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A NEW SPECIES OF *COLOBODACTYLUS*, WITH NOTES ON THE DISTRIBUTION OF A GROUP OF STRANDED MICROTEIID LIZARDS (SAURIA, TEIIDAE)

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Abstract

Colobodactylus dalcyanus, *sp.n., is described from the Itatiaia massif in Eastern Brasil. The genus* Colobosaura *is considered to be closely related to or synonymous with* Colobodactylus; Heterodactylus *and* Anotosaura *are thought to belong to the same assemblage. The distribution of the taxa is discussed in terms of paleoclimatic cycles; the conclusion is that the group, with the exception of one species, flourished under a drier and cooler climate, and is presently surviving through unfavorable times, in atypical refuges.*

Introduction

Amaral (1933:70) described the microteiid *Colobodactylus taunayi*, gen. nov., spec. nov., from localities on the coastal plain and on the Atlantic plateau of the state of São Paulo. The species has subsequently been collected in the same areas, in the Serra do Mar and on some coastal islands of São Paulo.

We now have from the Serra do Itatiaia twelve specimens of what we consider to be the second species of the genus, *Colobodactylus dalcyanus*, sp.n. The locality of this new form raises interesting problems about the distribution of a group of related microteiid genera.

Generic assignment

The systematics of microteiids is going through a period of flux; the absence of convincing generic criteria is glaring, as shown by the blurred contours of Montanucci's (1973) concept of *Pholidobolus* and by the comments of Oftedal (1974) on *Anadia*. We do not consider it profitable to enter systematics at the generic level on a piecemeal

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basis; in order to justify the generic assignment of the new species we only note that it shares with *Colobodactytus taunayi* the following characters:

1. Body slender, tail very long, limbs short.
2. Hind limb pentadactyl; pollex absent or reduced to a small clawless tubercle.
3. External ear opening present.
4. Prefrontal scutes absent.
5. Dorsal scales hexagonal or lanceolate, keeled, in transverse rows, becoming broader, leaf-shaped, less sharply keeled and finally smooth down the flanks. Ventral scales smooth, imbricate, arranged in longitudinal rows and, not consistently, also in transverse rows.
6. Adult males with well developed pores, one preanal and a femoral series extending to the knee fold; pores indicated as shallow impressions in juvenile males; females with 1-4 shallow impressions, of the preanal pore and of the distal ones.
7. Tongue with scale-like papillae, less evident near the tip.
8. Lower eyelid with a large transparent disk.

These characters, commonly employed in the Boulengerian tradition (to us still the most convenient) to define microteiid genera, place the new form squarely in *Colobodactylus*. Additionally, the following shared characters seem to us to confirm the closeness of the relatioship between the two species: (i) two pairs of enlarged nuchals, with one or two small median scales between rows; (ii) last row of gulars with a free edge, but not forming a conspicuous collar; (iii) ventrals in four longitudinal rows, the median ones narrower than the outer; (iv) scales on the dorsal aspect of the fore limb large, flat, smooth, not differentiated into brachials and antebrachials, on the ventral surface small but not quite granular; (v) antèrior half of thigh (from the dorsal to the ventral midline) with large flat scales, posterior half with flat granules, arranged in rows; (vi) the same type of color pattern; (vii) teeth tricuspid.

Colobodactytus taunayi Amaral, 1933

Colobodactylus taunayi Amaral, 1933: 70, figs. 41-45; 1937: 1739; 1938: 188. Barbour & Loveridge, 1946: 94. Hoge, 1950: 152. Mertens, 1955: 314.

Colobodactylus taunay: Hoge, Belluomini, Schreiber & Penha, 1960: 23.

Colobodactylus taunayi: Peters & Donoso-Barros, 1970: 98. Vanzolini, 1972: 105. Beçak, Beçak, Napoleone & Reis, 1973: 219.

Holotype: Iguape, SP, no further data, ♂, number 787 in the lizard collection of the Museu Paulista (now Museu de Zoologia da Universidade de São Paulo, MZUSP).

Paratypes: S. Paulo (Ipiranga), SP, date not recorded, Luederwaldt leg., Museu Paulista 789B (now MZUSP 40083), ♀; "Brasil", Museu Paulista (now MZUSP) 803, ♀; São Bernardo, SP, Bicego leg., date not recorded, Museu Paulista 793, ♂, exchanged with the Museum of Comparative Zoology.

COMMENTS ON THE LITERATURE

Amaral 1937 and 1938 are two versions of the same checklist. Barbour & Loveridge (1946) simply mention the paratype in the MCZ collection.

Hoge (1950) reports on the occurrence of the species on Queimada Grande Island; his sample is now MZUSP 4689-4713. Hoge compared his specimens with the type materials, and cast doubts on the identity of the holotype and one of the paratypes, but they were unfounded: the specimens are authentic and closely agree with Amaral's description and measurements.

Mertens (1955) simply reports collecting the animal at Queimada Grande. Hoge & al. (1960) also mention its occurrence on the island, *passim*. Peters & Donoso-Barros (1970) list the species in their Catalogue. Vanzolini (1972) reports on specimens collected at Ilha Vitória. Beçak & al. (1973), in an abstract of a communication to a congress, refer to the DNA content of a female; their specimen is now MZUSP 28199, deposited to document the identification.

SPECIMENS EXAMINED

All numbers refer to the lizard collection of the Museu de Zoologia, USP. All localities are in the state of São Paulo.

Mainland. Iguape, 787, ♂, holotype. Barra do Icapara, 17474, 12.v.1969, A. M. Olalla leg., ♀. Poá, 11963, 17.x.1965, E. X. Rabello leg., ♂. São Paulo, 40083, paratype, ♀. Boracéia, 10965, ♀.

Islands. Queimada Grande, 28.ix-5.x.1974, Instituto Butantan leg.: ♂♂, 4690, 4693-4696, 4698, 4700, 4701, 4703, 4705, 4708-4710; ♀♀, 4689, 4691, 4692, 4697, 4704, 4707, 4711, 4712. Queimada Grande, no further data, received from Instituto Butantan: ♀♀, 6903, 28199; unsexed, 3300, 3301. Alcatrazes, 17.ii.1948, Instituto Butantan leg.: ♂♂, 4719, 4722; ♀♀, 4718, 4720, 4721. Vitória, 14-28.iii.1964, Departamento de Zoologia leg.: ♂, 10821; ♀♀, 10581, 10822.

No data: "Brasil", 803, ♀, paratype.

DESCRIPTION: MAINLAND SPECIMENS

Body slender, roughly prismatic, with flat dorsum; head blunt, canthus rostralis moderate. Tail very long, limbs short.

Rostral broad and low, but well visible from above. Fronto-nasal a little larger than the frontal, hexagonal, its suture with the frontal straight or slightly arcuate. Prefrontals absent. Frontal pentagonal, with angle directed backward, nesting between the frontoparietals, which are polygonal, roughly isodiametric, meeting on the midline. Interparietal hexagonal, parallel-sided, elongate, its hind tip reaching beyond the parietals, that are broad, iregularly polygonal. Two pairs of nuchals; among then, on the midline, one or two small scales, in contact or not with the interparietal. Supraoculars three, the first smallest, briefly meeting the anterolateral angle of the frontal. Two or three supraciliaries, the anterior broadest, the middle one very short.

