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TWO SIBLING AND SYMPATRIC SPECIES OF *GYMNOPHTHALMUS* IN RORAIMA, BRASIL (SAURIA, TEIIDAE)

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Introduction

During an ongoing herpetological survey of the Brasilian state (until recently Federal Territory) of Roraima, one of us (C.M.C) noticed that two forms of Gymnophthalmus *seemed to be sympatric in the area, distinguishable by physiognomy and color pattern. Examination of the materials in the Museum collection, however, failed to reveal any clear-cut bimodality. Broad variation was noticed in the color of the ventral parts, but it was apparently continuous, and not associated with any pholidotic characters.*

It was later remarked by C.M.C. that one the forms he could distinguish in the field seemed to inhabit only open formations, while the other occurred in forest, regardless of the distribution of the two types of environment in the research area, the northeastern quarter of Roraima. To test this provoking possibility, collections were obtained at ecologically well characterized localities, and examined with this bias. The results of the examination disclose, as hereafter reported, besides the actual existence of two sibling species, a cluster of fascinating biological questions, to be addressed by various techniques and strategies, and demanding much additional collecting and research.

Literature

The genus *Gymnophthalmus* has a very broad distribution, from the Lesser Antilles and the Isthmus of Tehuantepec south through cis-Andean South America to northern Argentina, a span of some 45 degrees of latitude. It is not known from the Atlantic forests of Brasil, but is widespread in other Brasilian morphoclimatic domains. It has been reported from Chile, but we reject this record (v.i.).

Boulenger's (1885: 427) generic diagnosis continues to be valid: "Tongue moderately elongate, arrow-headed. Head with large regular shields: frontonasal separating the nasals; praefrontals present; no frontoparietals; nostril pierced in the middle of a single nasal. No eyelids. Ear exposed. Limbs well developed; inner finger absent. All the scales rounded-hexagonal, imbricate, smooth or feebly keeled, arranged quincuncially. No collar fold. Tail cylindrical. Males with, females without, femoral pores".

From the viewpoint of geographical distribution, as currently understood, three groups of forms may be discerned:

1. Insular forms: *G. lineatus* in the Dutch Leeward Islands; *G. pleii* (three subspecies) in Martinique and St. Lucia.

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2. Purely continental forms: *G. rubricauda*, from Bolivia and Mato Grosso do Sul (one specimen in MZUSP) to northern Argentina; *G. multiscutatus* in northeastern Brasil.

3. Forms occurring both on the continent and on islands: *G. speciosus* (three subspecies), from Central America, as far north as the isthmus of Tehuantepec, to Venezuela and also in Isla Margarita; *G. underwoodi*, in Barbados, Trinidad, Tobago, the Guianas and Brasilian Amazonia.

The latter species is our special concern, but there are so many minor mistakes and misapprehensions in the literature that we find it convenient to take a survey of the history of the systematic and zoogeographic concepts of the whole genus, emphasizing, of course, northeastern South America.

The first species of *Gymnophthalmus* to be known was described by Linné (1758: 209) in the tenth edition of the Systema Naturae, as *Lacerta lineata*. He mentions a type in the royal Swedish collection, a specimen still extant (Andersson, 1900: 16). A Seba plate is also mentioned in the original description, and from it the type locality "Zeilona" was taken. In the twelfth edition of the Systema, Linné (1766:371) changed the name to *Lacerta 4-lineata*, and this name, usually spelled "quadrilineata", being morphologically more suitable, prevailed until Andersson's (1900) review of Linnean types. Of course all authors were cognizant of *lineatus*, and both names were frequently cited side by side, often with equal weight, but the nomenclatural step was formally taken by Andersson.

Gmelin (1788: 1076) copied the twelfth edition of the Systema, but for no explicit reason changed the distribution to "America Septentrionali". Lacépède (1788: 492), without reference to actual specimens, promoted *Lacerta quadrilineata* to the status of a North American salamander. Bonnaterre (1789: 81), however, averred that *Salamandra Quadrilineata* was at the transition between salamanders and lizards. Daudin (1802: 266) reinstated the species among the lizards, in the genus *Scincus*, no doubt on account of the quincuncial arrangement of the body scales. Sonnini (in Sonnini and Latreille, 1802: 252; for date and authorship, see Vanzolini, 1977: 14) returned *Lacerta lineata* to the salamanders; for the first time the species was assigned, albeit without any supporting comments, to South America.

As this early point the history takes a sharp turn. The hazy and idiosyncratic systematic concepts so far put forward in the literature were replaced by much better work, as Merrem (1820: 74) erected the new genus *Gymnophthalmus*. His diagnosis is good and has interesting implications. It reads (italics in the original): "Palmae tetradactylae. Plantae pentadactylae. Truncus et Cauda squamosa. (Dentes *conici in maxillis*. Lingua *bifurca*. Palpebrae *nullae?*)".

Among these characters, the first four, hands with four and feet with five digits, head with scutes (as opposed to scales), body and tail scaly, had been previously mentioned in the literature, and are correct and apt. However, conical teeth on both jaws and a bifurcate tongue, heretofore unmentioned, clearly indicate autopsy. "No eyelids" also indicates direct examination; the attached question mark may be interpreted either as uncertainty about the actual condition, or as wonder about its novelty, or both. It is remarkable that exactly this character is behind the etymology of the generic name, "naked eye".

There is no clue in the Tentamen as to the specimen conceivably seen by Merrem. There is a conjecture by Cocteau (1836, v.i.) but, as will be discussed, this is better ignored.

Merrem placed *Gymnophthalmus* among his Squamata Gradientia, i.e., the lizards, between *Scincus* and *Seps*, thus squarely among the present Scincidae. This placement was to last until Boulenger (1885) put the genus in the family Teiidae.

Wied (1825: 198) cited *G. quadrilineatus* from the Atlantic forests of Brasil (Mucuri, on the coast of southern Bahia), but it was a misidentification of what was subsequently described by Reinhardt and Luetken (1861: 211) as *Gymnophthalmus maximiliani*. This species is the type of the genus *Micrablepharus* Boettger, 1885, type by original designation *Micrablepharus glaucurus* Boettger, 1885, a synonym of *maximiliani*.

Cocteau (1836) published a series of small monographs on scincids, as then understood. These are in a way excellent papers, with detailed reviews of the literature, careful descriptions and measurements, and accurate illustrations; specifically, the paper on *G. lineatus* (for which Cocteau proposed the new name *merremii*) is important for its treatment of the old Paris specimens. However, Cocteau was given to conjecture and digression, both frequently hazardous.

In his paper, a documented locality is for the first time proposed for *G. lineatus*: Martinique, Plée coll. These specimens, however, were later made the types of *G. pleii* Bocourt, 1881.

Cocteau (1836: 8) further surmised that Sebas's specimen cited by Linné in the Systema Naturae was preserved in the Paris collection. His reasons for the conjecture were two: (i) the bottle in which the specimen had been originally preserved ("avant les derniers rangements de la collection") bore labels similar to those of the collection of the Stathouder, "qui comme l'on sait, renfermait les originaux de Séba, et a passé en vertu de traités politiques au Muséum de Paris"; (ii) the specimen had a color ("brun marron") characteristic of reptiles in Dutch collections, due to a long sojourn in weak spirits.

It is well known (e.g. Boeseman, 1970; Pieters, 1980) that, in the plunder of Amsterdam by the French in 1795 (Cocteau's "Traités politiques", analogous to those that took to Paris the Brasilian materials preserved in Lisbon and seized by Junot) a large part, but not all of the collection of Stadholder William V of Orange was taken to Paris. It is also certain that part of Seba's collection (a little less than 10 per cent, according to data in Boeseman, 1970) had been purchased at auction by A. Vosmaer, curator of the Stadholder's cabinet, and eventually found its way into the latter. This, however, hardly justifies the sweeping assertion that Williams's collection "renfermait les originaux" of Seba. It is common knowledge (11.cc.; also Strauch, 1889; O. Thomas, 1892) that most of Seba's collection ended in St. Petersburg, now Leningrad, purchased by Peter the Great.

We are indebted to Dr. Ilya Darevsky, of the Zoological Institute, Academy of Sciences at Leningrad, for information on the matter. Until World War II, when they were destroyed, there were at the Academy two specimens of *Gymnophthalmus* from the Seba collection, neither one with locality data besides "Amer. mer.".

The point in itself has very little importance: a type exists, and Seba's specimen, with an obviously spurious locality, is irrelevant both to the systematics and to the distribution of the species. The matter, however, came to acquire some relevance: it was later (Bocourt, 1881, q.v.) used to associate the species with Brasil. As a matter of fact, the association began with this same Cocteau paper, which contains a lengthy digression on what could have been the "Americima" of Marcgrav (1648), which is actually unidentifiable, even today, by ourselves Brasilians.

Finally, Cocteau (1836: 10) proposed that Wied's Bahia specimen would have "à ce qu'il parait, servi de type aux notes de Merrem." If this were true, *Gymnophthalmus* would be a genus based on an erroneously identified species, with all the dreary attending nomenclatural consequences (Article 70 (b) of the Rules). We think this conjecture, for which no evidence was presented, is better left alone.

Duméril and Bibron (1839: 820) described, under the name *G. quadrilineatus*, the already mentioned specimens of what is now *G.p. pleii*. They state: "Patrie. Cette espèce se trouve au Brésil et à la Martinique, nous possédons des individus provenant de ces deux pays". The Brasilian specimens were not, however, specified, either in the Erpétologie Générale or in the subsequent catalog of the Paris Museum reptiles (Duméril and Duméril, 1851: 191). In the latter they cite only Antillean specimens (Martinique: Plée; St. Lucie: Bonnecour), and none from the mainland, much less from Brasil. The Seba specimen is not mentioned, either.

We consulted Paris on the matter, and Prof. Edouard Brygoo was kind enough to put the matter to rest. By 1839 there were in the Muséum National four examples of *Gymnophthalmus*: nº 3093, the Seba specimen, recorded as from Brasil, ns. 1409 (2 exs.) and 3094, the Martinique lizards collected by Plée. Between 1839 and 1851 was added to the collection the Ste. Lucie specimen (nº5614) from Bonnecour.

Four specimens identified as *G: quadrilineatus* were reported from Caracas by Lichtenstein (1856: 20); this is the first documented reference to specimens from the continent. However, Caracas was at the time a noted "shipping locality", one from which dealers mailed specimens, not individually labelled, gathered from a wide area. Thanks to the kindness of Dr. Rainer Günther, Museum für Naturkunde, Berlin, we were able to see these specimens. The collector is said to be "Moritz". The specimens should, according to current litterature, be assigned to *G. speciosus* (Hallowell, 1861), the next species to be described. Our examination, however (see below) has disclosed some complicating features.

Blepharactisis speciosa Hallowell, 1861, g.n., sp.n., has type locality "Nicaragua" (no further data), and was collected by the North Pacific Exploring Expedition (thus on the west slope). Its distribution as now understood extends southeastward through Colombia into the llanos of Venezuela; we'll discuss below our reasons to question this.

Reinhardt and Luetken (1861: 226) described *Gymnophthalmus nitidus*, from the Danish West Indies, now U.S. Virgin Islands. The species was put by Boulenger (1885: 427) in the synonymy of *G. quadrilineatus*, which was never disputed. Curiously enough, it has never since been reported from the Lesser Antilles (e.g. Maclean, Kellner and Dennis, 1977; Schwartz and Henderson, 1988). Dr. Jens B. Rasmussen, of the Copenhagen Museum, has kindly informed us that the two specimens described by Reinhardt and Luetken were sent to the Museum by a man known to have lived in Saint Thomas, but that there is no other evidence that the specimens actually came from there. Albert Schwartz (in litt.) agrees with us that the types were not from the Virgin Islands.

There follow two additional Central American forms. Cope (1871: 557) described *Tretioscincus laevicauda*, from "Occidental Department, Nicaragua", J.A.MacNeil coll. Barbour and Loveridge (1929:351) cite three cotypes in the Museum of Comparative Zoology, collected by MacNeil at Polvón, Nicaragua, which can be thus taken as the type locality. This form is now considered a strict synonym of *speciosus*.

Epaphelus sumichrastii, g.n., sp.n., described by Cope (1876:115) has not an explicit type locality. Stuart (1939:6), however, cites a personal communication from E.R. Dunn, to the end that the cotypes, in the U.S. National Museum, were labelled "near Ventose Bay, Sumichrast". This is certainly Bahia Ventosa (16°11'N, 95°08'W), in Oaxaca. The form is considered at present a subspecies of *speciosus* (Peters & Donoso Barros, 1970: 138).

