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ON *TROPIDURUS HYGOMI:* REDESCRIPTION, ECOLOGICAL NOTES, DISTRIBUTION AND HISTORY (SAURIA, IGUANIDAE)

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ABSTRACT

Tropidurus hygomi *was collected sympatrically with* T. torquatus *at the type locality, on the coast of Sergipe. It was also found among materials identified as* torquatus *from Salvador, Bahia. It is restricted to white sand areas with clumps of vegetation including ground bromeliads. Problems related to the history of species inhabiting this type of environment are discussed.*

INTRODUCTION

In the nineteenth century the city of Maruim, at the head of the estuary of the Rio Sergipe, was the most active port in the area, exporting sugar and importing manufactured goods. From this area, in the first half of the XIX century, a Danish sea captain, V. Hygom, for a period of years sent herpetological materials to the Copenhagen Museum. These were eventually published by Reinhardt & Lütken (1861), in a paper mostly based on Reinhardt's own Brasilian collection (for which see Papavero, 1973), but including other materials from Brasil in Copenhagen. It is an excellent paper, very well illustrated, but rather hard to translate, and for this reason it has not been widely consulted.

Reinhardt & Lütken (1861: 226) list three species of *Tropidurus* in the former's collection: *torquatus,* obtained at Lagoa Santa and Rio de Janeiro, and two species described as new, collected by Hygom in the Maruim area ("ved Maruim", "i Omegnen af Byen Maruim"): *Tropidurus macrolepis* and *hygomi.* They rightly considered the three forms as very close, and dealt with them by means of differential diagnoses, epitomized in a short Latin key, that can be translated as follows:

"*α*) snout and snout scales somewhat convex.

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T. torquatus, dorsal scales small, supraoculars in 5-6 rows, hexagonal, varying in size, those of one the rows dilated, broader than long.

T. macrolepis, scales larger, supraoculars in 4 rows, the scales of the two extreme rows small, those of the other two larger, broader than long.

β) snout and snout scales flat.

T. hygomi, dorsal scales mediocre, supraoculars in 3 rows, the scales of the marginal ones small, those of the remaining row characteristically and extremely widened."

On their plate V the heads of the proposed new species are shown in dorsal view.

Boulenger (1885: 177), in the British Museum Catalogue, included *T. macrolepis* in the synonymy of *T. hispidus* (Spix, 1825) and maintained *T. hygomi,* of which he had a female syntype, saying: "The only important difference distinguishing this species from the preceding [*torquatus* (Wied, 1820)] is the greater width of the band-like supraoculars, which cover nearly entirely the supraocular region, being separated from the supraorbitals by one and from the supraciliaries by one or two series of very small scales. The scales on the body a trifle larger than in *T. torquatus.*"

Mertens (1928: 31) mentioned a "halfgrown" specimen of *hygomi* collected near Salvador, Bahia. The collector's notes on color in life allow no doubt about the correctness of the identification.

Since then the species has been present in check lists and catalogs, but no new facts or specimens mentioned, except for a rather pointless comment by Burt & Burt (1931: 297) in one of their worst moments.

We have now observed and collected the species a few kilometers from Maruim, and are in a position to redescribe it, to comment on its habitat and on some implications of its geographical distribution. The occasion of our find was a brief preliminary survey of the reptile fauna from a site at which the government of Sergipe intends to establish an industrial complex.

DESCRIPTION

(Plates 1 and 2)

Materials

MZSUP 49526-49541: Santo Amaro das Brotas (Gravatá), Se, 21-25.iii.78; 49658-49674: Santo Amaro das Brotas (Aldeia), Se, 23.iii.78; 49675-49680: Santo Amaro das Brotas (Estiva), Se, 25-27.iii.78.

Scales on top of snout small, flat, polygonal, irregular, irregulary imbricate. Occipital large, irregular, usually asymmetric, frequently scalloped or overlapped by small surrounding scales. Scales on the sides of the occipital similar to those on the top of the snout, those behind it similar to the dorsals, but unkeeled.

Canthus rostralis formed by two posterior square scales, extending equally on the top and on the side of the snout and a distal one, indented above by the nasal, which is round and swollen, with the nostril on the posterior half. The anterior supraciliaries, that occupy 4/5 of the edge, are elongate, very thin, and dip forward, while the posterior ones are shorter and dip back.

Supraocular area with a patch of small, flat irregular scales in front; surrounded by a row of 1-2 such small scales. The enlarged supraoculars are band-like, strikingly broad, in a single row, at least on the posterior 2/3 of the area.

Rostral low and broad. Supralabials six. Two to four rows of loreals. Infraorbital moderately large, in narrow contact with or separated from the fifth labial. Temporal scales small, imbricate, keeled on the distal half, some of them distinctly mucronate. A row of long aciculate scales on the anterior margin of the ear, the upper ones frequently spanning the opening. On the sides of the neck two deep pockets, obliquely arranged, lined with granules, and often containing mites; behind them a variable antehumeral fold not reaching the ventral surface.