Nostril near the lower edge of a very large nasal, that incorporates the loreal. Freno-orbital from small to barely differentiated. One large, narrow, median infraorbital; one or two scales in front of it, the anteriormost at times well developed; a variable number behind, grading into the temporals. Palpebral disk large, with a few opaque granules on the anterior and posterior angles. Supralabials six, the first large; the second small; the third very long, about as long as the infraorbital; fourth and fifth high, polygonal, similar to and in continuation with the temporals; sixth low, reaching the ear. Temporals large, flat, smooth, polygonal, with sunken sutures. Ear opening rounded or, more frequently, with a straight hind edge, lined with slightly prominent granules.

Symphysial short and broad. Unpaired post-symphysial pentagonal or heptagonal. Two pairs of large post-symphysials in full contact on the midline (in the male from Poá the second pair is separated), reaching laterally the lower labials; a third pair of narrow, oblique scutes, also meeting on the midline but not reaching the labials. Infralabials six, in one specimen the first and second fused on both sides; second to fourth small, fifth very small, reaching the ear. Gulars smooth; one or two irregular transverse rows in contact with the postsymphysials, followed by 5-6 pairs of very broad scales, the last row not forming a definite collar.

Scales on the nape broad, with sharp even keels. Scales between ear and arm flat, smooth, leaf-shaped. Scales on the flanks broader than the dorsals, leaf-shaped, losing progressively the keel. Ventrals smooth, imbricate, arranged in transverse rows; the two median rows narrowest. The row of ventrals between the arms composed of 3-4 irregular scales on each side and a central triangular scale, usually longer than the others. Anal flap very variable, the most frequent configuration being two narrow median scales flanked on each side by a large lateral element. Scale counts (2 ♂♂, 3 ♀♀): dorsals, from second pair of nuchals to level of posterior margin of thighs, ♂♂ 31-33, ♀♀ 34; ventrals, from last row of gulars to anal flap, ♂♂ 19-22, ♀♀ 20-24; scales around midbody, ♂♂ 30-32, ♀♀ 29-30 (actual distributions in Tables 1-3).

Fore limb, on the upper side, with uninterrupted rows of large smooth scales from the shoulder to the wrist; on the lower side with small smooth scales. Fingers in the following order, from smallest to largest: II,V-III-IV. Infradigital lamellae smooth, somewhat irregular.

Posterior half of thigh with irregular rows of flat granules; anterior half with large flat smooth scales; on the dorsal contact between the two areas, 2-3 rows of narrow keeled scales. Scales on the dorsal aspect of the leg pointed, submucronate, keeled; on the ventral surface smooth. Toes in the following order: I-II,V-III-IV. Infradigital lamellae smooth, somewhat irregular. Total number of pores 15 in both male specimens.

Dorsal and ventral scales of tail similar to the dorsals of the trunk, forming regular rings.

The color pattern of the head and trunk shows three very distinct areas: dorsal, lateral and ventral. The ground color of the dorsum is grayish tan, with fine black punctuations, in a salt- and pepper effect, with a tendency toward the formation of very fine transverse bars. The top of the head and nape are a warmer, darker reddish brown, with a varying amount of heavier, scattered black markings.

Between the back and the flank, along the dorsolateral edge, runs a white line, that begins on the superciliary region and goes all the way to the tail; it is distinct on the head and neck, much less evident, at times obsolete, at midbody, and again more vivid at the level of the sacrum. It is bordered below by a dark line, that begins on the nasal, is interrupted at the supraciliary edge, becomes less evident, even interrupted, at midbody, and better defined near the tail. Below this line the neck and flanks are sooty, to the edge of the ventrals; the lower half of the upper labials is whitish, with some dark spotting.

TABLE 1

Colobodactylus, number of dorsal scales

	males						females						
	Iguape	Poã	Queimada	Alcatrazes	Vitória		Icapara	São Paulo	Boraceia	Queimada	Alcatrazes	Vitória	
	taunayi					*dalcyanus*	*taunayi*						*dalcyanus*
31		1		1	1								
32			9	1							1		
33	1		5								1	1	
34			1				1	1	1	10	1	1	
35						3							
36						2							2
37						1							2
38													1
39													–
40													1

The dorsal surface of the forelimb shows heavy, well defined large black spots on the upper arm, and heavy marblings on the forearm and hand. The dorsal surface of the hind limb is strongly variegated.

The ventral surfaces (tail again excepted) are creamy white. There are usually a few dark markings on the sides of the chin and, in one specimen, fine markings on the preanal region.

The tail is dorsally darker than the body. Proximally there is, on each side, in continuation with the dorsolateral white stripe, a light line, continuous or in the shape of a series of white spots. Otherwise the dorsal pattern is one of narrow dark bars (one per scale row) over a slightly lighter background. These bars continue ventrally as rings, the ground color of the under surface being a lighter gray.

Largest male, 51 mm snout to vent; largest female, 60 mm. Only specimen with intact tail, a female, 59 + 176 mm.

TABLE 2

Colobodactylus, number of ventral scales

	males						females						
	Iguape	Poã	Queimada	Alcatrazes	Vitória		Icapara	São Paulo	Boraceia	Queimada	Alcatrazes	Vitória	
	taunayi					*dalcyanus*	*taunayi*						*dalcyanus*
19	1		2	1	1								
20			6	-			1			1	1		
21			4	1					1	3	2	2	
22		1	2							4			
23			1							1			
24						2		1					1
25						-							-
26						-							2
27						3							1
28						1							-
29													2

INSULAR POPULATIONS

Queimada Grande. We have before us 27 specimens from Queimada Grande (15 ♂♂, 10 ♀♀, 2 unsexed, because poorly preserved), 5 from Alcatrazes (2♂♂, 3 ♀♀) and 3 from Vitória (1 ♂, 2 ♀♀).

With regard to pholidotic characters, the sample from Queimada Grande shows some significant peculiarities when compared with the mainland. Most striking of all is the condition of the second pair of post-symphysials. The scutes are completely separated on the midline in 10 out of 14 males, and partly separated in four; only one male has the second pair in contact on the midline. Out of 10 females examined, seven have the scutes in contact; in one case they are partly, and in two completely separated. The third pair is separated in seven males and one female.

TABLE 3

Colobodactylus, number of scales around midbody

	males						females						
	Iguape	Poá	Queimada	Alcatrazes	Vitória	*dalcyanus*	Icapara	São Paulo	Boraceia	Queimada	Alcatrazes	Vitória	*dalcyanus*
	taunayi						*taunayi*						
27													1
28													-
29								1			1		-
30		1					1		1		1	1	-
31										4	1	-	-
32	1			1						3		1	1
33			4	1		4				2			3
34			7		1	1				1			-
35			3			1							1
36			1										

In four males the frontoparietals are separated by a contact between the interparietal and the frontal; in no female was this condition observed.

A large, well formed freno-orbital was found in seven males and two females. Loreal scutes were found in one male and two females, but not very regular, somewhat asymmetric and not associated with especially well developed freno-orbitals.

The number of scales around midbody is decidedly higher in the insular sample.

Regarding color pattern, the Queimada samples show two main statistical differences from the continent. There is a decided tendency towards the presence of a white nuchal bar, joining the two white dorso-lateral stripes. This transverse bar was found, with varying degrees of distinctiveness (from white to mottled) in about one half of the specimens, seemingly unrelated to sex. There is also much more ventral mottling than on the continent: eight specimens have dark markings on the gulars, four on the belly and seven on the preanal region. One specimen is slightly mottled from chin to vent.