Bocourt (1881: 466) was the first to attempt a review of the ensemble. His treatment is important in several respects. The basic systematic framework has been added to, but not fundamentally altered. The two forms he described (*pleii* and *luetkeni*) are currently valid. He was apparently the first to notice femoral pores as a secondary sex character in the genus. However, in what refers to the distribution in mainland South America, his notions have caused a good measure of confusion. He says about *G. quadrilineatus* (1881: 469): "Trois individus nous ont servi à faire cette description. Le premier est originaire du Brésil et provient, d'après Cocteau, du Cabinet de Séba. ... Les deux autres exemplaires on été acquis comme provenant du continent américain, sans indication précise de localité. ... D'après les divers auteurs que nous avons cités dans notre synonymie, il résulte que l'on peut considérer le *Lacerta quadrilineata* de Linné comme originaire du Brésil."

This is a most extraordinary and fully gratuitous reasoning. It has already been shown that no explicitly Brasilian specimens had been previously mentioned as kept in the Paris collection. The matter hangs on the Seba specimen, that, between 1734 and 1839, somehow changed its allegiance from Ceylon to Brasil, without explanation.

Of the "divers auteurs" whose authority would support Bocourt's assertion, not one actually does so. Marcgrav (1648) described an unidentifiable "Americima", which Cocteau (l.c.) discussed inconclusively. Ray (1693) did no more than transcribe Marcgrav. Seba (1734), as seen, attributed the lizard to Ceylon. With regard to the nineteenth century authors, Daudin, Merrem, Wied (1825) and Cocteau have already been discussed. Wagler (1830: 157) simply copied Merrem. Gravenhorst (1851: 354. p.36) mentions five specimens, originally in the Lampe collection, then in Breslau, but cites no localities. Wied (1824; actually 1829, see Vanzolini, 1977: 30) shows a figure of his Bahia specimen, that belongs to *Micrablepharus*, not to *Gymnophthalmus*.

Boulenger (1885: 427 *seq.*), in the second volume of the British Museum Catalogue, kept close to Bocourt's scheme. He accepted four species: (i) *quadrilineatus*, of which he saw four no locality specimens; (ii) *sumichrasti*, of which he had specimens from Guatemala (received from Bocourt) and from Venezuela (no further data); (iii-iv) the insular forms *pleii* and *luetkenii*, not seen. He maintained *laevicauda* (also not seen) as a valid species of *Tretioscincus*.

Van Lidth de Jeude (1887: 133) firmly established the occurrence (and abundance) of *G. quadrilineatus* in Curaçao. This was confirmed and reinforced by several succeeding authors, so there is no further need, in the present context, to consider the literature on this species. Cope (1887: 46) synonymized *sumichrastii* and *laevicaudus*, and maintained Hallowell's genus *Blepharactisis*. Boettger (1893: 76) reported *G. Sumichrastii* from Caracas: the specimen, however, was apparently bought (marked "Gek." in the Senckenberg catalog) from dealers; the record is not above suspicion (see below, however). Boulenger (1902: 337) described the very distinctive *G. rubricauda* from Cruz del Eje, in Córdoba, Argentina.

In the sequence, data began to accumulate on the distribution of the genus in northern South America. Ruthven (1922: 64), in his classic Santa Marta paper, cited *G. sumichrastii* from several localities on the Caribbean slope of Colombia. His description of the animal does not quite agree with Boulenger's, which is understandable, since Ruthven presumably had *speciosus*. Nicéforo-Maria (1930: 103), in his list of the reptiles of Honda, cited *G. sumichrastii*, and commented on the coloration of the tail (pink) in formalin.

Burt and Burt (1930: 33) identified as *G. laevicaudus* one specimen from San Juan de los Morros, Aragua, Venezuela, preserved in the U.S.National Museum. In their ensuing review of the South American lizards in the American Museum of Natural History (Burt and Burt, 1931:339) they recorded *G. laevicaudus* from Santa Rosa de Osa (= Osos) in Colombia, and from Tofo, (= El Tofo, in Coquimbo) Chile. The latter is a zoogeographic aberration that has been calmly accepted and uncritically reiterated by many authors (exceptions are Taylor, 1956 and Peters, 1967) but never confirmed by additional specimens from this well explored area of Central Chile.

In their next paper Burt and Burt (1931:339) summarize, as an adjunct to a key to the species of *Gymnophthalmus*, their understanding of the distributions. In the case of the continental forms this would be: (i) *rubricaudus*, northern Argentina and Bolivia; (ii) *laevicaudus* (including *sumichrastii*), western America from Central Chile, northward to southern Mexico; (iii) *lineatus*, Brasil, northeastern South America and the Dutch Leeward Islands. This scheme was repeated in Burt and Burt's (1933) checklist of the lizards of South America and, in spite of its lack of foundation, became received wisdom.

We have already seen that there was thus far no uncontrovertible, or even plausible, evidence of any species of *Gymnophthalmus* occurring in Brasil, in fact anywhere east of Caracas. Otherwise, the idea of a westernmost species extending from Chile to Mexico may have looked plausible on a map, but it rested on the evidence of a single Chilean specimen, disjunct from its nearest neighbor by some 35 degrees of latitude, a pattern with no known parallel.

The supposed bipolar pattern, one western and one eastern forms, further led the Burts (1931: 341) to think it probable that *G.laevicaudus* would turn out to be a subspecies of *lineatus*: "Therefore, in consideration of the fact that their respective types of coloration are found to approach each other very closely in at least the intermediate region of northern South America, it seems very probable that *laevicaudus* will ultimately be regarded as at least a subspecies of the previously described *lineatus*". The remark about the approach between color patterns can only be understood as pointing to the Santa Rosa de Osos specimen, described as having a faint dorso-lateral streak on each side. Santa Rosa (06°39'N, 75°3'W) on the Cordillera Central of Colombia, can hardly be said to be in an intermediate geographical position.

In reality, the distributional data then available were not sufficient even to demonstrate that an eastern and a western forms existed, much less to support or suggest any hypotheses about their geographic differentiation. Additionally, Burt and Burt (1931:339) found no sharp diagnostic differences between the two forms, which they (couplet 4 of the key) contrasted, if the term can be applied, as follows: *laevicaudus*, back and sides without light lines, or with only a faint dorso-lateral streak on each side; *lineatus*, back and sides lined, at least a faint pair of lateral light stripes on each side.

This rather detailed examination of Burt & Burt (1931) is made necessary by the influence it had on subsequent work, and chiefly on the next paper, the first specifically concerned with our area. Parker (1935: 518), in his summary of the herpetology of Guyana (then British), had at hand eight specimens, seven from Georgetown and one from the Mazaruni. These specimens were identified as *G. laevicaudus*, based on "Burt, 1931a, p. 339." This is a misquotation. In Parker's References Burt 1931a is Bull. U. S. Nat. Mus. cliv, pp. 1-286, the revision of *Cnemidophorus*. Reference should have been made to Burt and Burt, 1931, Bull. Amer. Mus. Nat. Hist. 1xi, pp. 227-295. Parker remarked that the discovery, "in the center of the supposed range of *lineatus*" of specimens of *laevicaudus*, which, if it were a subspecies of the former, should not occur east of Santa Rosa de Osos, necessitated a reconsideration of the concept of two geographical races: either there was a single dichromatic species or there were two species, distinguished only by colour, with overlapping geographic ranges.

Parker found "no evidence pointing to either of these possibilities as being the more likely...". One sees that, even after Van Lidth de Jeude (1.c.) and subsequent authors, linking *lineatus* to Curaçao and later to Bonaire (e.g. Werner, 1925), the myth of Brasilian *lineatus* persisted. It is also of interest that Parker did not compare his Guyanan specimens with Central American ones, but based the identification solely on "recent descriptions (Burt, 1931a, p.339)." The misquotation of the Burt's work has already been noted; the description referred to is actually a key, involving all of three characters.

This conjecture of Parker was several times repeated in the literature. It was not noticed that it was a hybrid concept: on one side, specimens actually seen, on the other a scheme uncritically adopted from the literature.

Meantime Amaral (1933: 73) had described, from northeastern Brasil, the very distinctive *G. multiscutatus*, later shown to be widely distributed in the caatingas (Vanzolini, Ramos-Costa and Vitt, 1980).

It will have been noticed that the Central American forms, *speciosus*, *laevicaudus* and *sumichrastii*, had not been so far discussed with base on specimens. Stuart (1939), on the occasion of describing a new species from Guatemala (*birdi*, now a subspecies of *speciosus*), reviewed the whole genus. It became an influential paper, but it is actually full of problems.

Stuart accepted without question the then current distributional scheme. Having seen specimens, he seems, however, to have paid scant attention to the literature. He states, for instance, about *G. merremii*, that "Cocteau recognized it as synonymous with *G. quadrilineatus* of Linnaeus." Cocteau in fact expressly proposed a *nomen novum*, because he believed (partly on account of Wied's specimen, which, it has been repeatedly mentioned, is a *Micrablepharus*) that the pattern of four light stripes was not constant, and did not justify the epithet "four-lined". Stuart also criticized, and rather sharply, the Burts, for having synonymized *laevicaudus* (=*speciosus*) and *sumichrastii*. This they did not do; Cope did (1887), the author of both species. Stuart (1939: 5) relied on a diagnostic character: *speciosus* always (with the exception of one side of the head in one of the types) would have five supralabials to the level of posterior margin of the eye, against four in *sumichrastii*.

Schmidt & Inger (1951: 453) recorded *G. quadrilineatus* from Baixa Verde (now João Câmara), Rio Grande do Norte, Brasil. Dr. J. Vindum (California Academy of Sciences) was kind enough to check the identification; it is, as it should be, *multiscutatus*.

Mertens (1952: 56) reported on two Central American specimens from El Salvador, with comments on the head scutellation. Due to one specimen having 4/5 supralabials, he reduced *birdi* to the subspecific level. Taylor (1956: 227), in his review of the lizards of Costa Rica, on the basis of three specimens, presented a very good description of *speciosus*, the first and only full one to be had. He commented on the suspect Chilean record.

The next significant paper is the description of *Gymnophthalmus underwoodi* by Grant (1958: 227). He mentions the color pattern of 24 specimens of *speciosus* from Panamá, and describes *underwoodi*, based on a sample of 14 examples from Barbados. The following characters are mentioned: (i) no femoral pores, suggesting the sample to be composed of females only (the possibility of parthenogenesis was not then raised); (ii) a larger ventral scale count (from the central interbrachial to the vent) in *speciosus* with means of 28.1 in 6 males and 32.1 in 8 females, against 23.9 in *underwoodi*; (iii) ditto dorsals, from parietals to rear of thighs, respectively 37 and 38 against 32; (iv) possibly, the presence of a larger number of keeled distal caudals in *underwoodi*. (Keeled caudals mean a regenerated tail).

Underwood (1962: 93, 178), in his paper on the reptiles of the Eastern Caribbean, refers, without comment, *G. underwoodi* from Barbados, Trinidad and, "perhaps", British Guiana. Richard Thomas (1965), in a review of Lesser Antillean *Gymnophthalmus*, with the description of a new subspecies, gives much information on mainland specimens, although he (justifiedly, we think) felt unsure enough about identifications to mention "presumed *speciosus*" from Colombia, and to write "*speciosus*" always within quotation marks.

Hoogmoed (1973: 273), in his monograph of the lizards of Surinam, formally identified the lizard occurring in the country as *G. underwoodi*, and presented a detailed description, with illustrations and summary differential diagnoses from *lineatus* and *speciosus*. This placed the taxonomy of the group on a firm footing. The distribution, however, was still insufficiently documented. Before Hoogmoed's monograph, a handful of *speciosus* records had been published:

Test, Sexton and Heatwole (1966), Donoso-Barros (1968), and the Sociedad de Ciencias Naturales La Salle (1970, under the name *lineatus* with doubt), for Venezuela; Medem (1969) for Colombia. After Hoogmoed there was a slow but steady sedimentation of more or less reliable distributional and ecological data on both *underwoodi* and *speciosus.*

Gasc (1975: 674; 1976: 29; 1981: 314) and Gasc and Lescure (1981: 33) reported localities and habitats of *underwoodi* in French Guiana. Vanzolini (1976: 177) extended the known distribution of the species to northern Roraima, to the middle Rio Negro in the state of Amazonas and to the right bank of the Amazon in Pará. Cunha (1981: 17) also reported on specimens from Roraima. Staton and Dixon (1977: 19) recorded *speciosus* from definite localites in the llanos of Venezuela, with notes on habitat preferences. Finally, Ayala (1986: 571) published a state list of Colombian examples of *speciosus* preserved in museums, with mention of the respective collections.