Symphysial roughly pentagonal, narrower than the rostral, followed on each side by a divergent row of enlarged scales, that may or may not grade into the gulars. The first post-symphysial may be separated or not from its fellow, but always contacts the first labial; the second may be in partial contact with the first labial; from then on successive series of elongate sublabials intervene. Gulars flat, small, imbricate.

Dorsals keeled, mucronate, the keels forming oblique lines. No differentiated scales on the midline. Ventrals smaller than dorsals, rounded, smooth, imbricate. Scales of the anal flap more or less enlarged, surrounded by smaller scales on the three sides.

Scales of the dorsal aspect of the arm and of the posterior surface of the forearm similar to the dorsals; dorsals of the forearm with light keels; carpals smooth. Ventral scales of the arm small and smooth, of the forearm spiny, of the palm less so. Infradigital lamellae with three spines.

Dorsal aspect of the thigh with keeled mucronate scales, aligned in front obliquely towards the back, then turning progressively along the axis of the limb. Hind side of thigh with small mucronate scales, pointing upward. Dorsal aspect of tibia with mucronate scales longitudinally arranged. Tarsals diamond-shaped, smooth, little imbricate, sometimes notched at the tip. Ventral scales of thigh and leg similar to those of the body. Sole moderately spiny. Toes in the order I-II-V-III-IV. Basal lamellae of toes V and IV forming a strong, thick serrated ridge, much less well developed on the other toes. Infradigital lamellae spiny, variable.

Dorsal scales of the base of the tail much wider than the trunk dorsals, with slight keels but distinctly mucronate. Distally they become progressively similar to the dorsals of the body and then more elongate, with high keels. Scales on the sides of the tail smooth, with pointed and notched tips, distally becoming similar to the dorsals. Median ventral scales at the base of the tail smooth, large, with pointed tips, soon acquiring keels and mucrons, and finally becoming similar to the dorsals; thus the scutellation of the distal part of the tail is homogeneous.

On dorsal view the young has a rufous brown head, well set off from the neck, which is sooty brown, with white and black punctuations, the former occupying a whole scale (and no more), the latter one scale or less. On the back there are two ill defined longitudinal gray stripes, separated by 12-14 scales. The median area is light brown, with punctuations like those on the nape. The gray stripes, 4-5 scales wide, begin in front of the shoulder, and reach the base of the tail. Below each gray stripe there is a dark one, with some spotting, then a grayish area on the flank, with a few spots, and then the belly, which is light gray, immaculate. The dorsal aspect of the limbs is streaky brown, with black spots.

The nasal and loreal regions are reddish brown. There is one longitudinal white stripe, beginning under the anterior angle of the eye, running above the upper lip, widening and becoming grayish in front of the ear, where it merges with the throat color. There is a very characteristic black spot on the eyelid; it is frequently triangular, with base on the supraciliary edge and tip on the lip; it may also be rectangular, as in the plate; it is always set off by white areas in front and behind it on the lid. The lips and gular region are densely reticulated with dark, the remainder of the lower surfaces uniform grayish.

The adult female basically resembles the young, with the following differences: on the anterior part of the back there appear one or a few interrupted transverse narrow black bands, bordered with white behind; on the sides of the neck there is a black area, below the beginning of the gray stripe, that enters into and sometimes borders the antehumeral fold.

The adult male is much duller; the gray stripes may disappear, and the whole back acquire a salt and pepper appearance. The sides of the head and lid are also much less vividly marked, sometimes unpatterned.

The ventral sex markings in the male are the usual ones in the genus, on the ventral face of the thighs and on the anal flap. They are not very heavy. On the lower face of the thigh there is a narrow triangle pointing distally, some 3-5 scales wide at the base, 16-20 oblique scale rows long. The marking on the flap has 15-20 scales on the hind edge, 7-9 on the midline. The scales which form the marking are a rich black, with a very narrow light border, which gives the marking a tesselate appearance.

COMPARISON WITH SYMPATRIC TORQUATUS

The relative size of the scales on top the snout differs sharply in the two forms; in *hygomi* one can count, between the occipital and the rostral, slightly to the side of the midline, from 12 to 18 scales; in sympatric *torquatus* the count is 8-10. The shape of the scales also differs; those of *torquatus* are polygonal, juxtaposed, quite unlike the uneven scales of *hygomi.*

The condition of the supraoculars is also very distinctive in this region: each band-like scale of *hygomi* corresponds to two polygonal scales of *torquatus.*

There is a further difference in the folds on the sides of the neck. In *hygomi* there are two definite pockets in front of the antehumeral fold; in *torquatus* the lower pocket is absent or at most faintly indicated.