Largest male 51 mm; largest female 57 mm.

Vitória. One of the three Vitória specimens shows a very anomalous pattern on the top of the head; there is a small azygos frontoparietal, the interparietal is narrower behind than in front, the first pair of nuchals is partly fused and the second pair is very large and irregular. It has also distinct loreals. These characters are not present in the other two specimens, which, however, show well developed freno-orbitals. There are no apparent differences from the continent in scale counts. With regard to color pattern, the Vitória specimens resemble those of Queimada, but the ventral surface is distinctly smudged in the two adults, and the beginnings of such a pattern are visible in the young. One male 38 mm; largest female 58 mm.

Alcatrazes. The Alcatrazes sample does not differ noticeably from the continental ones. Both males 43 mm; largest female 58 mm.

Colobodactylus dalcyanus, sp.n.

TYPE MATERIAL

All specimens were collected at the Brejo da Lapa, Itatiaia (see below), on the Rio de Janeiro-Minas Gerais border.

Holotype: MZUSP 42908, ♂, 18.i.1976, W. R. Heyer.

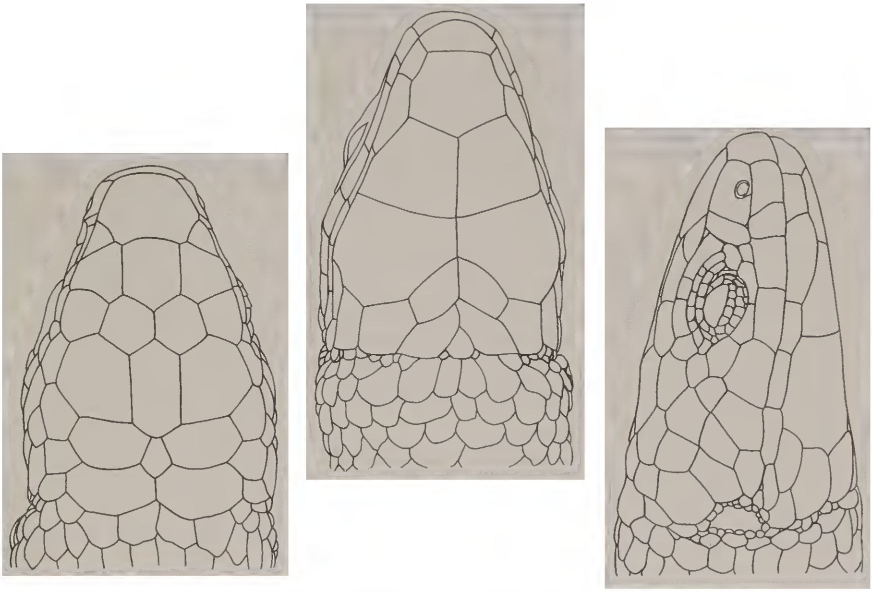
Paratypes: USNM 199223, ♀, collected with the type; MZUSP 21471, ♂, 3.ii.1971, I. P. Sazima; MZUSP 43073, ♀, 28.iii.1976, P. E. Vanzolini, F. Val & U. T. B. Meneses; MZUSP 45698-45700, 1 ♂, 2 ♀♀, 5.i.77, E., L., M. & W. R. Heyer, and F. Val; USNM 203359-63, 3 ♂♂, 2 ♀♀, same collectors.

Etymology: Named after Dalcy de Oliveira Albuquerque (Museu Nacional, Rio de Janeiro), in recognition of his help in this and numerous other occasions.

DESCRIPTION

Rostral broad and low, well visible from above. Frontonasal large, hexagonal, with slightly sinuous front edge, much larger than the frontal. Frontal pentagonal, almost isodiametric, with convex front edge, its posterior angle nesting between the frontoparietals, that are pentagonal, isodiametric. Interparietal parallel-sided, hexagonal, except when met by a small inter-nuchal scale. Parietals large, polygonal, not reaching behind the level of the tip of the interparietal. Two pairs of large nuchals; on the midline a small scale that may meet or not the interparietal. Supraoculars three; the first may meet or not the frontal. Supraciliaries three, the first very broad, the second very small.

Nasal large, corresponding to the first labial; nostril almost on the lower suture. Freno-orbital small, usually smaller than the first infraorbital. Loreal narrow, high, touching the second labial and the frontonasal. Palpebral disk large, without opaque granules. Infraorbital series variable; the median element may be broken up; one or two scales in front of it, the anteriormost large; a variable number of scales behind, grading into the temporals. Supralabials seven; the first large; the second high and narrow; the third, fourth and fifth below the eye; the sixth similar to the temporals; the seventh low, reaching the ear. Temporals polygonal, with well marked sutures, the upper scales larger than the lower ones. Ear opening narrow, oval or with straight hind edge, lined with small granules.



Colobodactylus dalcyanus, sp.n., MZUSP 42908, Holotype

Symphysial and unpaired (in one specimen longitudinally split) post-symphysial short and broad. First pair of post-symphysials very large, in full contact on the midline, reaching laterally the labials. Second pair also large, but with median margin smaller than outer margin, either in short contact on the midline or separated. Behind the second pair a row of elongate scutes, followed by another row (or just a median patch of scales), behind which there is a well defined sulcus. Laterally the sulcus shows a series of granules that continue on the lining of the hind margin of the ear opening. Infralabials six, the second largest, the last reaching the ear. Gulars smooth, those of the first 3-4 rows small, irregular, the median pair of scales of the next 4-5 rows enlarged, but not very regular, with free margins but not forming a conspicuous collar.

Scales on the nape broad, prominent, with tubercular or at least very broad keels, becoming regular at about arm level. Scales between ear and arm swollen, imbricate, very irregular in shape and size. Dorsals hexagonal, with a broad, rounded keel. Scales on the flanks leaf-shaped, above with broad keels, then grading into the ventrals. Ventrals in 4 longitudinal, and also in transverse rows (numbers below), the scales of the two median longitudinal rows broadest at midbody, so that longitudinal lines of sutures are broadly curved. Scales between the arms forming an irregular row. Anal flap variable. Scale counts (6 ♂♂, 6 ♀♀): dorsals, from second nuchal to level of posterior of thighs, ♂♂ 35-37, ♀♀ 36-40; ventrals, from last gular row to anal flap, ♂♂ 24-28, ♀♀ 24-29; scales around midbody, ♂♂ 33-35, ♀♀ 27-36 (actual distributions in Tables 1-3).

Fore limb, on the upper side, with uninterrupted rows of large smooth scales from the shoulder to the wrist; on the lower aspect with small scales. Fingers in the following order from smallest to largest: V-II-III-IV. Infradigital lamellae smooth, regular. Posterior half of thigh with large flat granules arranged in rather regular rows, on the top of the limb reaching the midline, or a litte beyond; 2-3 rows of large flat scales on the front half of the thigh; dorsally, separating them from the granules, one row of small keeled scales. Scales on upper aspect of leg rounded, with a few dull keels. Males (6 specimens) with a total of 12-14 pores (Table 4).

TABLE 4

Colobodactylus, males,
total number of pores

	Iguape	Poá	Queimada	Alcatrazes	Vitória	
	taunayi					*dalcyanus*
12					1	3
13			1			1
14			2			1
15	1	1	8	1		
16			1	1		
17			1			

Tail scales forming regular rings, the scales on the dorsal aspect similar to the dorsals, those on the ventral aspect squarish next to the vent, becoming hexagonal and indistinctly keeled after 4-5 rows.