Parthenogenesis. Thomas (1965: 146) dissected over sixty specimens of *underwoodi*, all of which lacked femoral pores, and found that all specimens large enough for the gonads to be diagnosed were females. Since then it has been generally accepted that the species is parthenogenetic. However, given the relative rarity of the lizard, not much work has been done on this subject. Vanzolini (1976) chanced to find some specimens from Roraima with well developed, functional pores; careful examination of the materials in the São Paulo collection revealed less obvious but undeniable pores in specimens from northern Surinam. It was his guess that parthenogenesis in *underwoodi* had not followed inter-specific hybridization, but was due to some other mechanism. Cole, Dessauer and Townsend (1983), in a study involving 21 loci of lizards from Surinam and Trinidad, concluded, on the contrary, in favor of hybridization, since, in spite of a diploid karyotype, they considered the amount of heterozygosity detected by electrophoresis to be excessively high. At the time they suggested no parents for the hybrid.

When we started this work, then, four species were known from mainland South America: *underwoodi*, usually parthenogenetic but locally bisexual, occurring in Barbados, Trinidad, the Guianas, Roraima and Brasilian Amazonia east of 65°W; *speciosus,* in Colombia and Venezuela; *rubricauda*, from Bolivia to northern Argentina; *multiscutatus*, in northeastern Brasil. The latter three forms were known only from open formations; *underwoodi* had been collected both in open formations and in forest.

THE GEOGRAPHIC AND ECOLOGICAL SETTING

Relief and vegetation

Roraima, formerly a part of the state of Amazonas, then separated from it as the Territory of Rio Branco (from the name of the major river and in those days the only access), next renamed the Territory of Roraima, and now a full state, is the northernmost one of Brasil, extending from 01°24'S to 05°16'N and from 58°50' to 64°38'W. It is bounded to the north and west (Venezuela) and to the east (Guyana) by old mountains that may in places surpass 2,000m, but are generally lower, 600-1,000m high, and are always much dissected. Otherwise the relief is moderate, with residual ridges, mesas and inselbergs rising over extensively planed surfaces. Over 94% of the state's area is below 600m above mean sea level (m.s.l.); less than 1% is above 900m (Guerra, 1957: 8).

A fair amount of information is available on the environment in Roraima and the areas in direct continuity; it has been recently compiled, with new research, by Projeto Radambrasil (1975). From the zoological viewpoint, the most important ecological feature of Roraima is the interplay, at present and in past climates, of open and forested formations.

Of the state's 230,660 sq km, 85% are covered by forests of various descriptions. In the south, on the floodplains of the great rivers Branco and Negro and of some of their larger tributaries, stands the only area of Roraima where deposition exceeds denudation, about 50,000 sq km of varzea (seasonally flooded) forest. Otherwise it is all terra firme (never flooded). The varzea forests are a continuation of the general Amazonian hylaea; they are not of concern to this paper. The terra firme forest is largely continuous with that of the low plateau that reaches south almost to Manaus (Braga, 1979). The forest shows, in response to topography and lithology, several regional facies, differing in such aspects as the height and closeness of the canopy, conspicuousness of palms, vines and bamboos, etc. (Projeto Radambrasil, 1975). It should also be remembered that in all terra firme areas, even in incised river valleys, there is always some amount of varzea, however small and disjoined (disarticulated). We shall touch again on these points when discussing the individual collecting localities.

The northeastern corner of the state is covered with open formations, totalling approximately 35,000 sq km in area (Fig. 1). These were known of old as "Campos de São Marcos", from a famous government cattle ranch. In time they became, and still are, widely known in Brasil as "Campos do Rio Branco". In the international literature the most popular name is the "Rio Branco-Rupununi savannahs", given by Myers (1936). We do not adopt the designation "savanna" for reasons to be explained; whenever the term is used it is as a literal citation.

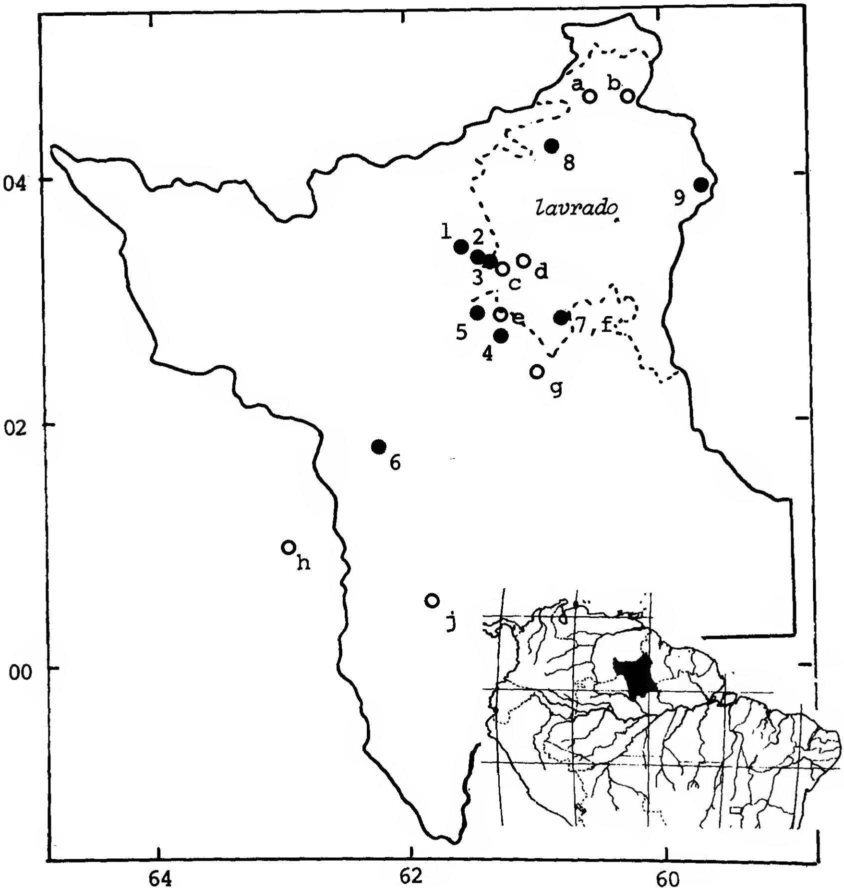


Fig. 1. Collecting localities: 1, Ilha de Maracá. 2, Fazenda Salvamento. 3, Maloca Mangueira. 4, Apiaú. 5, Cachoeira do Paredão. 6, Cachoeira do Cujubim. 7, Boa Vista. 8, Surumu. 9, Normandia.

Meteorological stations: a, Bandeira Branca. b, Uailan. c, Boqueirão. d, Taiano. e, Fazenda Fé e Esperança. f, Boa Vista. g, Serra da Prata. h, Barcelos. j, Santa Maria do Boiaçu.

In contrast to the forests, which in Roraima are found in every sort of geomorphic situation, the campos are restricted to the northern half of one of the major Roraiman morphostructural units, the "Rio Branco-Rio Negro Pediplain" (Projeto Radambrasil, 1975: 159). Due to their extent and individuality, these campos are an extremely important ecological unit, as we hope will become apparent in what follows.

The pediplain (Fig. 2) occupies in all some 196,000 sq km, about 75% of Roraima. The part lying north of 02°N, the area of the campos proper, is the result of the very recent, probably Pleistocene or even later (1.c.: 176), planing of the loose clayey and sandy conglomerates of the Pliocene Boa Vista Formation. Other sub-units of the same morphostructural unit are the result of the planing of other geological formations, Pre Cambrian and Tertiary.

The topographical surface of the campos is relatively flat (80-160 m); it is in the initial stages of dissection by the drainage (Fig 3). The resulting low hills are called "tesos", a general old Portuguese term for such features. The landscape is studded with small granitic, gneissic, and migmatitic inselbergs. There are several larger, more complex denudation features generally known as "serras".

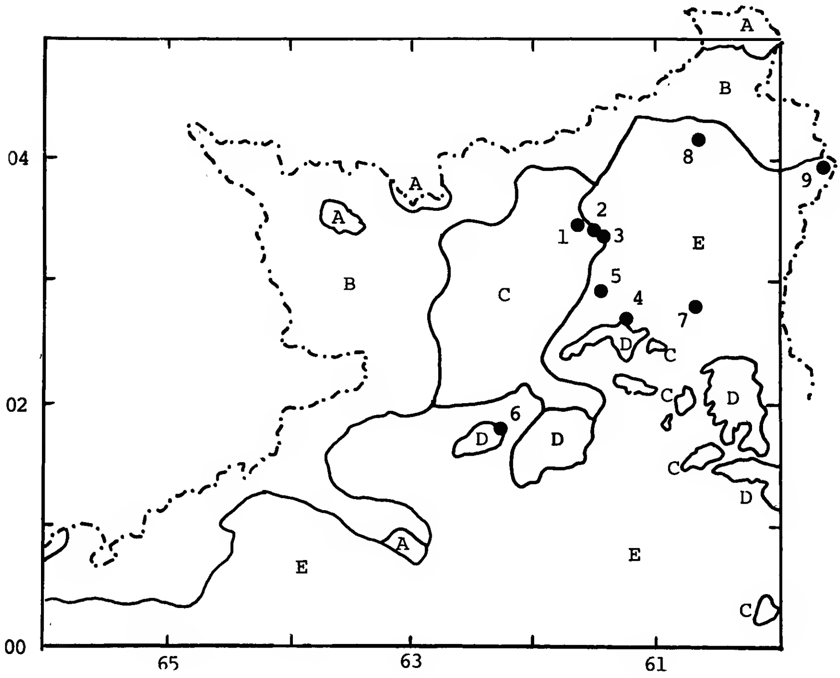


Fig. 2. Morphostructural units of Roraima (adapted from Projeto Radambrasil, 1975): A, Roraima Sedimentary Plateau. B, Plateau of the Amazonas-Orinoco Divide. C, Northern Amazonian Dissected Plateau. D, Residual Plateaus of Roraima. E, Rio Branco-Rio Negro Pediplain.

Localities: 1, Ilha de Maracá. 2, Fazenda Salvamento. 3, Maloca Mangueira. 4, Apiaú. 5, Cachoeira do Paredão. 6, Cachoeira do Cujubim. 7, Boa Vista. 8, Surumu. 9, Normandia.

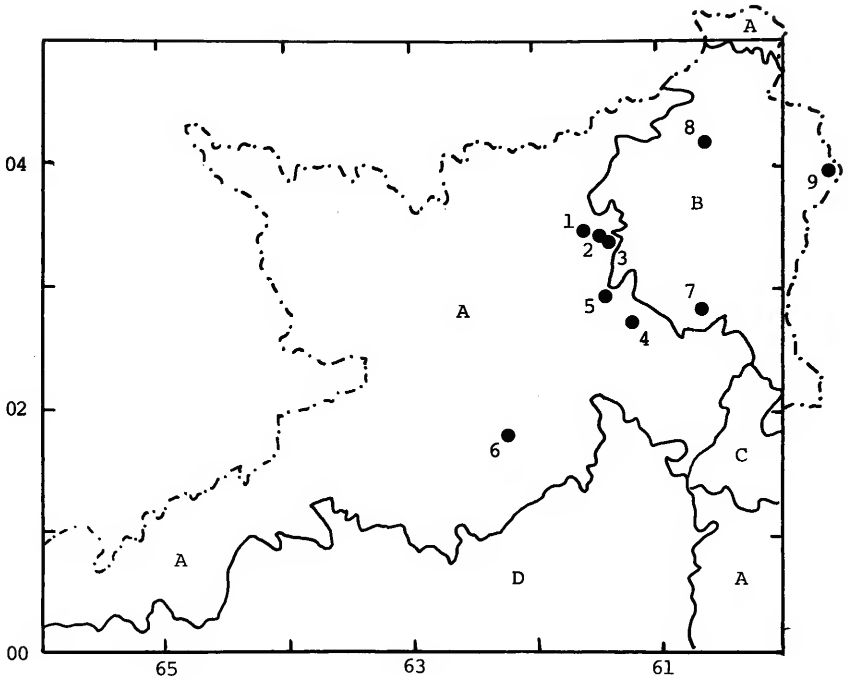


Fig. 3. Morphoclimatic units of Roraima (adapted from Projeto Radambrasil, 1975): A, Dissected plateaus and pediplaned surfaces. B, Erosive levels and pediplaned surfaces. C, Transition belt on residual plateaus. D, Transition belt in areas subject to annual floods.

