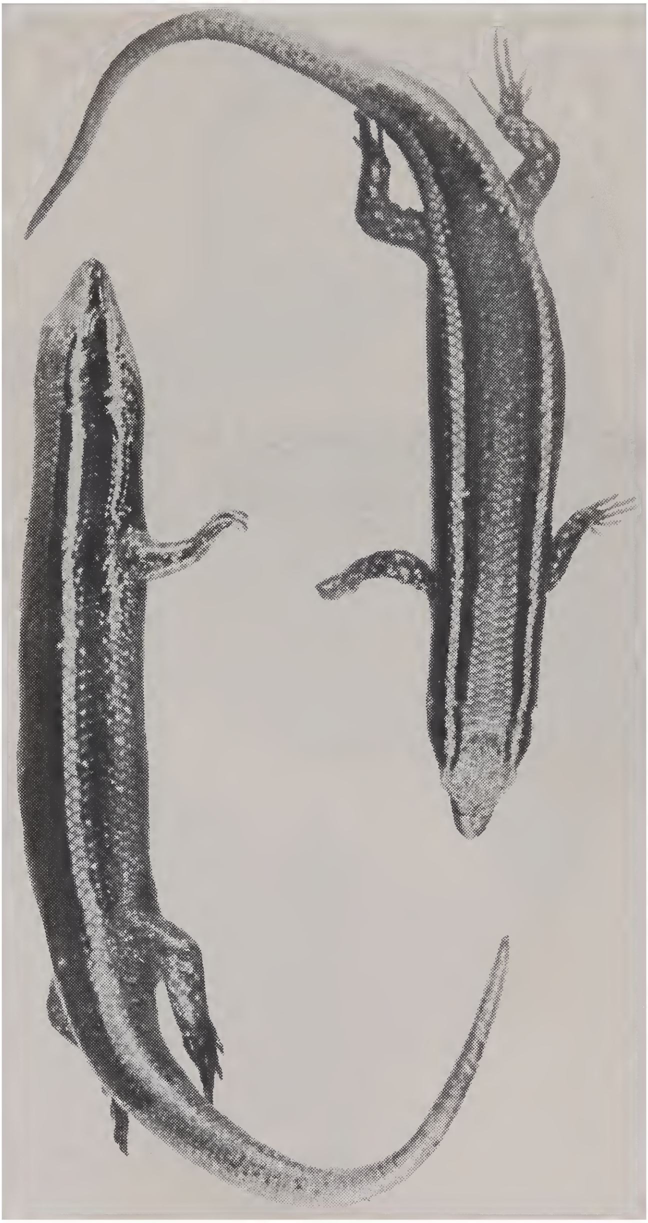

Plate 5. South Coast color pattern. MZUSP 24021, Peruíbe.

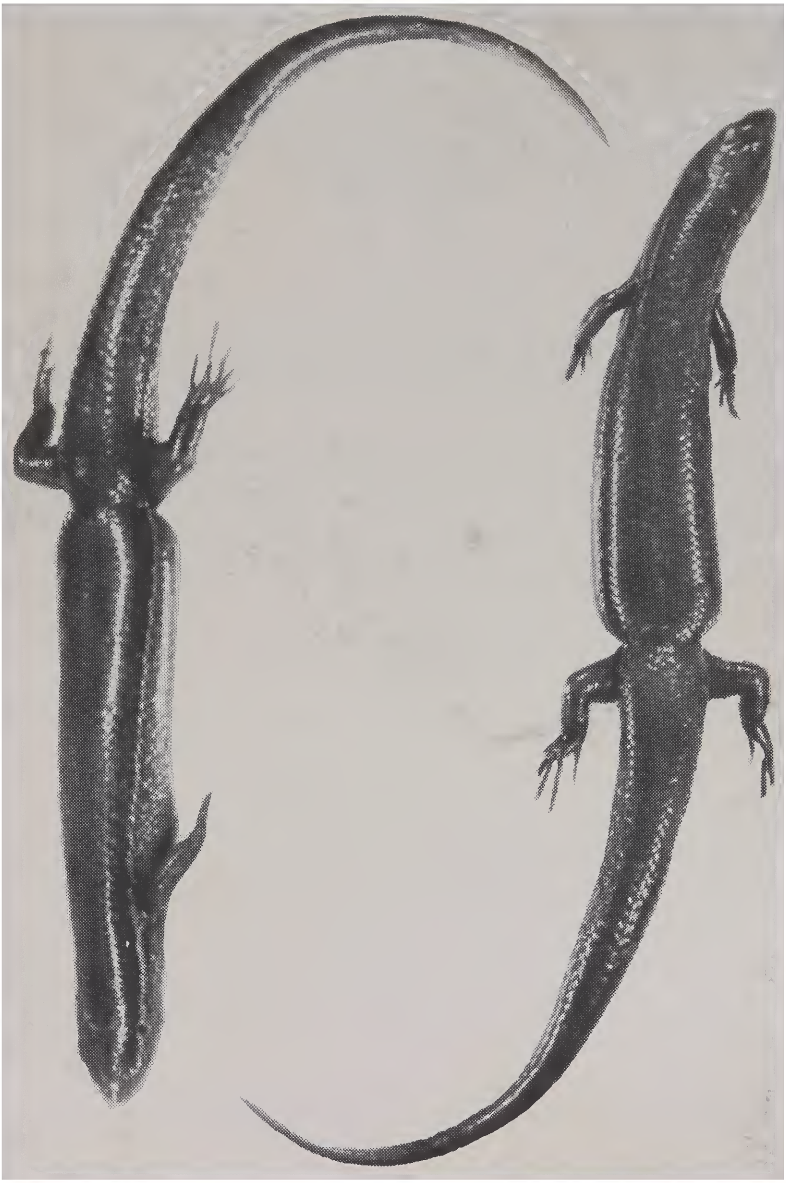

Plate 6. Guanabara color pattern. MZUSP 7312, Guanabara.

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