The color pattern comprises three distinct zones: dorsal, lateral and ventral.

The dorsal ground color is grayish brown, warmer on the head, that is heavily vermiculated with very dark brown. On the nape there are faint traces of a median longitudinal dark streak. The trunk scales show fine punctuations, arranged in thin sparse transverse lines. The dorsal aspect of the members is mottled with darker and lighter brown. The upper aspect of the tail is of about the same ground color as the dorsum, and has a similar, but more distinct, pattern of tranverse lines; there is at the base a longitudinal dark streak more evident than the cervical one.

The sides of the head are black, mottled with brown; the sutures between the posterior supralabials (starting below the middle of the eye) are white, continuing on the lower lip.

Between the back and the flank runs a light line (white in two males and one female, tan and less distinct in one female) that starts on the suture between the parietal and the anteriormost temporal, follows along the upper temporals, becomes less distinct on the trunk, and marked again on the sacrum and tail. The sides of the neck are sooty, with light spots that vary in degree of contrast from specimen to specimen. The flank below the light dorso-lateral line is also fuliginous, with light mottling that again varies from specimen to specimen, perhaps in relation with sex (in the males the white spots are quite clear and more or less arranged vertically; in the females there is less pattern). The dark lateral band continues on the tail, where it is bordered below by a white line.

On the ventral aspect of the body and limbs there are characteristic dark markings (resembling ink blotches) on the middle of all scales, excepted the gulars, that show a denser reticulation. The ground color of the ventral aspect of the tail is smudged light gray; the anterior tip of each scale is darker, forming a pattern of transverse bars, not exactly corresponding to the dorsal ones.

Largest male, 45 mm snout to vent, tail 88 mm (the holotype); largest female 50 mm snout to vent; one further male with complete tail, 43 + 92 mm.

SYSTEMATICS

MAINLAND TAUNAYI AND DALCYANUS

At first sight *Colobodactylus taunayi* and *dalcyanus* differ sharply in color: the former is a tan animal, with virtually or nearly immaculate ventral parts, while the latter has a dark brown dorsum and heavily patterned ventral parts. This difference is quite diagnostic. However, the general pattern is the same: a dorsal area, with thin cross bars made of sparse punctuations, separated from the dark flank by a light line that continues on the tail; even the heavy blotches of *dalcyanus* are foreshadowed by the markings of the more heavily patterned specimens of *taunayi*. As far as color pattern goes, *dalcyanus* can be broadly described as a *taunayi* with melanistic tendencies.

With regard to scale counts, present materials show marked differences in the three main microteiid scale counts: dorsal, ventral and midbody scales (Tables 1-3); both samples are very small and further materials may conceivably blur a little the picture, but at least a statistical difference is certainly true.

As to qualitative pholidotic differences, some are very sharp, diagnostic, and one would expect them to be steady; others are somewhat subtler, but seem no less real.

1. *C. dalcyanus* has a definite gular sulcus, absent in *taunayi*.
2. *C. dalcyanus* has a well formed loreal, absent in *taunayi*.

3. The dorsals of *taunayi* are lanceolate, and have sharp keels; those of *dalcyanus* are definitely hexagonal, and have blunt keels.
4. The scales on the dorsal surface of the tibia of *taunayi* are pointed, sub-mucronate; sharply keeled; in *dalcyanus* they are flat, dull-pointed, with just a few blunt keels.
5. The lower caudals of *taunayi* are just as sharply keeled as the dorsal ones; in *dalcyanus* they are very indistinctly keeled.
6. On top of the thigh, between the granules of the posterior surface and the anterior large scales, *taunayi* has 2-3 rows of distinctly keeled scales, *dalcyanus* only one, more feebly keeled.
7. The granules on the posterior aspect of the thigh of *dalcyanus* are larger and better organized in rows than those of *taunayi*.
8. *C. taunayi* has, on the anterior and posterior angles of the palpebral disk, a group of flat opaque granules, that do not occur in *dalcyanus*.

These differences do not permit to establish a line of descent between the two species. In reality, only three characters can be considered from the viewpoint of degree of primiteveness; (i) presence (against absence) of a loreal, (ii) presence (against absence) of a gular sulcus, and (iii) degree of melanism. *C. dalcyanus* would be more advanced in having a heavily spotted belly and more primitive in retaining a loreal. The meaning of the gular sulcus is not clear at present, as it is not a general microteiid feature, and should thus be considered advanced, but is present in more specialized related genera (*Anotosaura*), and could then be primitive for the group. In general, it can be said that both forms have diverged little from a common ancestor.

THE INSULAR SAMPLES

It has been said above that Queimada Grande *taunayi* differ statistically from all others. Vitória may also have its own personality, as indicated by the color pattern. There is at present no evidence that Alcatrazes differs from the continent.

It is regrettable that, with the exception of Queimada Grande, the species is so poorly represented in collections. It seems to be authentically rare on the continent, as some of the localities from which it has been reported (the city of S. Paulo and neighborhood; Boracéia) have been intensively collected for many years, and only a few specimens turned up. Anyway, a reasonable analysis of the geographical differentiation of *taunayi* is not possible at present, and, in accordance with the guidelines of our continuing research on the coastal islands (Vanzolini, 1973; Rebouças-Spieker, 1974) we deliberately refrain from taking any formal action about the insular populations.

The main information of general import that the insular samples afford is the frequent presence of a loreal. This, as said, is presumably a more primitive state than the absence of the scute, and we have thus an example of a conservative character on islands — quite the contrary to what is usually expected from small isolated populations, but very much in keeping with Rebouças-Spieker's (1974) findings in *Mabuya macrorhyncha* on these same islands. The fact that the loreal is present in part of the insular specimens seems to indicate that the species as a whole is tending to lose the scute, but that the insular populations are either evolving more slowly or have reached a stable polymorphism.

C. dalcyanus also has a loreal, and the same comments of course obtain, especially since mountain-top distributions have some points of analogy with insular ones.

In no other pholidotic character there is special agreement between *dalcyanus* and the insular samples.

On the color pattern side, the slight melanistic tendency of the ventral aspect found in Vitória is certainly independent from that of *dalcyanus*. In the island the tendency is towards a smudged pattern, very different from the very definite ink spots of *dalcyanus*.

DISTRIBUTION AND ECOLOGY

The known distribution of *C. taunayi* on the mainland of São Paulo encompasses the coast (Iguape, Barra do Icapara), the Serra do Mar (Boracéia) and the Atlantic plateau (São Paulo, Poá, São Bernardo). There are no habitat data on the specimens. Additionally, it is not possible to infer much from the list of localities. Those on the coast present a full range of environments from sand beach to Atlantic forest. Boracéia is in the Atlantic forest. Poá, on the contrary, was already completely deforested when MZUSP 11963 was collected, in 1965, in a farm. The São Paulo and São Bernardo specimens are old ones, and it would be unwise to base any strong deductions on them, but they almost certainly were not collected in forest. This distribution will be discussed below.

C. taunayi is further known from three coastal inslands (for data on which see Vanzolini, 1973): Queimada Grande, Alcatrazes and Vitória. The Queimada specimens were collected in grass (Hoge 1950), the Vitória ones in grass and on the ground of poor second growth forest (Vanzolini, 1972).