Localities: 1, Ilha de Maracá. 2, Fazenda Salvamento. 3, Maloca Mangueira. 4, Apiaú. 5, Cachoeira do Paredão. 6, Cachoeira do Cujubim. 7, Boa Vista. 8, Surumu. 9, Normandia.

The drainage is characteristically dendritic. The creeks flow, from the source in small swamps at mid slope, between ranks of Mauritia palms, well known for liking to keep their feet wet. This is called, everywhere in Brasil, a "vereda". As one proceeds downstream, other kinds of trees join the palms on the levees, and progressively the vereda becomes a gallery forest.

Structurally, the campos are open formations, having at their fullest three strata of vegetation, grassy, shrubby and arboreal, which is why they are referred to as savannas. The ground stratum is composed of grasses and sedges, in varying proportions; there may be globose cacti. The middle stratum is composed of erect or recumbent shrubs, dispersed. The upper stratum is composed of low trees, usually very dispersed but locally clumped. The arboreal stratum may be so rarefied as to be practically absent; otherwise, the trees may be clumped in round groves, called "capões". Columnar and branching cacti (*Cereus*) are present with varying density.

The physiognomical resemblance of the Roraima campos to Central Brasilian cerrados is striking and has been noticed since the beginning of the European occupation, in the seventeenth century. This is why the name "campos" has been unvaryingly and unambiguously given to them, campos being the Portuguese generic term for open formations, with modifiers added for sharper definition: "limpo", open; "fechado", "cerrado", "coberto", closed. The similarity, which goes beyond physiognomy, and includes floristics, has been a long-standing preoccupation of botanists, and, recently, of zoologists. It is in fact an intrinsic part of our discourse, and we think it pertinent to review some high points of the evolution of these concepts.

Huber (1900) was the first professional botanist (and a first rate one) to publish a survey of Amazonian campos and to attempt an explanation of their genesis. Working from Belém, he had personal acquaintance with the Lower Amazon and with the large islands at the mouth of the river, as well as with the "Guyane brésilienne", i.e., Amapá. His genetic hypothesis was, to modern eyes, somewhat eccentric: the campos would occupy former large river and lake beds. His work, however, is very valuable in that he compared objectively, as analogous, the "campos cobertos" of the Lower Amazon and the cerrados of Central Brasil, and compiled a very pertinent annotated list of woody plants. He went as far as to extend his flúvio-lacustrine hypothesis to the core area of the cerrados.

Ducke (1913), in a review of several years' field work in the Lower Amazon, described, among much material on other types of open formations, the flora of some "campos firmes" (above seasonal flood level, as opposed to "campos de varzea") and, curiously enough, called attention to the presence of rattlesnakes, as a zoogeographic link with Central Brasil.

Oliveira (1929: 13), one of the geologists of the old school whose work characteristically contained a wealth of ecological information, gives a good description of the campos of the Rio Branco and speculates that, being poorer in number of species, they should be younger than their Central Brasilian counterparts.

Bouillenne (1930) is frequently cited on the subject of Amazonian campos. His work is valuable for the lists of plants of the areas he visited (Santarém and Monte Alegre). Otherwise, it is full of misinformation: e.g., he has the sources of the Tapajós in the caatingas; he writes "Herbert et Smidt" for H.H. Smith; etc.

Myers (1936) published and excellent physiographic, phytophysiognomic and floristic characterization of the campos of the Rio Branco and their continuation in Guyana. His viewpoint was mainly that of human exploitation; he did not attempt to correlate the area to other open formations. He was firmly convinced that these campos were a climax vegetation determined by fire.

Ducke and Black (1953: 10), in what remains a fundamental paper on Amazonian plant geography, based on unexcelled field experience and sound systematics, refer to the campos as a natural category: "The true "natural" campos are grasslands inhabited by a flora foreign to the hylaea, of species widely distributed over the continent or belonging to the "cerrado" of Minas Gerais, Mato Grosso, etc." They, however (l.c: 21), did not consider the campos as proper cerrados, but only as analogous to them: "shrubland or more or less open "campos" resembling the "cerrados" of Central Brazil."

Beard (1953) undertook a broad review of "the savana vegetation of northern tropical America", including Central America, the West Indies, the llanos, the Guianas and the Rio Branco, and the Amazon basin. Of course, the quality of the information and the level of personal acquaintance vary widely from case to case. He proposed a classification of savanna types and a theory of savanna origin. Nowadays this work has historical value only, as the information available at the time was clearly insufficient; for example, Beard's only cited source on the cerrados was Waibel's (1948) notoriously superficial paper.

Braun and Ramos (1959), in a study, mostly agrogeological, of a series of small enclaves of campos between the rivers Purus and Madeira at about the latitude of 07°30'S, emphasized the cerrado analogies, especially with regard to soils. The importance of hard pans (lateritic crusts) was also stressed; this has turned out to be a matter of great relevance to paleoclimatology.

Lima (1959) collected intensively in the Monte Alegre area, which had previously been worked by the Museu Goeldi botanists. He sums up his impressions as follows (our translation from the Portuguese): "The vegetation of this plateau is of the savanna type, characterized by thin herbaceous cover, with scattered small, contorted trees, many species having thick bark and leathery leaves. It appears identical, in physiognomy and species composition, to the campos cerrados of Central Brasil and to the "tesos" of Marajó".

Egler (1960) published on a highly interesting enclave in the middle valley of the Rio Trombetas, the "campos do Ariramba" (01°10'S, 59°55'W), which had also already been visited by Museu Goeldi botanists. It is a fairly detailed work; some of the conclusions are of great interest (translation):

"The most important fact found in these campos is, however, the occurrence of floristic elements typical of the flora of the campos cerrados, although represented by a small number of species and individuals. *Curatella americana* L., "lixeira" or "caimbé", one of the most regularly occurring species of the campos cerrados, is found as isolated individuals. *Salvertia convalliodora* is also found, although less frequently. Some *Qualea* were found, but in the sterile phase, except for some *Q. grandiflora*, which bore the first flowers. Trees and shrubs with suberous bark and leathery leaves, similar to those typical of campos cerrados".

"The occurrence of such species does not mean that these dry grasslands must be considered as degraded campos cerrados; it only permits one to accept the hypothesis that they may have had, in former times, direct connections with the great open areas south or north of the Amazon". This seems to us an eminently sensible opinion. We have extremely interesting materials from the area.

A similar position to Egler's was held by Pires & Rodrigues (1964: 243), on the "campos de terra firme" in general (translation): "These campos are also characterized by a large number of endemisms, which vary from region to region, besides a fair number of elements from the cerrados of Central Brasil...".

Takeuchi (1960) published a study of the Rio Branco campos at two localities (in reality, two transects). He describes two facies, "campo limpo" and "campo cerrado", with lists of species and life forms and a brief mention of differences from the Central Brasilian cerrados, his information on the latter being derived from works of a broad, unspecialized description. Goodland (1966) published a comparison between the savannas of the Rupununi and those of Calabozo (llanos of Venezuela, Estado Guárico), with no new data.

The review in Projeto Radambrasil (1975: 329) stresses the essential uniformity of the open formations appearing as enclaves in the forests above the Equator; the Amapá and Tirió (on the Surinam border) savanas would show the closest relationships with the core area. To explain the general distribution of these enclaves, they hypothesize that savanna trees are ecotypes of forest forms adapted to less favorable conditions.

Eiten (1977), in an attempt to formally define the cerrados, made a survey of the formations outside Central Brasil, among them "campos e savanas amazônicas". He lists seven types of intra-Amazonian open formations that had already been or might have been considered as cerrados. The Rio Branco and Rupununi campos are included in his group 7 (translation):

"7) Dry campos ("campos firmes") never flooded and never saturated on account of poor drainage or emergence of ground water. Woody plants are either lacking or form an open or sparse covering of low trees and shrubs. These campos occur wherever there is a moderate dry season and rainfall may reach a yearly average of 1500mm."

Among three sub-types in this category, the Rio Branco-Rupununi would belong in the most widespread one, occurring "over blocks or pebbles of laterite or quartz mixed with a fine soil". Besides our area, this subtype includes open formations in Amapá, in southwestern Amazonia (Puciari-Humaitá, see above Braun and Ramos), in the Monte Alegre area, and in "thousands of small areas scattered over interfluvia all over Amazonia".

Eiten (l.c.: 131) believes that there might be cause enough to consider the dry campos of his group 7 as cerrados. However, he ponders the danger that this would entail an unwholesome broadening of the concept, encompassing so much gradual variation that it would become impossible to draw diagnostic lines. His final conclusion is that the information then available was insufficient to establish criteria firmly linking the Amazonian campos with the Central Brasilian cerrados, and that, with the exception of the southwestern campos of the Puciari-Humaitá, it would not be advisable to classify as cerrados any of the Amazonian open formations.

The botanical works mentioned do of course emphasize physiognomic and floristic resemblaces. There are two other aspects, however, first stressed by Ab'Saber (e.g., 1977), that are of prime interest, so much so that he uses them in the very definition of the morphoclimaic domain of the cerrados. Gallery forests, beginning as Mauritia palm veredas, are an essential element of the concept of the domain. The Rio Branco gallery forests are so similar to those of the core area that it is impossible to tell them apart in photographs.

The dendritic drainage is another essential element of the diagnosis of the domain of the cerrados. In Roraima it is possible to map the campos with precision in aerial photographs or radar images by means of the drainage, the dendritic pattern being further set off in the latter images by thin light lines along the creeks, disclosing the presence of Mauritia (Projeto Radambrasil, 1975: 159).

In our opinion, the similarities between core area cerrados and northern campos is extremely important, especially when considered from the historical viewpoint, i.e., of changes in distribution patterns linked to paleoclimates. It would be wrong, however, to underrate the differences. There are, as we see it, three major ones.

Firstly, the ground cover. Sedges are cited the literature as components of the lower stratum of the cerrados, but they are never very conspicuous, the grasses always predominating. On the contrary, in all Amazonian campos of which we have experience, Cyperaceae, particularly species of *Bulbostylis*, are very common and frequently preponderant. Among the grasses, there is also much overlap in the species lists; it is remarkable that, although the genus *Trachypogon* occurs in the core cerrados, it never reaches the density seen in the Rio Branco campos, where it is dominant. This is an important matter because it raises the problem of the relationships of the Rio Branco campos with the Venezuelan Gran Sabana.

A second major phytoecological difference between core cerrados and northern campos is the abundant presence of cacti in the latter. Occasional psammophilous forms are found in the cerrados, but in Roraima cacti are a conspicuous element of the landscape.

Finally, cerrado soils never show the superficial layer of rock fragments, mostly quartz and broken lateritic (hard pan) crust, exposed by removal of top soil and characteristic of the Rio Branco area.

We think these differences are important enough to warrant individual treatment for the northern campos. Egler's (1960) and Eiten's (1977) points seem to us well taken: the relationships are clear and relevant, but placing both formations in the same category would dilute much that is important and characteristic.

The same may be said, on stronger grounds still, about the term "savana". It includes so many disparate ecosystems, American and African, that it ends by having the sole physiognomic connotation of "open formation", with the loss of important criteria, such as depth of soil and movement of the water table, water economy of the plants, summer deciduousness, etc.

In the particular case of the Rio Branco we prefer to use the local term "lavrado". This used to mean, in old Portuguese, a treeless plain. In this sense the word is lost, preserved only in dictionaries. In Roraima, however, it is currently applied to the campos, except the very closed ones. We have found it convenient to use it as definite ecological term, equivalent in rank to "cerrado", and including the plural, "lavrados", to introduce a degree of generality and an awareness of facies and subtypes.