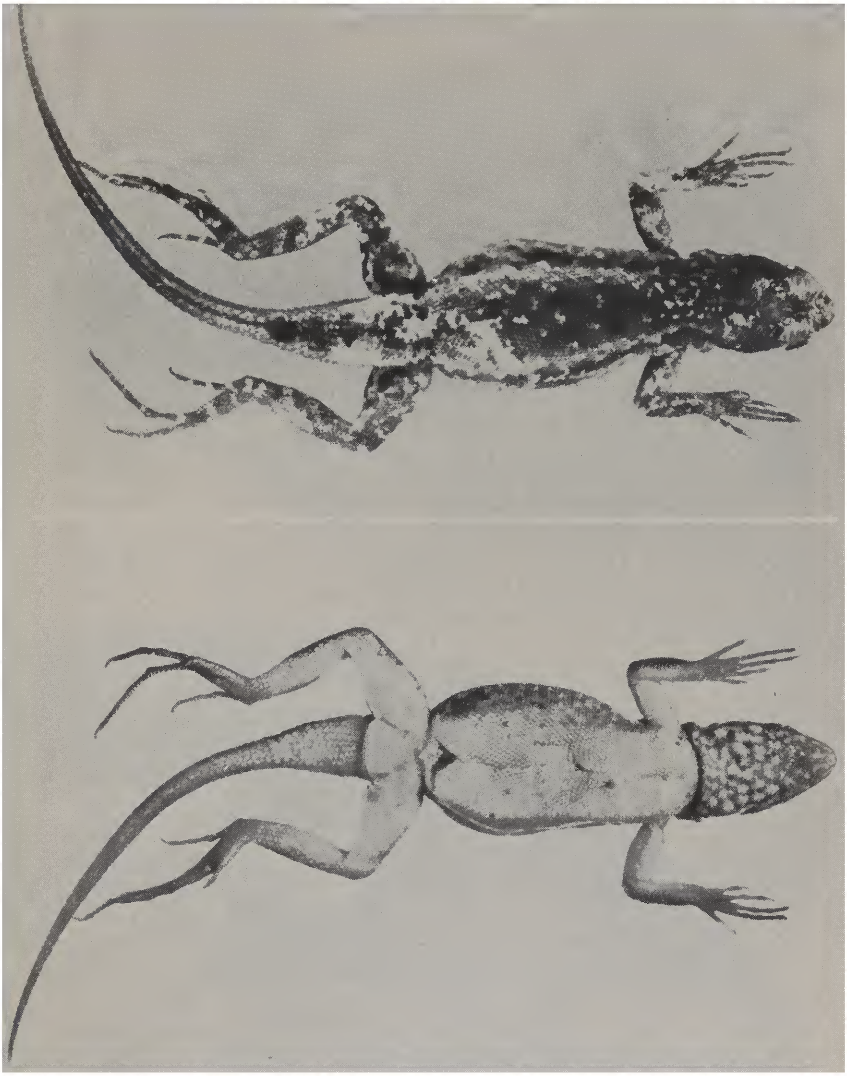


Plate 1. *Tropidurus hygomi,* MZUSP 49532, Santo Amaro das Brotas (Gravatá), Sergipe, ♀, 52 mm body length.