C. dalcyanus is so far known only from the type locality, Brejo da Lapa, on the NW flank of the Itatiaia massif. The massif is a stock of intrusive alkaline rocks, with an approximate area of 220 square kilometers, rising to a plateau 2300-2500 m high, and to needles that reach 2787 m. The actual locality (Brejo da Lapa) is not on usual maps but can be found on the chart published as an appendix to the 1967 papers of Ribeiro and of Penalva (q.v.). It is a bog at about 2100 m, some 150 m below the tree line on that flank of the massif. The forest around the Brejo is low and thin, very different from the Atlantic forest (Brade, 1956:24-26) that covers the lower slopes. The specimens caught by Heyer and the one collected by our group were on the roadside, under rocks.

As the remainder of the area has been reasonably well explored (Pinto, 1951; Brade, 1956), it would seem that the species is restricted to the type locality or at most extends to the north. Two papers deal specifically with Itatiaia reptiles. Miranda-Ribeiro (1905) lists a small collection of four species of snakes and two of lizards — one *Mabuya* and *Tupinambis*. Barth (1956) purports to give a complete faunal list of the Itatiaia National Park; he cites two microteiids (no precise locality): *Heterodactylus imbricatus* and *Euspondylus* (alias *Pantodactylus*) *quadrilineatus*. Both identifications are plausible, but the work should be viewed with extreme caution, as it is very amateurish. (For example, *Chelodina longicollis*, a chelid turtle from Australia, is cited as occurring in Itatiaia). It is not impossible that one of the microteiids cited by Barth is really a *Colobodactytus* collected somewhere else on the massif.

Map 1. Approximate distribution of *Colobodactylus*. 1, Itatiaia. 2, Boracéia. 3, São Paulo and Poá. 4, Ilha dos Búzios and Ilha Vitória. 5, Ilha dos Alcatrazes. 6, Ilha da Queimada Grande. 7, Iguape and Barra do Icapara.

The general picture of the distribution of *Colobodactylus* is then, on the basis of present materials: (i) one species, *taunayi*, occurs in southeastern São Paulo and on coastal islands; (ii) a second species, *dalcyanus*, has a very restricted montane distribution; (iii) the presently known range of *taunayi* does not encopass the massif where *dalcyanus* occurs, the nearest locality, Boracéia, being some 170 km away; given the rarity of the species on the mainland, though, this datum must be viewed as provisional; (iv) all specimens with habitat data were collected in grassland or second growth, but the possibility remains that *taunayi* may occur in rain forest.

SOME RELATED GENERA

We will briefly discuss next three genera that we consider related to *Colobodactylus*: *Colobosaura, Anotosaura,* and *Heterodactylus. Bachia* is considered by Dixon (1973) to be close to the latter two genera, but we will leave it aside here because it is a specialized subterranean group, rather heterogeneous, and with an Amazonian and peri-Amazonian distribution.

Colobosaura Boulenger, 1887

Boulenger's name is only a *nomen novum* for *Perodactylus* Reinhardt & Luetken, 1862, preoccupied. Three species have been described: *modesta* (Reinhardt & Lütken, 1862), the type; *kraepelini* (Werner, 1910); and *mentalis* Amaral, 1933. We will not discuss *kraepelini,* known only from the type material (apparently one male and one female from Puerto Max, Paraguay), because the original description, first, is too laconic, and, second, mentions explicitly a plicate tongue of the *Alopoglossus* type, certainly not present in the group we are dealing with. The animal has to be seen again before anything sensible can be said about it.

Colobosaura modesta differs at once from the two *Colobodactylus* in having well developed prefrontals. Otherwise, the similarities overweigh the differences. The lateral and ventral pholidosis of the head and neck are very similar to that of *dalcyanus*; there is even a short sulcus ventral to each ear opening. The dorsals are hexagonal--lanceolate, with broad low keels. The tail scutellation also resembles closely that of *dalcyanus.* The pollex varies from tubercular, clawless, to relatively well developed. The dorsal scutellation of the thigh also approaches that of *dalcyanus.* The color pattern again comprises a dorsal, a lateral and a ventral area. The dorsum is buff, with fine punctuations (heavier than in *taunayi*) condensed in transverse bars. There is a dorso-lateral white stripe. The flanks are dark, with light mottling. The ventral parts are immaculate.

Colobosaura mentalis has prefrontals, an extra pair of small chin-shields in front, and is otherwise very similar in scutellation to the forms already discussed. The gular sulcus is almost as distinct as in *dalcyanus.* The pollex is well formed but clawless. It is hard nowadays to make out the color pattern of the types (and only specimens known), but from Amaral's description it seems to be similar to that of *taunayi,* with the exception of a median black bordered light stripe, on the head and nape.

As said above in the introduction, we do not deem it profitable to go into systematics at the generic level at this time, but it appears

Map 2. Approximate distribution of *Colobosaura*. 1, Senhor do Bonfim. 2, Morro da Garça. 3, Santos Dumont. 4, Nova Europa. 5, Ribeirão Claro.

that these forms are closely related and there would be even grounds for fusing the two genera.

Heterodactylus Spix, 1825, and **Anotosaura** Amaral, 1933

The two species of *Heterodactylus* differ strongly in size: *lundii* (Reinhardt & Lütken, 1862) is not known to reach 50 mm snout to vent, and is slender: *imbricatus Spix*, 1825, is stout and usually surpasses 100 mm. However, they are rather alike in scutellation.

With regard to *Anotosaura*, as noted by Dixon (1974), in his review of the genus, two of the three species (*collaris* Amaral, 1933, and *vanzolinia* Dixon, 1974), are similar (in fact he calls them subspecies, but see Vanzolini, 1976a) and the third (*brachylepis*

Dixon, 1974) so strikingly different from them that his initial response was to place it in a different genus. However, I agree with Dixon that they have enough in common to be kept in the same genus at this stage of our knowledge, and it is possible to compare them with the *Colobodactylus*-*Colobosaura* complex as a unit, with recourse to eventual parentheses.

A very obvious character of *Heterodactylus* and *Anotosaura* is the absence of an ear opening, which Boulenger used in the British Museum Catalogue to define one of his subgroups of microteiids. Closure of the external ear opening is an adaptation to a burrowing life, and goes together with body and tail elongation and limb shortening, as it does in *Anotosaura, Heterodactylus* and *Bachia* (Dixon, 1973). In extreme cases (*Bachia,* amphisbaenids) of fully subterranean small animals, there is also a diminution of the number and an enlargement of the area of head (and other) scutes, as a further means of lessening friction against the soil.

What one does not see commonly mentioned in the literature is that, as in any case of loss of an organ, there are what might be called degrees of earlessness. Thus in *Heterodactylus* and *Anotosaura* there is at the site of the ear opening a clear depression lined with small irregular scales. In *Bachia* the condition varies; some forms

Map 3. Approximate distribution of *Heterodactylus*. 1, Serra do Cipó. 2, Serra da Piedade. 3, Santa Rita. 4, Serra do Caraça. 5, Mariana. 6, São Pedro do Pequeri. 7, Rio Preto. 8, Macaé. 9, Piedade.

(e.g. *monodactyla*) show no signs of the closure, while others (e.g. *bresslaui*) do.