CLIMATE

What we in Brasil broadly call "Amazonia", i.e., the domain of the hylaea, is an area of sub-continental proportions, measuring, inside the country, some 4.5 million square kilometers (Soares, 1953). It is only natural to expect that climates within it vary spatially. Given the generally moderate relief and the relatively narrow latitudinal span, temperatures are fairly homogeneous over the land and during the year. On the contrary, the great extension causes rainfall, determined by the interplay of powerful air masses (Nimer, 1979), to vary spatially and seasonally.

Figure 4 shows the annual isohyets for northern Brasil. It is immediately apparent that the Amazon in general is not an area of very high pluviosity. Nowhere are seen the four meters of rain observed on the coastal range of São Paulo (Nimer, 1979: 97); much less the seven meters that fall on the Colombian Chocó (Atlas de Colombia: 118). The general scheme is one of two high pluviosity areas, at the northeast and northwest corners of the region, with yearly totals between 3,000 and 3,500mm, separated by a broad NW-SE trending belt of pluviosity below 2,000mm. Haffer (1969) first called attention to this belt, stressing its great biogeographical and paleoecological importance.

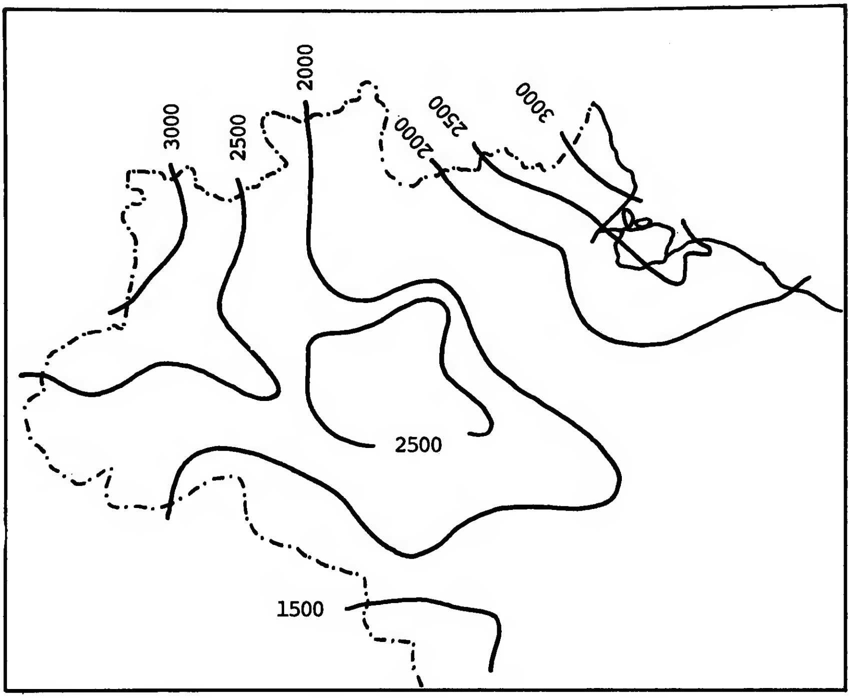


Fig. 4. Isohyets for northern Brasil (from Guerra, 1959).

In fact, inside the belt are found several enclaves of campos; it has otherwise been noted as a floristic divide (Ducke & Black, 1953) unaccompanied by any physiographic features; it is thought (e.g. Vanzolini & Williams, 1970) to have been one route of spread of open formations in Amazonia during the dry legs of climatic cycles. About three fourths of Roraima is inside this belt. Evidence of much drier paleoclimates is abundant, independently obtained by several approaches (Projeto Radambrasil, 1975).

Meteorological stations with adequate time series are scarce north of the Amazon. In order to reach an understanding of the climate as an ecological factor in Roraima we shall have to make do with two stations only, Boa Vista, ideally situated for our purposes, and Barcelos. The latter, in the state of Amazonas, on the middle Rio Negro (00°58'S, 62°56'W), at an altitude of 50m above m.s.l., represents well enough the hylaea of southern Roraima, and allows a comparison with the lavrado at Boa Vista, 490 km to the northeast.

There are additional data (Lameiro and Coimbra, 1988) from a number of Roraima stations with short runs of pluviosity records. These data do not match exactly those of the Serviço Nacional de Meteorologia, which are based on adequate time series. An idea of the discrepancy can be had by comparing the figures for Boa Vista in both series. These data afford, however, a fair idea of the climatic rhythm and of the seasonality. It has already been noted that the important spatial variations in Amazonian climates refer to precipitation, not to temperatures. In addition, some of the stations (Fig. 1) are very favorably situated relative to our localities. The data these for stations are listed in Table 2 (the statistics are ours).

Table 1 shows the march of temperature and rainfall for Boa Vista and Barcelos, plus Manaus and Belém, two well known localities, included for comparison. As mentioned, the climates are remarkably isothermic: the individual ranges of monthly averages vary from 1.8 to 2.8 degrees; the coefficients of variation (standard deviation as percentage of the mean) vary from 1.4 to 3.5, which are very low values (compare the same statistic for the pluviosity). The difference between the extreme stations (Boa Vista and Belém) is only 1.9°C, i.e., 7% of the highest temperature. Boa Vista is the hottest locality and has the most seasonal climate of all.

With regard to pluviosity, the annual ranges and the coefficients of variation are strikingly high, the latter reaching 88 in Boa Vista: all climates are markedly seasonal. The difference in total precipitation between Boa Vista and Barcelos is large, 20% of the latter total. This difference can be further analyzed by a consideration of Fig. 5, which shows the march of temperature, rainfall and evaporation in the two localities. It is quite apparent that in Boa Vista during six months of the year evaporation exceeds precipitation. This is exactly what happens in the cerrado, whose plants, however, do not have to resort to water-saving devices, either morphological (wax, hairs, thorns, succulent parts) or physiological (closure of stomata), because there is sufficient water stored in the deep soils to maintain a normal balance during the dry season. We know of no studies of the ecological physiology of the lavrado, but the likeness in facies with the cerrado strongly suggests that a similar scheme of water economy obtains.

We have not found data on lavrado soil depths comparable to those available for the cerrado, but Projeto Radambrasil (1975: 207), in a comment on yellow dystrophic latosols under savanna in the Boa Vista area, pronounce them to be "very deep".

To further the lavrado-cerrado ecological comparison we show on Fig. 6 hiterograms (Setzer, 1946, after Knoche and Borzacov, 1940) from Boa Vista and Barcelos, and from Porto Nacional, a locality in the northern cerrados (10°42'S, 48°25'W). It can be seen that the distinctly seasonal climate of Boa Vista resembles that of Porto Nacional; the dry season, however, is less severe. Furthermore, in the cerrado the driest months are also the coolest, while the contrary happens in Roraima. That the dry season is from May to November in Central Brasil and from November to April in Roraima is only to be expected, since they are in opposite hemispheres.

LOCALITIES

Forest localities

Ilha de Maracá. We have only one productive forest locality, the island of Maracá, on the Rio Uraricoera, at 03°24'N, 61°38'W. It is not a river-deposited island, but one under structural control. The Uraricoera follows a general WSW-ENE direction, a little north of the 03°N parallel. At about 61°53'W it splits its course into two arms, along a system of fractures and faults. One of the arms, Furo de Maracá, continues the general trend. The other arm, Furo de Santa Rosa, turns to the northeast to a point at 03°33'N, 61°38'W, where it bends sharply to the southeast, almost in a straigth angle, and rejoins the Maracá at 61°23'W. The island is a fairly regular triangle, measuring approximately 57 km along the base, the Furo de Maracá, and 25.5 km in height. The area is about 713 sq km.

As said, the island is not river deposited, but part of the dissected landscape of the Northern Amazonian Dissected Plateau (Fig. 2), one of the major morphostructural units of the area (Projeto Radambrasil, 1975: 152), resulting from erosion of the granites, gneisses and migmatites of the Early Pre Cambrian Guianese Complex. Accordingly, the island has an undulated and incised relief, the downstream (eastern) tip being a little flatter.

Maracá is on the eastern edge of a forested morphoclimatic unit, "Dissected Plateaus and Pediplaned Surfaces" (Projeto Radambrasil, 1975: 165), in direct contact with the campos of the Rio Branco. Across the river from the eastern end of the island is the western edge of the lavrados in the area.

A very good ecological description of the island is presented in Moskovits's (1985) unpublished thesis on the ecology of the two species of *Geochelone* (Testudines, Testudinidae) that inhabit the area. Moskovits (l.c.: 160) recognizes in the island eleven types of habitats, occupying individually from less than 2% to almost 25% of the area. There are six types of habitat occupying

Table 1. March of precipitation and temperature, 4 Amazonian stations

	Boa Vista		Barcelos		Manaus		Belém	
Jan	32	27.9	201	26.0	260	26.0	352	25.1
Feb	38	27.9	155	26.2	245	25.8	440	24.9
Mar	54	28.1	205	26.2	271	25.7	458	25.0
Apr	120	27.7	256	25.8	272	25.9	332	25.4
May	298	26.6	300	25.6	194	26.1	305	25.7
Jun	377	26.0	240	25.5	106	26.3	173	25.7
Jul	354	26.0	183	25.4	64	26.6	138	25.7
Aug	206	26.5	120	25.9	38	27.4	130	25.8
Sep	98	27.6	124	26.0	60	27.6	126	25.7
Oct	60	28.4	127	26.3	118	27.6	87	26.0
Nov	66	28.8	131	26.4	150	27.2	88	26.2
Dec	48	28.3	135	26.5	218	26.5	177	25.9
Year	1751		2177		1996		2808	
Range	32-377	26.6-28.8	120-300	25.4-26.5	38-270	25.7-27.6	87-458	24.9-26.2
x	145.9	27.48	181.4	25.98	166.2	26.56	233.8	25.59
V	88.4	3.5	33.0	1.4	52.9	2.7	58.1	1.6

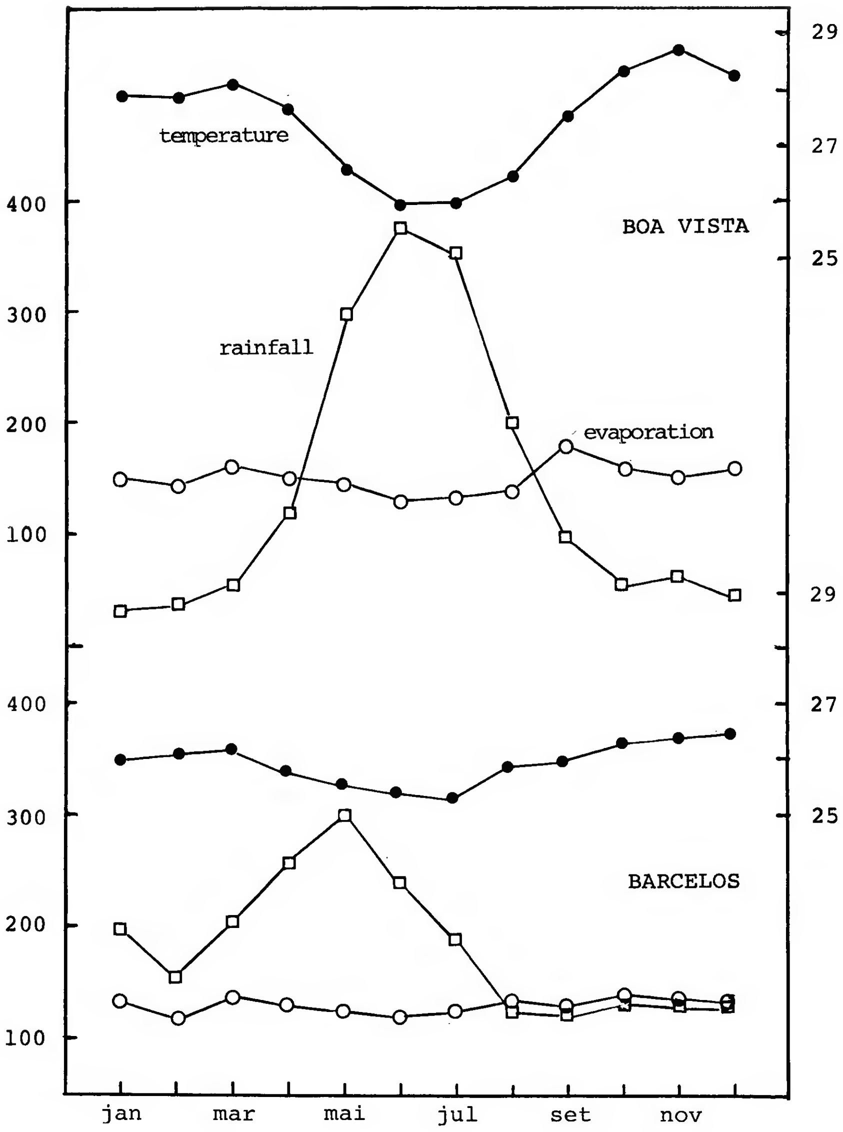


Fig. 5. March of temperature, rainfall and evaporation for Barcelos and Boa Vista (data from Serviço National de Meteorologia).