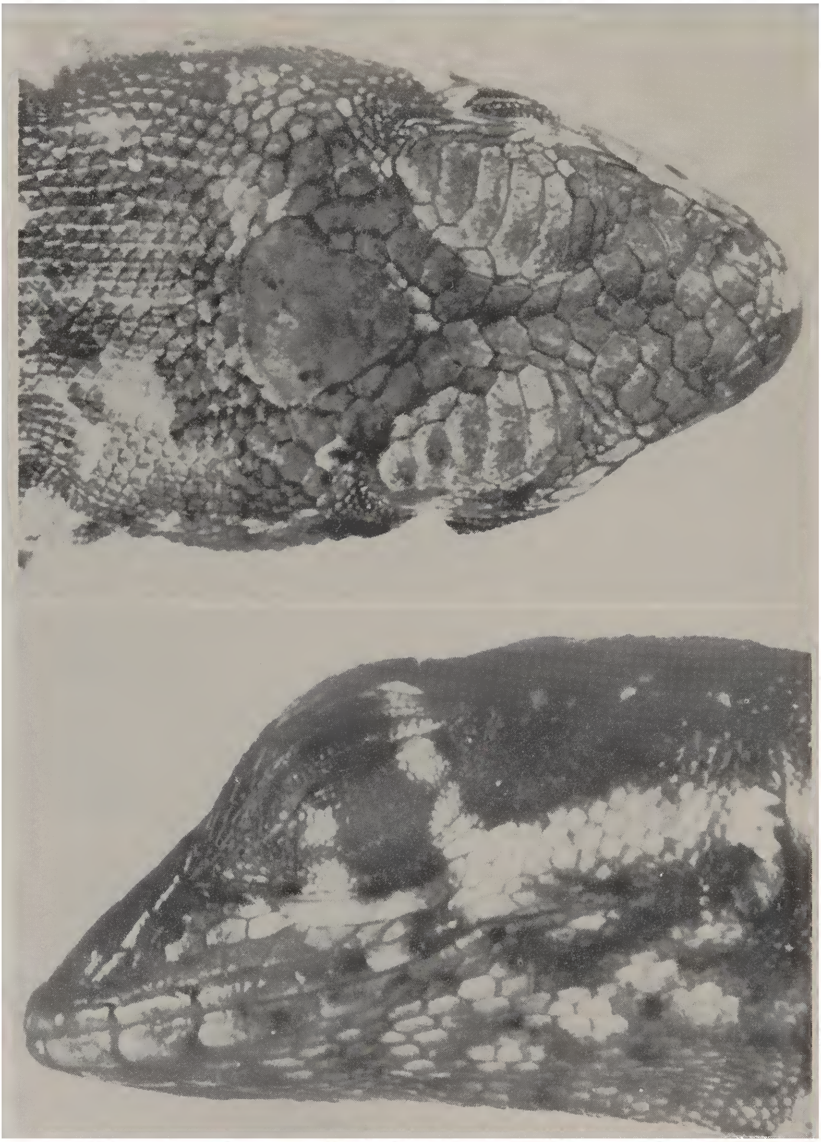


Plate 2. *Tropidurus hygomi*, MZUSP 49532, Santo Amaro das Brotas (Gravatá), Sergipe, ♀, 52 mm body length.

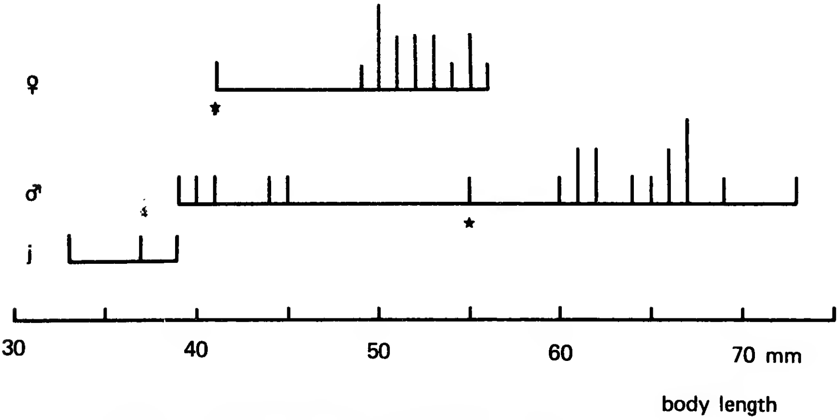
The color pattern of the young and of the female show strong differences, quite visible in the field, especially the dark, white-edged palpebral markings of *hygomi*, absent in *torquatus*.

In *torquatus* of all sizes the black punctuations on the back tend to form transverse bars, irregularly edged with white behind. The transverse bar on the interscapular region curves down and forward and continues in front of the arm as the black collar that gives the species its name. In *hygomi* the antehumeral fold may be marked in black, but a collar is not evident, and the back is never barred behind the shoulders.

Finally, *hygomi* reaches at most 60% of the body length of sympatric *torquatus*, and has a different breeding season, as will be seen below.

BIOMETRICAL DATA

All specimens but three, 33 to 39 mm body length, could be sexed by dissection of the gonads. Graph 1 is a bar diagram showing (better than any histogram we could devise) the distributions of frequencies of body length. The asterisks indicate the smallest female with yolked eggs and the smallest male with the adult color pattern. Some facts can be inferred from this graph.



Graph. 1. Distributions of frequencies of the body length.

T. hygomi is probably the smallest species of the genus, our largest male measuring 72 mm, snout to vent length; sympatric *torquatus* reaches 119 mm; only the transandean *T. occipitalis* and *theresiae* (Dixon & Wright, 1975) approach it in size, but are slightly larger. The small size is of course reflected in the reproductive strategy: as the graph shows, females mature very early, quite possibly in their first year.

Adult males are larger than ripe females, with scant overlap. Whether they mature later or simply grow faster the present data do not permit to infer; a larger sample might. In spite of a gap of

10 mm body length between the largest unpatterned and the smallest patterned male, the shape of the distribution tends to indicate that the regalia are assumed at about 55 mm body length.

Twelve out of 15 females had either large yolked follicles or oviductal eggs. Among 69 females of *T. torquatus* simultaneously taken in the same area, no signs of female reproductive activity were seen.

HABITAT

(Map 1)

The study area is a coastal plain in the state of Sergipe. The coast line, ca. 28 km long, is fairly straight, running a little W of SW-NE (220°-40°). The limit to the south is the lower course of the Rio Sergipe, that enters the sea at 10°55'S, 37°02'W; to the north the Rio Japaratuba, whose mouth is at 10°45'S, 36°53'W. The inland limit is the edge of the low Tertiary plateau (Barreiras Group), that converges towards the coast on the north. The trapezoid thus encompassed measures approximately 300 km^2. The city of Maruim is at the western corner of the area, where the Rio Sergipe leaves the Tertiary hills and receives the Ganhamoroba; a few kilometers down it receives the Cotinguiba and enters its present estuary proper, an old interiorized ria.