It is obvious that adaptive loss of an organ is not in itself proof of relationship; convergence and parallelism are well known phenomena. But when relatedness has been made probable by other characters, adaptive loss of organs acquires status as a group trend, and so as an additional indication of relationship. In the case of the earless genera, and especially in that of *Anotosaura* and *Heterodactylus*, Dixon (1973, 1974) has shown that the general pattern of scutellation indicates that they are actually related. I think, for the same reasons, that *Colobosaura* and *Colobodactylus* represent evolutionary stages of the same stock previous (but possibly on the way) to earlessness.

The body and tail scutellation of *Heterodactylus lundii* is extremely close to that of *Colobodactylus*, both in shape and arrangement of scales. The same can be said of *Anotosaura*: the hexagonal dorsals are broader (very short in *brachylepis*) and not keeled, but the same pattern is found of complete rings of scales around the body, the shape of the scales changing from hexagonal to squarish down the flanks.

The general pattern of the head scales is also rather uniform in the group, taken into account the lability of the prefrontals and

Map 4. Approximate distribution of *Anotosaura*. 1, Agrestina. 2, Senhor do Bonfim. 3, Capitão Enéas. 4, Serra do Cipó.

frontoparietals in microteiids. The parietal region and the side of the head show the least intergeneric variability, with the exception of *H. imbricatus,* which has a reduced inter-parietal. On the chin region, the number of post-symphysials in contact on the midline varies much, but one always finds a triangular gap between the last pair of large post-symphysial and the transverse sulcus that reaches the ear on each side; this gap is usualy filled with a pair of elongate scales and a variable number of irregular elements. On the other hand, the condition of the gulars in *Anotosaura* differs markedly from that of all other forms. *A. collaris* and *vanzolinia* have gulars arranged in regular transverse rows, with free hind margin; the last row (the collar) has the longest scales and the most extensively free edge. In *brachylepis* the morphology of the gulars is the same, but there is no prominent free edge; they are simply imbricate.

The color pattern of both *Heterodactylus lundii* and *Anotosaura vanzolinia* is closely reminiscent of that of *Colobodactylus taunayi*: back brown (with dark punctuations but also some lighter mottling), a dorsolateral light line, sooty flanks with some light mottling, and a light belly with dark punctuations (as in Ilha Vitória *taunayi*). *H. imbricatus* shows the same pattern, but the differences in tone between the dorsum and the flank are not so marked; the dorso-lateral line is less evident, especially at midbody. The color pattern of *collaris* is not kwnon. That of *brachylepis* is sui generis, and presents a problem. The types (2 specimens) are light brown with dense minuscule dark vermiculations. The only other known specimen, from another locality, is decidedly melanistic, but still shows the fine vermiculations (Vanzolini, 1976a).

The comments made above about earlessness apply also to a trend towards loss of digits found in this group. *Heterodactylus imbricatus* has a tubercular, clawless pollex; *lundii* no pollex; both forms five toes. *Anatosaura collaris* and *vanzolinia* have five digits, *brachylepis* four, in all limbs.

A final peculiarity of *Anotosaura,* noticed by Dixon (1974) is that it shares with *Bachia* simple conic (peg-like) teeth, instead of the tricuspid ones found in the other genera.

Summarizing *Hetorodactylus* is a homogeneous taxon, in spite of the size disparity. *H. imbricatus* would be more advanced with regard to size, color pattern and some details of head scutellation not discussed here, and less advanced in still having a rudimentary thumb. *Anotosaura* is not very homogeneous, but presents some peculiarities of its own that permit the three species to be kept together.

DISTRIBUTIONAL PATTERNS

We do not forget that the present study is based on 77 specimens (27 of which are *C. taunayi* from Queimada Grande), from 26 localities, plus 4 literature citations, from 4 localities. The meagerness of this inductive basis is heightened by the fact that in recent years some important finds have been made (the new species *C. dalcyanus, A. vanzolinia* and *A. brachylepis,* the Serra do Cipó *H. lundii* and the Capitão Enéas *A. brachylepis*) and more can be confidently expected for the near future.

The scarcity of specimens is felt less acutely than might be expected in the area of taxonomic decisions; the only case is that of *Anotosaura brachylepis*. As said by E. E. Williams (in litt.), a good species can be recognized on one specimen, as even a genus.

It must be remembered that we are employing only external characters, which is unavoidable in a group of rare animals. However, even if it comes to be proved that the two groups (genera with and without external ear opening) we are here treating together are not really related, the zoogeographical argument is not weakened, as it really does not depend on phylogeny. It was indeed the distributional pattern that first called our attention to the possibility of taxonomic relationship.

THE DISTRIBUTION OF THE SPECIES

As said, *Colobodactylus taunayi* is known from the coast and coastal islands, from the Atlantic plateau and from the Serra do Mar in São Paulo, a set of ecologically disparate localities. *C. dalcyanus* is known from the Itatiaia massif, at 2100 m.

Colobosaura mentalis is known only from the type materials, from Senhor do Bonfim, Bahia (at the time of collection called Villa Nova). This locality is in a very diversified area geographically intermediate between caatingas and cerrados (Vanzolini, 1974), with some scattered spots of forest; it is impossible to infer anything about the ecological preferences of the lizard.

On the contrary, it is practically certain that *Colobosaura modesta* is a cerrado and probably Chaco species. The type locality is within the core of the domain of the cerrados (Vanzolini, 1970). Incidentally, it has been misspelled and incompletely quoted in the current literature. Actually, Reinhardt & Luetken (1862:218) say that the former collected the types in "an outhouse of an abandoned ranch", called "Ponte Pari", near the isolated hill Morro da Garça in central Minas Gerais (there is a town of the same name a few kilometers east of the hill, but Reinhardt refers explicitly to the latter). Peracca (1895) describes a specimen collected by Borelli, but does not cite the locality. Judging, however, from the other localities cited in the paper, the specimen was obtained somewhere along the Rio Paraguay, between the Rio Apa on the north and Resistencia and Corrientes on the south, i. e., near the southwestern end of the great diagonal of open formations.

We have two specimens from the state of São Paulo and one from Mato Grosso. One of the São Paulo specimens was collected by the late Karol Lenko, of this Museum, in cerrado, in an enclave near the town of Nova Europa; the other was sent to Instituto Butantan from Santos Dumont, SP, a village in the transition belt between the domain of the cerrados and the Atlantic forest (Vanzolini, 1970), in an area with many cerrado enclaves. The Mato Grosso specimen is from Ribeirão Claro, Mt, near the southern edge of the core area of the cerrados.

We have *Heterodactylus imbricatus* from the following localities: *Minas Gerais*: Mariana; Serra do Caraça; Rio Preto; Pequerí. *Rio de Janeiro*: Macaé. *São Paulo*: Vila Elvio (20 km from Piedade). The type locality is the interior of the province of Rio de Janeiro (Spix. 1825:25). The following locality records in the literature are reliable: Boulenger (1885), "Montequeira" (actually Mantiqueira) mountains near Rio; Burmeister (1853:379), Santa Rita, near Rio Acima, MG; Mertens (1930), Santa Tereza, ES. Barth's (1958) record for the Itatiaia is held in abeyance, given the unreliability of the paper.

This distribution is reminescent of that of *Colobodactylus taunayi*, in covering a variety of environments from the cerrados of Minas Gerais to the Atlantic plateau of São Paulo, the Serra do Mar in Espirito Santo, and the coast of Rio de Janeiro.