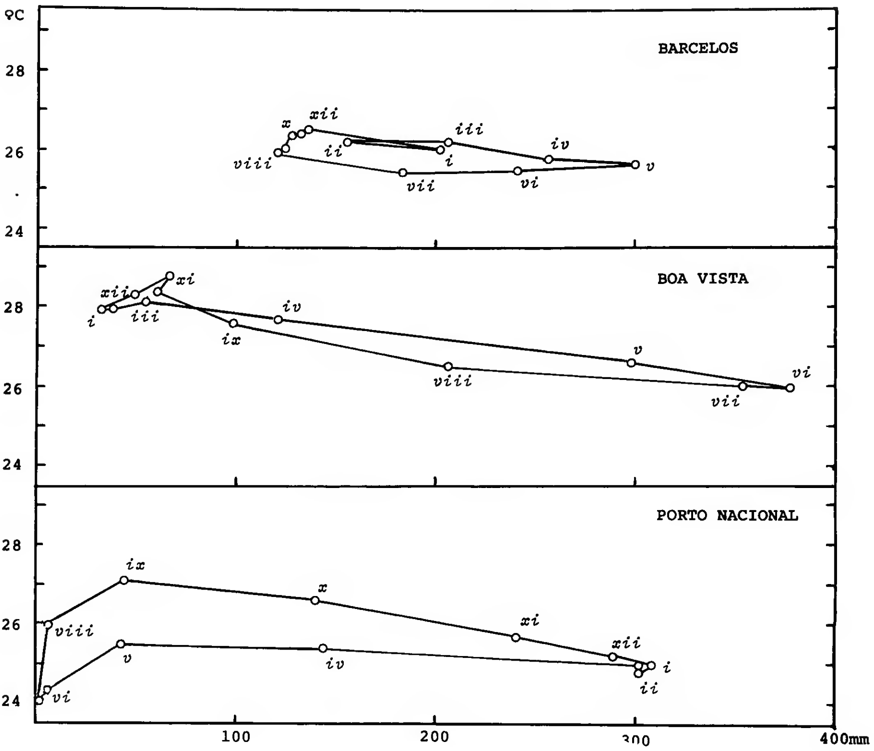


Fig. 6. Hiterograms for Barcelos, Boa Vista and Porto Nacional (data from Serviço National de Meteorologia).

9% or more each. The general picture is that of a mosaic, as all the eleven habitat types occur in a sample plot of 138.5 hectares.

About 85% of the island is terra firme, the remainder consisting of swamp with Mauritia palms, some ordinary varzea forest (small disarticulated patches), second growth, and grassy ponds. Palms, especially *Maximiliana regia*, are common, frequently forming thickets. There are areas with a high density of vines. Emergent trees are present, but in relatively small numbers.

We add that the soils, as could be expected from the nature of the bedrock, are sandy, and that treeless patches are frequent. The canopy, 20-25 m high, may be continuous, but is more usually broken, letting through a good amount of light. The understory may be quite uncluttered, but is more often shrubby. The leaf litter is usually thin, leaving bare sandy patches. Hemming et al. (1988) present excellent habitat photographs of the island.

An idea of the pluvial regime of Maracá and neighboring localities (Fazenda Salvamento and Maloca Mangueira) may be gathered by inspection of Table 2: Boqueirão, a Macuxi Indian village ("maloca") remains a few kilometers to the east. It is a rather dry area, with a long (September to March) and hard (295 mm in seven months) dry season. Maracá cannot be thought of as part of the hylaea, but as a rather special type of forest.

The Taiano station, on a low relictual hill, has almost twice the rainfall of Boqueirão. This is very probably due to orographic rains, a common feature in large areas of open formations: moisture-laden winds hit the hills and let out the water.

The best collecting sites at Maracá have been on the eastern end of the island, in patches of sunlight on the leaf litter.

Apiaú. Apiaú is a relatively old (founded 1944) agricultural colony, east of the Rio Apiaú, a tributary of the Mucajaí on its right (southern) bank. The area (Fig. 2) is part of the already mentioned Rio Branco-Rio Negro Pediplain (Projeto Radambrasil, 1975: 152), and is bounded to the south by the Serra de Mucajaí, one of the Residual Plateaus of Roraima resulting from dissection of the Guianese Complex. The base level is at about 300 m, the dissected ridges rising to 500 m. The whole area is under terra firme forest, with disarticulated minor sectors of varzea.

As usual in terra firme forests, the drainage has a coarse texture and poor hierarchy, i.e., small and spread out water courses run directly to the major rivers, without the interposition of intermediate-sized tributaries.

The forest at Apiaú is medium tall, the rather broken canopy reaching 20-25 m, with few emergents. The vegetation is very patchy. There are lower, more humid areas, with palms and giant arums (*Montrichardia*). On patches of stony soil, densely covered with irregular quartz pebbles, there are stands of non-forest trees; especially conspicuous is an area of several hectares bearing a pure stand of a thin, tall and very tough myrtaceous tree ("goiabinha"). In these small enclaves lichens are common. Rock (including boulders) and hardpan exposures are frequent; leaf litter is sparse.

The stations in Table 2 that allow an idea of precipitation at Apiaú are Fazenda Fé e Esperança and Serra da Prata, both forest localities in the same area. They approach Barcelos (Table 1) and the other hylaean station, Santa Maria do Boiaçu (Table 2) on the lower Rio Branco, in having much more rainfall than Ilha de Maracá.

The few *Gymnophthalmus* (in spite of much collecting effort) obtained is this area were caught in sunlighted spots in the leaf litter.

Cachoeira do Paredão. This is a falls on the Rio Mucajaí, at 02°57'N, 61°35'W, not far from Apiaú. The two areas are very similar, but at the falls the relief is more moderate, and rock exposures less common. The only specimen was collected in second growth, on the leaf litter, in a spot of sunlight.

Cachoeira do Cujubim. A falls on the Rio Catrimani, a large tributary of the Branco, at 01°45'N, 62°17'W. The upper course of the river cuts across some highly dissected plateaus, and has numerous falls. The vegetation is terra firme forest. The pertinent locality in Table 2 is Santa Maria do Boiaçu. The three specimens we have from Cachoeira do Cujubim were collected by a friend, Carlo Zacquini.

Localities in the lavrado

Salvamento. This is a small cattle ranch ("fazenda") on the right bank of the Rio Uraricoera (03°20'N, 61°24'W), downstream from but partially overlapping the island of Maracá across the river, which is here some fifty meters wide. In fact, our best collecting locality at Salvamento is a few hundred yards from the boat landing that serves the Ecological Station on the island. North and west of Salvamento begin the forests of the Northern Amazonian Dissected Plateau (Fig. 2).

Salvamento is typical lavrado of the northern half of the Rio Branco-Rio Negro Pediplain. The topography is undulating, with veredas running among tesos. There are occasional boulders and exposures of rock and hardpan. The ground is covered with rock fragments and the grass stratum is sparse. The dominant tree is *Curatella americana*, but it is nowhere dense, except in small copses on the tops of tesos. The climate has been commented in the paragraph on Ilha de Maracá.

Termite mounds (*Nasutitermes* sp.) are very frequent, and inside them all our specimens were collected. The mounds are fairly uniform in shape and size; they are small, 30-60 cm high and a little less in diameter, made of carton and soil. The lizards have been found inside the nests, in slightly widened spaces at about ground level; when the nest is overthrown they try to escape into the cavities and passages of the broken pieces, never to the outside. One to five (more commonly two) have been found per nest; none have been seen on the outside.

Maloca Mangueira. Maloca Mangueira is a Macuxi Indian village in the lavrado, very near the limit of what is called "mata geral", the general forest of the Northern Amazonian Dissected Plateau. It sits a little over 7 km SSE of Salvamento, and 12 km NW of Boqueirão (Table 2). In spite of being so close, and at the same altitude, Mangueira and Salvamento differ in some important particulars. The relief is flatter at Mangueira; capões (bush islands or copses), mainly of *Curatella*, are found at all levels. *Nasutitermes* nests are scarce. *Gymnophthalmus* in this area has been found only on the edge of capões, in the sparse leaf litter, at the foot of *Curatella* or other small trees, always exposed to sunshine.

Normandia. Our collecting locality, at 03°53'N, 59°37'W, is on the right bank of the Rio Maú (or Ireng), which makes there the border between Brasil and Guyana. The area is flat; according to Aziz N. Ab'Saber (pers. comm.) it is a low sandy plateau. The landscape is lavrado, but of an extremely dry description. *Curatella* is the dominant tree, but cacti are abundant, especially the large *Cereus jamacaru.* The vegetation on the actual bank of the Maú is an extremely xeric, very dense mixture of small contorted trees and cacti. An idea of the rainfall regime may be had from the data of Uailan and Bandeira Branca (Fig. 1, Table 2), which are also applicable to the Surumu area. The total pluviosity is low, the dry season long and harsh. Two specimens were collected here, one in a termite nest, the other on the bank of the Maú, walking in the sun. The termite nests (not yet identified) are apparently different from those at Salvamento.

Surumu. We have one specimen in the MZUSP collection, anterior to this project, labelled "Surumu". We are not sure of whether this is the town (the old Vila Pereira) or the general area. Whatever the exact locality, it belongs to the campos.

Boa Vista, the capital of Roraima, is on the right bank of the Rio Branco. The general area is low, in part swampy; there are many round depressions permanently or seasonally filled with water. The vegetation is in general lavrado; on the banks of the Branco it cannot be called a proper gallery forest, but is denser and contains more trees than the lavrado. *Gymnophthalmus* was collected on the ground, in a dry area of this river bank vegetation.

Taxonomic analysis

To investigate the presence of morphological differences between forest and lavrado populations, three carefully documented samples were collected, at Ilha de Maracá (forest), Fazenda Salvamento and Maloca Mangueira (lavrado). The original reasons for selecting these localities were accessibility and productivity, but their particular geographic disposition turned out to be very advantageous. They are in typical areas of the respective environments, additionnally in close spatial proximity: between Maracá and Salvamento there is the width of a medium-sized river, from Salvamento to Mangueira a few kilometers.

Examination of these three samples evinced no qualitative and no marked quantitative differences, but suggested three differences in color pattern.

(1) The upper lip of forest lizards was seen to be black or sooty, while in the lavrado it was white or showed a definite glossy, enamel-like longitudinal bar.

(2) All *Gymnophthalmus* have a white, dark-bordered stripe begining on the superciliary region and running dorso-laterally to the base of the tail. The stripe of lavrado specimens, especially at shoulder level, was vivid, very white, set off by the dark borders. In the forest specimens contrast was much less, the whole ensemble being frequently obsolete. This pattern may be seen in an outstanding photograph published by Hemming et al. (1988: 109), mislabelled "*Mabuya* sp."

(3) The underparts (for brevity hereafter called "belly") of the lavrado specimens were white or yellowish, unclouded, glossy. Those of the forest lizards ranged through several shades of gray, being in extreme instances dark bluish.

These three criteria were informally applied to sixteen specimens not seen before, and all were correctly identified as to habitat.

Finally, it was noticed at tabulation that there were no males (bearing femoral pores) in the forest materials, while they were present in diverse proportions in the lavrado. In previous studies of parthenogenesis no correlation has been mentioned between sex ratio and habitat.