The beach is backed by a narrow belt of dunes; in the alluvial plain behind, two rivers run to the Sergipe, parallel to the coast. Nearest to the sea (2-2.5 km) is the Pomonga, whose headwaters, on the NE, are connected to the Japaratuba by a short artificial canal. Parallel to it, some 1-2 km inland, runs the much shorter Parnamirim. Both rivers are of course shallow and meandering.

In the alluvial plain between the shore dune belt and the Tertiary hills, four physiographic and ecological components of the landscape can be discerned: (i) Tertiary surfaces lowered by erosion ("nível inferior dos taboleiros" of Brasilian authors); (ii) mangrove tidal plains; (iii) a network of rain-fed freshwater and brackish marshes and ponds; (iv) wave-built terraces or "restingas".

In the restingas we find two extreme types of soil, white sands and yellow clayey sands. The latter, whose clay component of course comes from the Tertiary sediments, by means of sub-Recent pedogenetic processes, are usually on the inland side, but some interdigitation seems to occur. They are relatively fertile, although not as much as those on the hills, and support some agriculture, mostly passion flower (*Passiflora*) and manioc (*Manihot*).

The white sands are covered by a characteristic type of vegetation, locally called "caatingas", but actually unrelated to the true caatingas of the semi-arid Northeast. This is where we found *Tropidurus hygomi*.

These "caatingas" are mostly distributed in clumps; the predominant species are shrubs and small trees of the genera *Coccoloba* (Polygonaceae) and *Pradosia* (Sapotaceae), palms of the genus *Attalea* and bromeliads of the genera *Hohenbergia* and *Aechmea*. Between the clumps there are patches of bare sand.

Between March 21 and 27, 1978, we worked on the caatingas for a total of some 14 hours, observing and collecting *T. hygomi* and other diurnal fauna. Our principal localities (Map 1) are Gravatá and Estiva. We also saw specimens at Curralinho and acquired a sample from local collectors at Aldeia.

The lizards, mostly small, were usually first seen on the bare sand, and predictably escaped towards the plant clumps. After a short run they stopped with cocked head; we saw no bobbing by these specimens. When further pursued they jumped sideways, with jerky motions. Large males were also found on bare sand, but frequently on low branches in the tangled vegetation. They seemed to do some bobbing, but we are not quite sure. Of a curious fact, however, we are reasonably confident: they became noticeably nervous and agitated, much harder to noose, in windy weather.

Map 1. Study area (after a sketch by E. R. dos Santos).

We found only two other lizards in the white sand restingas: the teiid *Cnemidophorus ocellifer* (Spix) and the scincid *Mabuya macrorhyncha* Hoge. The former has a very broad distribution, geographically as well as ecologically, in the open formations south of the Amazon (Vanzolini, 1974) and was common in other environments around the study area, especially towards the sea. The distribution of *Mabuya macrorhyncha* is relevant to the present problem, and will be further discussed below. A determined search was made for *Bogertia lutzae* Loveridge, a gekkonid associated with clumps of vegetation with ground bromeliads in Bahia, to the south, and Pernambuco, to the north: no specimens were found. *Tropidurus torquatus* was extremely abundant on the yellow sand areas, but no specimens were seen on the white sands.

Another stenoecious species found in the white sands was the bromelicolous hylid *Phyllodytes tuberculosus* Bokermann, 1966, of which more below.

Several species of snakes were obtained in the general study area. Among them were the confirmed lizard eaters *Chironius flavolineatus* (Boettger), *Leptodeira annulata* (L.), *Oxybelis aeneus* (Wagler), *Oxyrhopus trigeminus* (Duméril, Bibron & Duméril) and *Philodryas olfersii* (Lichtenstein)). The first named was caught actually prowling among the white sands clumps of vegetation. Other snakes collected were *Helicops leopardinus* (Schlegel), a water snake, and the batrachophagous *Dromicus poecilogyrus* (Wied), *D. viridis* (Günther) and *Waglerophis merremii* (Wagler). The only avian predator seen (infrequently) was the sparrow hawk, *Falco sparverius*. It would seem that the animal biomass of the area is mainly constituted by lizards and frogs.

THE TROPIDURUS TORQUATUS-HISPIDUS COMPLEX

Tropiduri without a differentiated vertebral row of dorsals, and with a black collar, ranging from Venezuela to Argentina, have been identified as either *T. torquatus* (Wied, 1820) or *T. hispidus* (Spix, 1825), according to criteria established by Boulenger (1885: 176-177) in the British Museum Catalogue: *T. torquatus* with "dorsal scales small, slightly larger than the ventrals" and *hispidus* "dorsal scales... at least twice as large as the ventrals". Additionally, *torquatus* would show "usually a more or less distinct light and a dark lateral dorsal band" against "no light bands along the body" in *hispidus*. Boulenger assigned to the two species broad and sympatric ranges: "Guianas; Brazil" and "Brazil; Venezuela".

Burt & Burt (1930: 26-27), without comment, considered both forms as subspecies of *torquatus*. Later Burt & Burt (1931: 297) said: "The intermediate character of the specimens of *torquatus* and *hispidus* from Bolivia and, thus, the geographic nature of their approach to each other, make it necessary to regard them as geographic races or subspecies".