The type locality of *H. lundii* is the bare and windswept top of the Serra da Piedade, Minas Gerais, an itabirite ridge almost 1800 m high. One of us (P.E.V.) collected several specimens there but could not find any below the top 50 meters. He thus used to believe this lizard to have one of the smallest ranges in the world (ca 2.5 hectares), when Otavio Froehlich, one of the collectors of *Anotosaura brachylepis*, brought in a specimen collected at 1300 m on the Serra do Cipó, approximately 75 km to the north of Serra da Piedade. We carefully compared this specimen with the topotypes and found no significant differences.

As to *Anotosaura*, data are also scanty. *A. collaris* is known only from the type locality in NW Bahia, Senhor do Bonfim, an area, as already said, so complex as to make useless any guesses about the ecological preferences of the form. *A. vanzolinia* has been so far collected only at Agrestina, Pernambuco, in euphorbia hedges in agreste (see discussion in Vanzolini, 1974).

The distribution of *A. brachylepis* is curious and not fully understood on the basis of present materials (Vanzolini, 1976). The types were collected on the western slope (ca 1300 m) of the Serra do Cipó, at the southern end of the great Proterozoic plateau of the Espinhaço. The general vegetation at the foot of the plateau is cerrado; higher up occur combinations of peculiar forms, dominated by Eriocaulaceae and Velloziaceae (Silveira, 1908). At the actual collecting site the vegetation was cerrado, near the thin gallery forest of the river (C. G. Froehlich, pers. comm.).

Another specimen, very similar to the types in pholidosis, but melanistic, was collected some 330 km to the north in a complex transitional area, with interdigitations of cerrado, caatinga and an agreste type of low forest (Vanzolini, 1976a).

GENERIC PATTERNS

We will attempt a description and interpretation of the distribution of the genera as presently defined (and of the group as a whole) based on the concepts of pulsations of the morphoclimatic domains caused by paleoclimatic cycles (Vanzolini, 1970), and on conventional models of geographic speciation (e.g. Mayr, 1970). It is our belief that cases exist that are not explainable in this simple orthodox fashion, i.e., cases of so called "ecological", "sympatric" or "parapatric" speciation, but that it is important to try first to explain each situation by conventional theory. Only thus we'll eventually have a residue left of hard evidence for alternative mechanisms, and adequate leads to analyze them. When this is done, we may have to go back and revise many of these preliminary analyses, but then no biogeographer should suffer from delusions of permanence.

In what follows the genera are ordered according to the conveniences of our argument, not taxonomically. This introduces no biases, as we are sure the distributional phenomena we'll be discussing are not relevant to systematics at the generic level.

A starting point, simple and least ambiguous, will be the distribution of *Colobosaura modesta,* a species restricted to the southwestern half of the great diagonal of open formations and to enclaves of the same in the area of transition with the Atlantic forest. The enclave specimens indicate that the form was present at a time when cerrados were more widespread than now, and that its former range was dissected by forest expansion. The absence of obvious signs of geographical differentiation speaks for the recency of the phenomenon.

Colobosaura mentalis should at this time be considered an element of the northern half of the diagonal, differentiated during a time when forest bridged the present gap between the hylaea and the Atlantic forest. This type of distribution argues for at least a lobe of forest, at Central Brasilian latitudes, at the time *modesta* and *mentalis* differentiated. The presence of disjunct but undifferentiated populations of *modesta* in the São Paulo enclaves indicates that the two species segregated during an older humid episode, not during the present one.

Heterodactylus imbricatus has a very "illogical" distribution from the viewpoint of general ecology. An East-West transect across its range cuts through cerrado, buffer forest, Atlantic forest, and ends on the coast.

This can be explained in more ways than one. For example: (i) *H. imbricatus* is a very versatile species, capable of colonizing many situations, helped by its quasi-subterranean habits; (ii) it is not now colonizing different habitats, but has only been capable of surviving ecological changes (forestation) in its old habitat, again under the protection of its habits; (iii) its distribution is not influenced by the general ecology of the area; (iv) it inhabits the network of open formations that permeates every forested area (Vanzolini, 1970).

We prefer the second hypothesis. The first one is made little probable by the relative rarity of the species and by its restricted range; these do not indicate an aggressive colonizer, but are compatible with a diehard holdover. As to the third hypothesis, it suffers from scarcity of analogies. Even purely suberranean reptiles (*Amphisbaena, Micrurus*) usually follow in their distribution the major plant formations; a major exception, *Amphisbaena alba* (Vanzolini, 1968), is a colonizer, with an enormous area of dispersal. Among non-subterranean forms we have extreme euryecy in a few forms, (e.g. *Ameiva ameiva* (Vanzolini, 1972) and *Iguana iguana* (Vanzolini, 1974); again these are aggressive colonizers, *Ameiva* a text-book case of penetration of the forest by an open formation lizard. The fourth hypothesis is made less probable by the occurrence of *imbricatus* on the mountains near Rio (the Boulenger record), where the forest is very dense; it cannot, bowever, be discarded on these grounds only.

Anticipating some data to be discussed below, we believe *H. imbricatus* to be in a sort of "seral" situation since the beginning of the present wet episode. It was an open formation lizard; when forest covered a part of its range, it became exposed to a diversity of environments, and the outcome of the process may either be its adaptation to forest conditions, or its disappearance from the area.

Both *H. lundii* localities are surrounded by cerrado. Serra da Piedade is on the edge of the distribution of *imbricatus,* Serra do Cipó disjunct from the remainder of the genus. This leads to interesting considerations. First, it tends to reinforce the idea that the group is basically a cerrado or, at least, open formation element, thus supporting the hypothesis we favor to explain the distribution of *H. imbricatus.* Second, the disjunction indicates it is a relict distribution, not one of ongoing colonization. Third, the restriction to mountains provides an additional paleoclimatic element — that the climate at the critical time for the establishment of the present pattern was not only drier, but also cooler than at present. Fourth, the lack of differentiation of disjunct *lundii* is parallel to that of *Colobosaura modesta.* Finally, we may again accept that the last climatic episode is not sufficient by itself to explain the existence of two species, which must date at least from the previous humid epoch.

The pattern of *Colobodactylus* agrees exactly with that of *Heterodactylus,* with one exception: *C. dalcyanus,* the montane form, is known from only one locality. Otherwise and, to us, very significantly, the distribution of *C. taunayi* has the same "illogical" character as that of *H. imbricatus,* and warrants the same explanations. The presently known distribution of *C. dalcyanus,* however, does not per force imply a former cycle of differentiation; it may have differentiated during the present wet episode.

The interpretation of the distribution of *Anotosaura* suffers most of all from the insufficiency of data. The two more primitive forms (this is the only group in which the concept can be used with some confidence) inhabit the northern end of the diagonal of open formations. No specimens are known from the caatingas proper, but only from their edge. *A. vanzolinia* was collected in the eastern transitional belt of "mitigated caatinga" known as "agreste", *A. collaris* in the southwestern belt, a more complicated one (Vanzolini, 1974, 1976), and cannot be said at present to be properly a cerrado species. It is not impossible that both forms are restricted to specific segments of the transitional belts, whose main characteristic (Ab'Saber, 1967, 1970; Vanzolini, 1976) is exactly extreme local diversity. This is one the reasons why one of us (Vanzolini, 1976a) has preferred to give species rank to *vanzolinia,* rather than to consider it a subspecies of *collaris,* as originally proposed by Dixon (1974). They may have originated, in a milder epoch than now, from a single continuous cerrado population, later dissected by the expansion of the caatingas to their present extent. Subsequently, the two populations would have been pushed into marginal situations. This is a hypothesis that has been previously suggested in a broader context (Vanzolini, 1974), and continues to seem plausible enough, but we must emphasize that much more collecting in the caatingas has to be done before we feel reasonably sure.