Table 2. March of precipitation, 8 short term stations

	Boa Vista	Sta Maria do Boiaçu	Uailan	Bandeira Branca	Boqueirão	Taiano	Fé e Esperança	Serra da Prata
Period	1970-1987	1975-1983	1978-1983	1975-1983	1979-1983	1979-1983	1975-1983	1984-1987
Jan	24	109	22	41	43	17	51	41
Feb	17	119	18	29	49	16	50	56
Mar	61	243	40	76	36	59	61	18
Apr	150	322	88	115	142	321	287	112
May	246	317	164	182	176	304	334	372
Jun	313	272	217	159	185	376	376	404
Jul	258	178	224	208	168	306	295	330
Aug	195	136	166	160	132	188	237	177
Sep	90	140	52	56	49	85	136	131
Oct	58	125	75	65	59	96	104	75
Nov	63	110	49	65	35	74	71	80
Dec	37	146	61	82	24	81	76	23
Year	1509	2117	1176	1238	1098	1923	2078	1819
Range	17-313	109-322	18-222	29-208	24-185	16-376	50-376	18-404
$\bar{x}$	125.8	176.4	98.0	103.2	91.5	160.3	173.2	151.6
V	82.0	52.3	71.1	58.0	68.9	82.0	71.3	91.9

It was obvious that these preliminary results should be verified in the whole of the materials at hand. In doing so (Table 3), difficulty was occasionally found in scoring the elements of the color pattern. Scoring was done blind, without knowledge of the lizard's locality; the samples were mixed for the purpose. In some instances there was a real intermediate state; in others preservation was not ideal. All such cases were lumped into a category "intermediate". Since our interest was discrimination, in the computations the intermediates were considered as different from the standard for the respective habitat (see below), thus understressing eventual statistical differences but avoiding circular reasoning.

Table 3. Sex ratio and color pattern, all forest and lavrado samples

		Lip			Belly			Stripe		
		N	B	W	D	I	L	V	I	D
Maracá	♀	65	63	2	57	4	4	1	11	51
Salvamento	j	6	-	6	-	3	3	6	-	-
	♂	22		22	1	1	20	21		
Mangueira	j	1	-	1	-	1		1		
	♂	2	-	2			2	2		
	♀	10	1	9	1	1	8	8		2
Apiaú	♀	2	2		2		-	-	-	2
Paredão	♀	1	1	-	1		1	-	-	1
Cujubim	♀	3	3	-	3	-	-	-	-	3
Surumu	♂	1	-	1	-	-	1	1	-	-
Normandia	j	2		2			2	2		
Boa Vista	♂	2		2			2	2		

Lip: B, black; **W,** white. **Belly: D,** dark; **I,** intermediate; **L,** light.
Stripe: V, vivid; **I,** intermediate; **O,** obsolete.

SEX RATIO

The lizards were sexed according to the presence or absence of femoral pores; dissection was thought neither necessary nor convenient. The smallest pore-bearing specimen was 32mm in body length; all examples shorter than this were scored as juveniles.

As said, no forest lizard was found to be a male. In the lavrado sex ratios varied, but the difference between Salvamento (35% males) and Mangueira (17%), seemingly high, is not statistically significant (p= 0.11).

There is no point in applying exact tests to the obvious differences between forest and lavrado sex ratios. We think the best quantification is to compute the exact confidence intervals (binomial distribution) for the number of males. The upper limit, at the 5% level, comes to 5.5% for Maracá and to 5.1%, for the pooled forest samples. It seems beyond doubt that the forest populations are really parthenogenetic: five per cent of males could be of no conceivable good to a lizard species.

As to the lavrado, the pooled frequency of males, 26/76 or 0.354, conspicuously deviates from 0.5. Since it seems natural to us, in the circumstances, to look for a loss of males, not for an eventual excess, we applied to the deviation a one-tailed test of the normal distribution. The associated probability is 0.007. Even the less compromised two-tailed test affords a probability smaller than 0.02. It is clear that there is in the lavrado a significant deviation, by deficit, from an even sex ratio.

Color pattern

Color pattern may be viewed, in our case, from three angles: coherence of elements, diagnostic value and biological meaning.

From the observed frequencies of the individual elements it is possible to calculate the probability of the eight classes that result from combining the two states of the three elements, and to compare observed and expected frequencies. This we have done (Table 4) for all specimens that could be unambiguously assigned, combining the sexes and juveniles, since no sex dimorphism was noted. The result is so striking that there is no point in computing statistics. Two classes comprise 97% of the individuals. These are classes that bring together the character states perceived in the preliminary inspection as distinctive of the forest and lavrado habitats (Table 3). We are thus led to the idea of a "standard" pattern for the forest (black lip, dark venter, obsolete stripe) and a complementary one for the lavrado (white lip, light venter, vivid stripe). It is quite understandable that these characters go together, as they are basically related to the general amount of melanin.

Table 4. Color patterns, observed and expected frequencies, all forest and lavrado specimens

Lip	Belly	Stripe	f	$\hat{f}$
Black	Dark	Obsolete	65	14.80
		Vivid	0	17.12
	Light	Obsolete	0	15.39
		Vivid	0	17.81
White	Dark	Obsolete	2	17.92
		Vivid	0	20.74
	Light	Obsolete	2	18.65
		Vivid	75	21.58
			144	144.01

In order to evaluate the diagnostic power of the color pattern, it is necessary to take into account, besides the deviant specimens listed in Table 3, fourteen other which were not tabulated because one of the elements either could not be ascertained or was scored as intermediate.

There are (Table 5) four specimens in which one element for the color pattern could not be determined. In each case, the other two elements agree with the standard. Taking the specimens with three scores, it is seen that color patterns may differ from the standard by one, two or all three elements. Adopting as a criterion that two out of three elements permit a decision, 149 of the 158 lizards in our sample could be correctly identified.

We believe that this good discrimination, plus the ecological, and not geographical, segregation, and the sex ratios, afford sufficient grounds for considering the two forms as distinct species. It is in the light of this concept that the aberrant color patterns will be examined.

Five specimens differ from their putative standard pattern by one element. Three of these are so scored for the sake of discrimination: they were initially classified as intermediates. It is reasonable to consider them as just showing marked intra-populational variation of the respective element, which is no cause for amazement in the case of chromatic characters, and of such a low relative

Table 5. Geographic distribution of color patterns

		N	Standard pattern	Differences from standard 1	2	3	Information incomplete
Maracá		64	57	4			3
Small forest samples		6	6	-			
Salvamento	j	6	3	3		-	
	♂	22	20	1	-		1
	♀	41	39	-	2	-	
Mangueira	j	1	-	1	-		
	♂	2	2	-			
	♀	10	8		-	2	
Small lavrado samples	j	2	-	-			
	♂	4	2	1	1		
		158	10	3	2	0	4

frequency. This reasoning may be extended to the two specimens in which the element in opposition to the standard is well defined — especially so since one of the specimens is a male. Otherwise, the mixture of characters might be interpreted either as intrinsic variation or as evidence of introgression. It should be noted that this latter line of thought demands reiterated hybridization to explain parthenogenesis.

The same argument must be extended to the two specimens, both males, that differ from the norm in two characters out of three.

In the case of two Mangueira females showing a full forest pattern, we must face one additional possibility: they might be variants of the lavrado form, or syntopic, intrusive, forest lizards, or still simply mislabelled specimens. The latter hypothesis cannot be offhand dismissed.

Both specimens were collected at the same time (December 3, 1985), at the start of the Roraima survey. During the same field trip collections were also made at Maracá. Both specimens are females, as all the Maracá sample. An explanation of the anomaly will have to be sought in continuing field work. If there are in fact two syntopic species, intensified collecting should not fail to reveal further cases; otherwise, hybridization in any form is likely to be detected by cytogenetic and biochemical methods. Failing these two hypotheses, we'll have to accept mislabelling.

Otherwise, it is not possible to assign unambiguously these two specimens to either form by statistical methods. We repeated all calculations for the Mangueira sample, both including and excluding these specimens: in no case there was significant change in the conclusions. We decided finally to omit them from computations, to be considered for the time being as forest lizards occurring, normally of fortuitously, in the lavrado, in numbers too low for statistical treatment.

MERISTIC CHARACTERS

Three meristic characters were studied (Table 6):

(1) Dorsal scales, counted between the occipital scale and the level of the posterior margins of the thighs;

(2) Ventral scales, between the interbrachial row and the anal plate (latter not included);

(3) Ventral lamellae of the fourth toe.

Table 6. Meristic characters: distributions of frequencies, forest and lavrado samples

	Maracá	Samall forest samples	Salvamento			Mangueira			Small lavrado samples	
			j	♂	♀	j	♂	♀	j	♂
Dorsals										
30	2				1					
31	4			2	-				1	1
32	19	1		2	1				1	
33	12		1	7	5		1		1	
34	12	2	1	5	10	1		1		-
35	6	1	1	2	4		-	2	1	
36	3	2	1	2	15		1	6		1
37	1		1	1	2					
38			1							
	59	6	6	21	38	1	2	9	4	2
Ventrals										
20	2	1								
21	8	4		4						1
22	24	-		6			1	1	1	-
23	12	1		9	7		-	2		1
24	10		2	3	7	1	-	1		2
25	4		2	1	14		1	2		
26	1				9			1	1	
27	1		1		3			2		
28	1		1		1					
	63	6	6	23	41	1	2	9	2	4
Fourth toe lamellae										
13								1		
14			1		2			1		1
15	7		1	6	9			1	1	1
16	22		2	10	14	1		3	-	1
17	21	5	2	6	12		2	4	1	1
18	14				3					
19					1					
	64	5	6	22	41	1	2	10	2	4

Scales around midbody were thirteen in all specimens.

We found it necessary to check the presence of correlation between the counts of dorsal and ventral scales (Table 7). In two cases (Maracá and Salvamento females) the correlation was significant, but the coefficient of determination (r^2) was in both cases very low, 0.13 and 0.23. It is permissible to treat separately the two variables.

Descriptive statistics utilized were the usual: range (R), mean $\bar{x}$, standard deviation (s), coefficient of variation (V); we also include I ($\bar{x}$), the 95% confidence interval of the mean, i.e., the mean plus and minus t (Student's) times its standard deviation.

Simultaneous comparisons were made of the samples with sufficient degrees of freedom (Maracá, Salvamento males and females, Mangueira females). Initially an analysis of variance was performed; when it was significant, the means were compared by Kramer's (1956) extension to samples with unequal numbers of Duncan's (1955) test for homogeneity of a set of means.

The raw data and descriptive statistics are shown on Tables 6 and 8. The final conclusions are drawn from Table 9, showing the results of Kramer's test:

(1) In dorsal and ventral scale counts there are significant sex differences in Salvamento; not so for lamellae.

(2) The dichotomy forest x lavrado is nicely shown in the females, in all cases. Salvamento males in two cases go with Maracá, in one with the rest of the lavrado. As could be expected from the correlations between dorsals and ventrals, lavrado has higher values in both cases.

Body proportions

It is customary in taxonomic studies to approach body proportions by means of a "dredging" operation, i.e., to look for eventual differences by methodically studying all available pairs of variables or by performing a multivariate analysis. In the present case, however, there is one guiding thread. Microteiids frequently adopt modes of life (as, in the case, leaf litter dwelling and termitarian inquilinism) that lead to attenuation of body shape and reduction of limbs, with loss of digits (Gans, 1986).

Modifications of shape are best studied by regression analysis. Attenuation, however, presents a practical problem. The girth of soft bodied animals (to make things worse, preserved at different times by different persons) cannot be reliably measured; head width, however, is a convenient proxy (Schmidt, 1977). Given the type of locomotion ot these elongate animals, the ideal independent

Table 7. Forest and lavrado samples: correlation between dorsal and ventral scale counts

		d.f.	F	r^2
Maracá		56	8.102**	0.1264
Salvamento	j	4	13.500*	0.7714
	♂	19	2.164 n.s.	0.2005
	♀	37	7.765*	0.3406
Mangueira	♀	7	4.762 n.s.	0.4049
Pooled		146	59.779***	0.2891

Table 8. Forest and lavrado samples: scale counts, statistics of the frequency distributions

		N	R	$\bar{x}$	s	V	I ($\bar{x}$)
Dorsals							
Maracá		59	30 - 37	33.1 ± 0.24	1.85	5.6	32.6 - 33.5
Salvamento	j	6	33 - 38	35.1 0.76	1.87	5.3	33.5 - 37.5
	♂	21	31 - 37	33.6 0.34	1.56	4.7	32.9 - 34.3
	♀	39	30 - 38	34.8 0.25	1.58	4.5	34.3 - 35.4
Mangueira	♀	9	34 - 36	35.6 0.24	0.73	2.0	35.0 - 36.1
Ventrals							
Maracá		63	20 - 26	22.7 0.19	1.48	6.5	22.4 - 23.1
Salvamento	j	6	24 - 28	25.5 0.67	1.64	6.4	23.8 - 27.2
	♂	23	21 - 24	22.6 0.22	1.08	4.8	22.1 - 23.1
	♀	41	23 - 28	24.9 0.20	1.27	5.1	24.5 - 25.3
Mangueira	♀	9	22 - 27	24.7 0.60	1.80	7.3	23.3 - 26.1
Fourth toe lamellae							
Maracá		64	15 - 18	16.7 0.12	0.95	5.7	16.4 - 16.9
Salvamento	j	6	14 - 17	16.7 0.48	1.17	7.4	14.6 - 17.1
	♂	22	15 - 17	16.0 0.16	0.76	4.7	15.7 - 16.3
	♀	41	14 - 19	16.2 0.17	1.10	6.8	15.9 - 16.5
Mangueira	♀	10	13 - 17	15.8 0.44	1.40	8.9	14.8 - 16.8

variable is total length (body plus tail). It is, however, a hard fact of herpetology that in any sample of elongate lizards the number of intact tails is never large, and is frequently insufficient for analysis; one has to have recourse to body length.