Considering that the type locality of *torquatus* is on the coast of the state of Rio de Janeiro, and that *hispidus* is said by Spix

(1825: 13), in the original description, to occur in Rio de Janeiro and Bahia, it is somewhat difficult to understand how the geographic nature of their approach to each other would include the Andes of Bolivia. In addition, the distribution given by the Burts for *hispidus* (northern South America) excludes Spix's localities. In spite of recent usage of this scheme, we think it does not deserve serious consideration.

There is no doubt that much variation is to be found both in scale size and color pattern in this group; it is practically certain that several species and well marked subspecies will be eventually recognized; it is not impossible that the names *torquatus* and *hispidus* will be found to be applicable to valid taxa. What seems unreasonable is to believe that the group is composed of two closely related species of such enormous and overlapping distribution. Our point is that the problem has not been faced yet, demands a broad geographical approach, preferably as a whole but at least covering large coherent areas, and that, until this is done, it is better to adopt only the oldest name, *T. torquatus,* explicitly as a general label for a complex group.

Accordingly, we had up till now considered the name *hygomi* as either referable to a local population of the *torquatus* group, or based on a few extreme specimens of general *torquatus.* It can no longer be thus treated; being biologically well differentiated and definitely sympatric with another species of the group, it poses questions that must be faced, especially those related to its geographical and ecological distribution and mode of speciation.

DISTRIBUTION AND ORIGIN

Our samples of *T. hygomi* are practically topotypical, as the localities may well be considered "in the neighborhood" of Maruim, in the only area where restingas are found. There is one more locality to be considered, Salvador, and the available specimens of course contribute to the understanding of the general problem. Finally, there are two other lizards, *Bogertia lutzae* and *Mabuya macrorhyncha,* and one frog, *Phyllodytes tuberculosus,* that also add to the analysis.

Tropidurus hygomi in Bahia

Mertens (1928) recorded one specimen from "Umgebung Bahia's" that, from the collector's notes (Rohde, 1926) must be interpreted as the environs of Salvador (ca. 13°S). This is a very plausible locality, as the same type of habitat is common in the whole area: wave-built terraces and dune belts, so characteristic of northeastern Brasil (Tricart, 1959), with clumps of vegetation prominently including ground bromeliads. The plant species are not the same (Vanzolini, 1972: 88), but the general physiognomy is very similar. Mertens's record led us to review all our series of *Tropidurus* from the Atlantic coast. The localities are, from north to south (Map 2): Morro Branco, Ceará, 147 specimens; Maxaranguape, Rio Grande do Norte, 664; Natal, Rio Grande do Norte, 25; Recife, Pernambuco, 26;

Pontal da Barra, Alagoas, 7; Carmópolis, Sergipe, 16; Salvador, Bahia, and neighborhood, 139; Porto Seguro, Bahia, 33; Ilhéus, Bahia, 4; Guarapari, Espírito Santo, 21; Cabo Frio, Rio de Janeiro, 67. Total, 1149 specimens.

Only in the Salvador area we found specimens, 30 in all, attributable to *hygomi:* Salvador, no further data, 21 specimens; Pituaçu, 10 km north of Salvador, 5; Itapoan, 15 km north of Salvador, 4. Seven specimens are juveniles (28-42 mm body length), 10 females (42-56 mm) and 13 males (60-72 mm). The Itapoan specimens were collected by Vanzolini and Rebouças-Spieker while looking for *Bogertia* in bromeliads on the dunes (Vanzolini, 1972: 88). The remainder were sent by helminthologists for identification; of course they are gutted and not prepared for herpetological purposes. Even so it is possible to compare this sample with the Sergipe topotypes.

There is good agreement between the two samples in the size and shape of the scales on top the snout and in the presence of two distinct mite pockets in front of the antehumeral fold. On the other hand, three of the main diagnostic characters are weak in Salvador: (i) 12 out of 29 specimens (41%) do not show a perfect pattern of slat-like supraoculars, in some cases the deviation being small, but in some pronounced; (ii) the distinctive juvenile and female eyelid pattern is absent in several specimens and weak in others; (iii) the auricular scales are feebly developed in 12 out of 29 specimens (41%) and fully developed only in 9 (31%). In all characters the deviant specimens approach *T. torquatus*. In fact, at some unspecified later time (K. Klemmer, in litt.), Mertens re-identified his specimen as *T. torquatus hispidus*. Vanzolini, who identified our Bahia *hygomi* as *torquatus*, would never have, *prima facie*, recognized *hygomi* on the strength of the Bahia specimens alone.

The two areas (Sergipe and Salvador) thus harbor populations of *Tropidurus* that differ from sympatric *torquatus* in the same characters, but do not agree themselves completely, even at this deliberately superficial level of analysis. The Bahia population may be suspected of being in the process of being swamped by *torquatus*, but this is not a matter to be broached with present materials and methods.