The circumstances of *A. brachylepis* are made less simple by the presence of a melanistic specimen in the lowlands. The area is one of interdigitations and enclaves, much disturbed by man; it is important, bowever, that the site of collection was unequivocally in open formations.

In the case of *Anotosaura*, we can theoretically think of two directions of colonization: from the lowlands to the mountain, and vice versa. In the first case the phenomenon may be in process and the respective populations of course still undifferentiated. There is one possible analogy: *Cnemidophorus ocellifer*, a widespread lizard in open formations of all types south of the hylaea, occurs on the Serra do Cipó at same heights as *Heterodactylus lundii* and higher than *Anotosaura brachylepis* (MZUSP collection). But *C. ocellifer* is again, from the distributional viewpoint, an aggressive species, while *brachylepis* is rare.

If we accept that the phenomenon is correlated whith a past climatic cycle, then we must face two possibilities: (i) that the species did not change morphologically in spite of the time span and of the ecological differences; (ii) that, more probably, further specimens will show differentiation between the montane and lowland populations, to the subspecific or specific level.

If we accept, on the contrary, the intrinsically not very probable hypothesis that a rare mountain-adapted form is now colonizing the lowlands, we are just throwing the problem back another episode, because at some time the mountain must have been colonized from below.

In conclusion, we think it more economical to believe that the distribution of *A. brachylepis* conforms to the general pattern of the group, and that eventually diferences will be found between the populations presently represented by the Cipó and Capitão Enéas specimens.

GENERAL PATTERN AND INTERPRETATION

This group of four genera with nine species contains only one reasonably widespread form. The range of *Colobosaura modesta* is a belt of open formations provedly some 1500 km long. This is really not too much on a continental scale, but is quite considerable for a microteiid. In cis-Andean South America this range is exceeded only by the pan-Amazonian forms, by *Micrablepharus maximiliani* (which inhabits the whole diagonal of open formations), and by *Cercosaura ocellata* and *Pantodactylus schreibersii* with their subspecies.

Otherwise, the longest distance between two *Heterodactylus imbricatus* localities is some 500 km; of *Anotosaura brachylepis* a little over 300 km; and of *Colobodactylus taunayi* about 200 km. The other four forms are so far extremely restricted geographically.

Again *Colobosaura modesta* is the only form clearly associated with a major system, the diagonal of open formations. *Heterodactylus imbricatus* and *Colobodactylus taunayi* have very heterogeneous ranges; as the areas are small this does not tend to indicate expansion but, as said, survival after a change to less than optimal conditions. The other species occupy marginal habitats. All in all one gets a strong impression of stranded species, i.e., of a relictual pattern, indicating that the present climatic phase is not optimal for the group.

The analyses above then afford several elements to interpret the general pattern in terms of paleoclimatic cycles.

It has been seen that the wet episode of a former cycle is necessary to account for the present distribution at the species level of, at least, *Colobosaura, Heterodactylus* and *Anotosaura*. Additionally, the obvious association with montane habitats (no other Brasilian group of microteiids reaches even the moderate heights these do) indicates that the subsequent dry period, during which the group reached the areas where it is now disjunct, must have been cool.

Brade (1956) has meteorological tables for two stations on the Itatiaia massif, at 816 and 2200 meters. The following data are abstracted from his tables:

	Temperature (°C)					
	Mean			Minimum		Rainfall
	Jan.	July	Year	Jan.	July	(mm)
816 m	21.0	14.5	18.4	7.0	0.0	1717
2200 m	13.4	8.2	11.3	3.7	—6.0	2417

The data permit to infer an approximate altitudinal gradient, and give an idea of the climatic conditions met by *C. dalcyanus*. As far as presently known, these are extreme for the group; Serra da Piedade and Serra do Cipó, within the same lowland isotherms as Itatiaia, reach lower heights (see, in the References, BRASIL, Ministério da Agricultura).

Vanzolini & Ab'Saber (1968) and Vanzolini & Williams (1970), on entirely other grounds, have already noted the biogeographical significance of a dry episode, dated by the Macedo shell-mound and the Saco da Tamburutaca hanging beach in Paraná, as 2680-3513 B.P. This is Period V of Fairbridge's revised (1976) "correlation of global sea level with specific indications from Brazil": "Period V lasted from 3400 to 2600 years ago and involves another striking cool cycle, judging from the high latitude palynological data (Late Subboreal)..." (loc. cit., p. 356). There is no reason to believe that rainfall fluctuation in the northern and southern hemispheres were parallel during the Holocene (Fairbridge, 1976), but it seems that major temperature events have been global in nature. Thus, we would say that the differentiation pattern of this group of microteiids is compatible with a wet-dry-wet climatic sequence, the dry episode being several degrees cooler than the present phase, and lasting from ca. 3400 to 2600 B.P.

An adaptation to cool environments would explain not only the montane addition of several forms, but also why the group does not occupy more fully the considerable geographic space of open formations that exists in the present climatic phase: it is probably too hot.

Still another bench mark is available. *Colobodactylus taunayi* is present on three islands of the coast of São Paulo. These islands were cut off from the coast by postglacial rising sea levels about 11,000 years ago (Bigarella, 1965; Vanzolini, 1973). This has been independently identified as an epoch of dry climates in South America by the presence of arkosic sediments in deep sea cores related to the Orinoco outflow (Damuth & Fairbridge, 1970) and would constitute the older dry episode, favorable to the group, completing the sequence; this seems to be as far back as we can make reasonable inferences.

A COMMENT ON REFUGES

These microteiids, as a group, are going through unfavorable times. It can be speculated that they might become successful during the next (coming) dry episode, as they have already lived through the wettest part of the cycle, the time when the Atlantic forest and the hylaea were directly connected. In this context it is interesting to note that the non-montane populations are not presently located in refuges as usually understood, i.e., isolated stands of a given plant formation. On the contrary, they are what we have called "stranded", restricted to marginal situations — transitional belts and heterogeneous areas. Whether they have spent the height of the wet episode in their present locations or these are already a result of climatic deterioration (for them of course an amelioration) is beyond present analytical resources. The point remains, however, that caution should be used in accepting geomorphological or paleopalynological demonstration of vegetational islands (conventional refuges) as sufficient proof that such areas were really the shelters of seed populations of species that survived unfavorable phases of climatic cycles. The animals themselves should be interrogated, as independently as possible from any other considerations, almost as an exercise in plane geometry with autecological tints, to be later superimposed on patterns arrived at by means of other disciplines.

A COMMENT ON MONTANE DISTRIBUTIONS

Mountains, even relatively low ones such as these in eastern Brasil, are traditional sites of endemism and of disjunct distributions. Cases in this geographical area have been discussed in other groups, e.g. birds (Holt, 1928; Pinto, 1951) and plants (Brade, 1956; Tryon, 1972). We attempted a broad comparative study, but ended up with just a list of examples; the circumstances of the several cases, and the levels of investigation are too diverse for an interdisciplinary study at this time. We hope with this comment to stimulate the collection of adequate samples and data, and to attract attention to a set of problems, apparently trivial but very rich in possibilities.

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