Other lizards (Map 2)

Bogertia lutzae Loveridge is a gecko known from the same dunes of Itapoan as *T. hygomi*, and from a similar locality in Pernambuco (Vanzolini, 1972), but not from Sergipe.

Mabuya macrorhyncha Hoge was originally described (see Rebouças-Spieker, 1974) from one of the coastal islands of São Paulo, Queimada Grande. Rebouças-Spieker (loc. cit.) discovered that it also inhabits all the neighboring islands and the coast from Santos (23°57′) south. The insular populations inhabit patches of ground bromeliads, mostly growing on bare rock. The continental ones prefer long flat sand beaches with low dunes and clumps of vegetation, also including bromeliads (these types of vegetation in São Paulo are discussed by Hueck, 1955). On the northern coast of the state, where beaches are short and steep, *M. macrorhyncha* is replaced by *M. caissara* R.-Spieker, a grass dweller: the bromeliad niche is there, but empty of lizards. According to Rebouças-Spieker's reconstruction of events, *macrorhyncha* would have been present on the whole coast of São Paulo before the last post-glacial rise of the sea level, when the coast was "a continuous gently sloping plain, with disarticulated hills". With the rise of sea level, starting some 13,000 years B.P., part of the coast changed its topography, and in this area appeared *Mabuya caissara.*

This reconstruction has been made more probable by the recent discovery (Rebouças-Spieker, pers. comm.) of scattered specimens of *macrorhyncha* from Rio de Janeiro to Alhandra on the coast of Paraíba. The specimen from the latter locality was collected by one of us (P.E.V.) in a situation very similar to that of southern São Paulo, except for an abundance of cashew trees (*Anacardium* sp., Anacardiaceae).

The frog

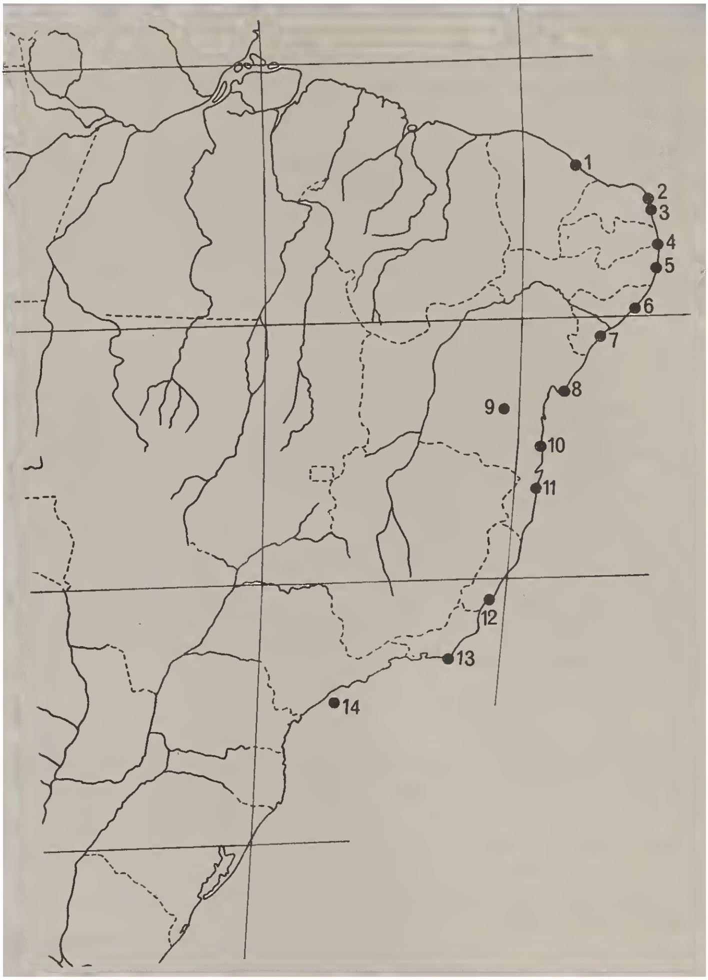
As to the hylid *Phyllodytes tuberculosus,* the genus is, so far as known, strictly bromelicolous (Bokermann, 1966, 1969). Of three Brasilian species two (*luteolus* and *acuminatus*) are known to occur exclusively on the coast; *tuberculosus,* on the contrary, had been so far recorded only from the type locality, Maracás, in one of the harshest caatingas (Vanzolini, 1972) of the state of Bahia. There is no doubt that, in spite of this extension to the interior, the distribution of the genus on the Brasilian coast belongs with those of the lizards mentioned — so much that the occurrence of one species in Trinidad (Bokermann, 1968) becomes intriguing. It is to be expected that other bromelicolous frogs will show the same type of distribution.

History

Tropidurus hygomi, Bogertia lutzae, Mabuya macrorhyncha and the species of *Phyllodytes* are thus linked to the extensive coastal beaches of Brasil. *Bogertia,* being a hemidactyloid gecko, might conceivably be an immigrant from Africa, but there is no direct evidence of that; there are, on the other hand, enough autochthonous South American hemydactyloids (Vanzolini, 1978) to ensure its treatment as a native.

"Entre Recife et Santos, le littoral oriental du Brésil frappe l'observateur par le contraste entre un énorme développement des formes d'accumulation sableuses, surtout au N de Rio de Janeiro, et la rareté des falaises et des formes d'abrasion. Les plaines marécageuses ourlées de magnifiques cordons littoraux de sable fin, se succèdent sur des dizaines et des dizaines de kilomètres, interrompues seulement çà et là par des collines rocheuses plus ou moins vigoureuses qui leur servent d'appui". (Tricart, 1959: 276).

This terse description, very true to life, brings out forcibly one fact: these lizards occupy, and very patchily, only a small fraction of an immense extent of apparently favorable and continuous environments. It is undoubtedly a relictual pattern. We know (Rebouças-



Map 2. Localities cited in the text. For coastal localities only the latitude is given. 1, Morro Branco, Ce (04°10'). 2, Maxaranguape, RN (05°30'). 3, Natal, RN (05°48'). 4, Alhandra, Pb (07°26'). 5, Recife, Pe (08°02'). 6, Pontal da Barra, Al (09°42'). 7. Carmópolis (10°40', 36°59'), Santo Amaro das Brotas (10°47', 37°04'), Maruím (10°44', 37°05'), Se. 8, Salvador, Ba (13°00). 9, Maracás, Ba (13°27', 40°26'). 10, Ilhéus, Ba (14°48'). 11, Porto Seguro, Ba (16°26'). 12, Guarapari, ES (20°40'). 13, Cabo Frio, RJ (22°50'). 14, Ilha da Queimada Grande, SP (24°29', 46°41').

-Spieker, 1974) that *M. macrorhyncha* existed in pre-Flandrian times, probably ca. 13,000 years BP. At this dry and cool time (CLIMAP Project Members, 1976; Ab'Saber, 1977) the sea-level being much lower, the coast line was to the east of its present position, had a gentler slope, less relief and a simpler compartmentalization. According to Tricart (1959), the rising seas of the Flandrian transgression reworked the latosols of the shelf, as they covered it, depositing the resulting fine sands (with minor contributions from other sources) on the new coast line. The present arrangement would have been completed (Tricart, 1959: 292) in the Dunkerquian. Tricart's scheme was published at a time when very little information and no dates existed on the evolution of the Brasilian coast line. Trying to bring it up to date we conclude that the final arrangement of the beaches was reached in Period VI of Hurt (1974), as elaborated upon by Fairbridge (1978), 2600-2200 yr BP. It is the period referred to in other contexts as Paranaguá Submergence, Abrolhos High, Limnaea Sea, and Early Subatlantic (Fairbridge, 1974, 1976). One could then say that a group of lizards and frogs had a peak in pre-Flandrian times, suffered severe restriction during the Flandrian transgression and were able to maintain a toehold on Dunkerquian beaches bearing some special types of vegetation. We find it impossible to say, on present evidence, whether they are recovering and re-expanding, or continuing a mediocre career.

Mode of speciation

If we accept, on the grounds of parsimony, that *T. hygomi* originated in the pre-Flandrian, we have a problem in explaining its mode of speciation. On the littoral as it is today, and with more reason on the simpler pre-Flandrian coast, it is not easy to imagine a new *Tropidurus* arising by geographical isolation; it is natural to consider other modes.

Speciation by means other than geographical isolation is not amenable to study by historical methods. One has to have recourse to genetical techniques, applied to crucial situations. At present, with regard to South America in general and to the inter-tropical segment of the east coast in particular, there is little to help in deciding which animals and places deserve investigation in depth. Judging from the surprises that even routine surveys such as the present one never fail to provide, a broad picture will take some time to assemble. However, certain scattered ecological data may help to define lines of research.

Vanzolini & Rebouças-Spieker (1976) have shown, for instance, that populations of *Mabuya caissara* on the coast of São Paulo, separated by a few tens of kilometers at most, may differ markedly in reproductive strategies, considered to be adaptive and under genetic control. In the Sergipe area surveyed we also collected the local representative of the *Tropidurus torquatus* complex. Our intention was simply to gather information on the most abundant lizard in the area, for future reference in monitoring environmental changes.

While busy with the sand restingas, we acquired *torquatus* at "lizard markets" in two localites ("Estiva" and "Aldeia", see Map 1), about 2 km apart, with no obvious ecological discontinuities in between. Before lumping the two samples we compared them statistically, as a matter of procedure, and to our great surprise found significant differences in maximum body length, relative tail length and incidence of mutilations.

The point we wish to make is that highly fragmented populations, with drastic restrictions to gene flow consequent upon deme structure and individual behavior rather than environmental features, are favorite candidates to speciation by means of radical chromosomal events. An especially attractive model, involving a *Sceloporus*, ecologically rather similar to *Tropidurus*, has been proposed by Hall (apud White, 1977, chapter 6). We are of course not in a position to propose this as a definite mechanism applicable to our type of geographical situation and historical process, but it seems the most potentially fruitful line of investigation.

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