The measurements we took were:

(1) Body length (snout to vent), taken with a ruler to the nearest millimeter.

(2) Tail length, similarly taken.

(3) Head length, taken with calipers, to the tenth of a millimeter, between the anterior rim of the ear opening and the tip of the snout.

(4) Maximum head width, taken with calipers, to the nearest tenth of a millimeter.

(5) Length of the hind limb, taken to the nearest millimeter by stretching the limb along a ruler perpendicularly appresed against the groin.

We preferred not to use multivariate statistics in order to keep closer to the physical nature of the variables. As to procedure, we follow Silva-Leme (1959), which is conceptually very clear and computationally very practical.

Table 9. Forest and lavrado samples: homogeneity of means of scale counts (Kramer's test)

Dorsals

Mangueira ♀	Salvamento j	Salvamento ♀	Salvamento ♂	Maracá
35.36	35.50	34.85	33.62	33.07

Ventrals

Salvamento j	Salvamento ♀	Mangueira ♀	Maracá	Salvamento ♂
25.50	24.93	24.67	22.73	22.61

Fourth toe lamellae

Salvamento ♀	Salvamento ♂	Salvamento j	Mangueira ♀	Maracá
16.20	16.00	15.83	15.80	15.56

Means that do not differ significantly are underlined

Tail x body length. (Table 10, Figs. 7,8). As said, a high proportion of our specimens have regenerated or broken tails. The only satisfactory sample is Maracá: one third (21) of the specimens have intact tails. More important still, the range of body lengths is very good, encompassing from newborn (less than 20 mm) to fully grown (over 40 mm) specimens. The other large sample, Salvamento, has fewer intact tails and a somewhat narrower range of body lengths.

The Maracá regression is linear (all regressions in this paper are) and has an excellent fit, the coefficient of determination r^2 exceeding 0.95. Two other forest specimens have undamaged tails and are shown by graphic inspection to adhere closely to the Maracá line, which justifies their inclusion in a pooled forest sample; this does not change the regression and adds generality. (In successive analyses this same type of pooling will be consistently done, with no further comment).

Table 10. Forest and lavrado samples: statistics of the regression analyses

Tail length x Body length

	N	R(x)	R(y)	b	a	F	r^2
Maracá	21	20-42	24-72	2.06±0.103	-16.1±3.31	398.394^{***}	0.9545
All forest	23	20-42	24-72	2.06±0.098	-15.7±3.18	432.969^{***}	0.9573
Salvamento j♂♀	7	25-39	42-80	2.35±0.438	-18.2±15.31	28.829^{**}	0.8522
Lavrado j♂♀	16	25-39	42-80	2.30±0.342	-17.7±12.19	45.188^{***}	0.7635
Head length x Trunk length							
Maracá	60	14.5-34.8	4.5-7.5	0.16±0.0051	2.0±0.13	960.582^{***}	0.9431
All forest	66	14.5-34.8	4.5-7.5	0.16±0.0047	2.0±0.13	1096.428^{***}	0.9448
Salvajento j♂	22	19.8-31.3	5.2-6.8	0.17±0.015	1.5±0.41	130.451	0.8671
j♀	46	19.8-35.3	5.2-6.7	0.10±0.0073	3.0±0.22	207.211^{***}	0.8249
Lavrado j♂♀	56	19.8-35.3	5.2-6.7	0.11±0.0073	2.9±0.22	213.383^{***}	0.7980
Head width x Head length							
Maracá	61	4.5-7.7	3.0-5.5	0.73±0.021	-0.2±0.13	1249.964^{***}	0.9549
All forest	67	4.5-7.7	3.0-5.5	0.72±0.020	-0.2±0.12	1319.388^{***}	0.9530
Salvamento j♂	25	4.8-7.3	3.1-4.5	0.65±0.022	-0.04±0.14	864.902^{***}	09734
j♀	46	4.8-6.7	3.1-4.5	0.78±0.049	-0.8±0.30	253.274^{***}	0.8520
Mangueira ♀	9	4.5-6.5	2.8-4.5	0.75-0.140	-0.5±0.85	28.750^{**}	0.8042
Head width x Body length							
Maracá	61	19-42	3.0-5.5	0.10±0.0041	1.1±0.13	589.742^{***}	0.9091
All forest	67	19-42	3.0-5.5	0.10-0.0040	1.1±0.13	589.682^{***}	0.9007
Salvamento j♂	23	25-38	3.0-4.6	0.11±0.0091	0.3±0.31	140.384^{***}	0.8699
j♀	47	25-42	2.0-4.5	0.080±0.0062	1.1±0.22	169.653^{***}	0.7904
Mangueira ♀	8	24-40	2.8-4.5	0.094±0.0190	0.6±0.70	24.668^{***}	0.8043
Head width x Total length							
Maracá	21	44-114	3.2-5.5	0.029±0.0017	1.8±0.14	284.095^{***}	0.9373
All forest	23	44-114	3.2-5.5	0.029±0.0016	1.8±0.14	311.126^{***}	0.9368
Salvamento j♂♀	5	68-119	3.1-4.4	0.025±0.0029	1.4±0.28	75.217^{***}	0.9617
Lavrado j♂♀	7	68-119	3.1-4.4	0.026±0.0026	1.3±0.25	98.356^{***}	0.9516
Hind limb length x Body length							
Maracá	63	19-42	6-16	0.40±0.016	-0.9±0.52	601.283^{***}	0.9079
All forest	68	19-42	6-16	0.38±0.016	-0.6±0.54	549.733^{***}	0.8928
Salvamento j♂	25	25-38	9-14	0.34±0.118	0.2±3.99	8.471^{*}	0.3439
j♀	40	25-42	9-14	0.30±0.64	1.0±2.29	22.502^{***}	0.3719
Hind limb length x Body length							
Maracá	21	44-114	7-15	0.12±0.012	1.9±0.98	98.242^{***}	0.8378
All forest	23	44-114	7-15	0.12±0.011	1.9±0.93	108.741^{***}	0.8381
Lavrado j♂	6	66-108	9-13	0.097±0.0289	2.5±2.68	11.286^{*}	0.7383
j♀	17	68-119	9-13	0.086±0.0222	3.3±2.11	15.141^{*}	0.7517
j♂♀	11	68-119	9-13	0.080±0.205	4.1±2.00	15.397^{**}	0.6311

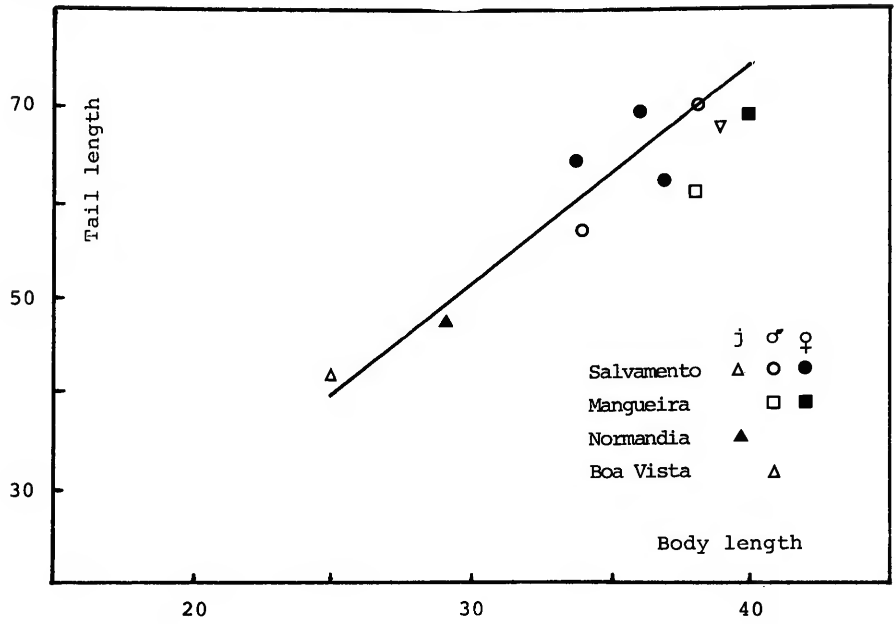


Fig. 7. Regressioin of tail length on body length, lavrado specimens.

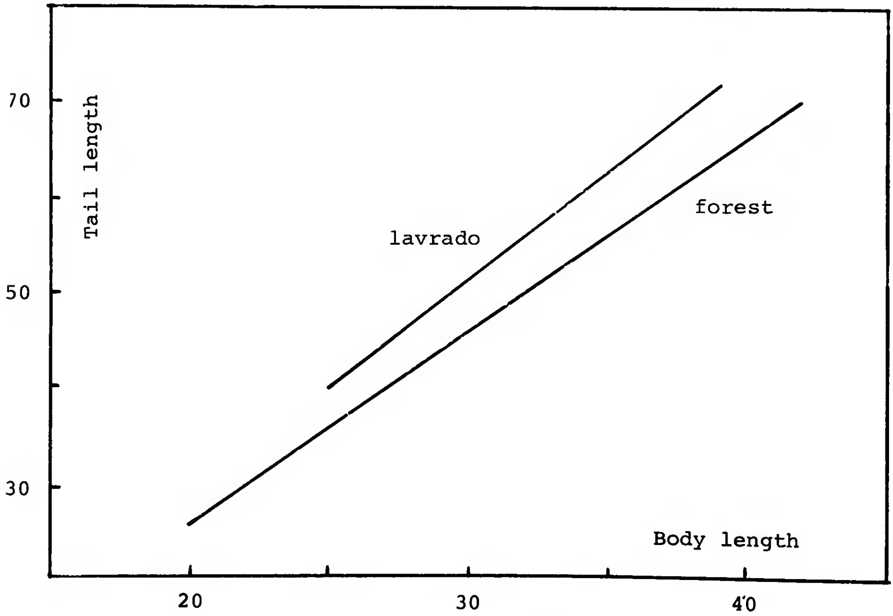


Fig. 8. Regression of tail length on body length, forest and lavrado samples.

On the lavrado side things are less simple. Inspection of Fig. 7 shows that it is permissible to assemble all males and females in a joint regression. Comparing analytically the pooled regressions for forest and lavrado (Fig. 8), it is seen that they may be considered as parallel; the intercepts, however, differ significantly, i.e., for any given body length lavrado lizards have longer tails.

Head length x trunk length (Table 10, Fig.9). The Maracá and pooled forest samples have excellent fits ($r^2 = 0.94$). The lavrado samples have slightly inferior fits, but are still useful.

Salvamento shows sex dimorphism, quite evident in the graph. Males have larger heads; as in the cases of dorsal and ventral scale counts, Salvamento males approach (but do not quite reach) the forest samples.

A pooled sample of lavrado females (Fig. 9) affords an adequate comparison with the forest lizards, that are shown to have relatively longer heads, with a significantly larger regression coefficient, i.e., the difference tends to increase as the individuals grow.

Head width x head length (Table 10, Fig. 10). In this character, as in others, the forest samples have the best fits, with r^2 above 0.90. Salvamento males have narrower heads than the females, which, on their turn, have narrower heads than Mangueira females, that have the broadest heads of all. In every case the difference lies in the intercept, the lines being statistically parallel.

Head width x body length (Table 10, Fig.11). The regressions are of the same general quality as the previous ones. All lavrado samples are homogeneous. The forest females, which have, as usual, an excellent fit, are significantly stouter than the others.

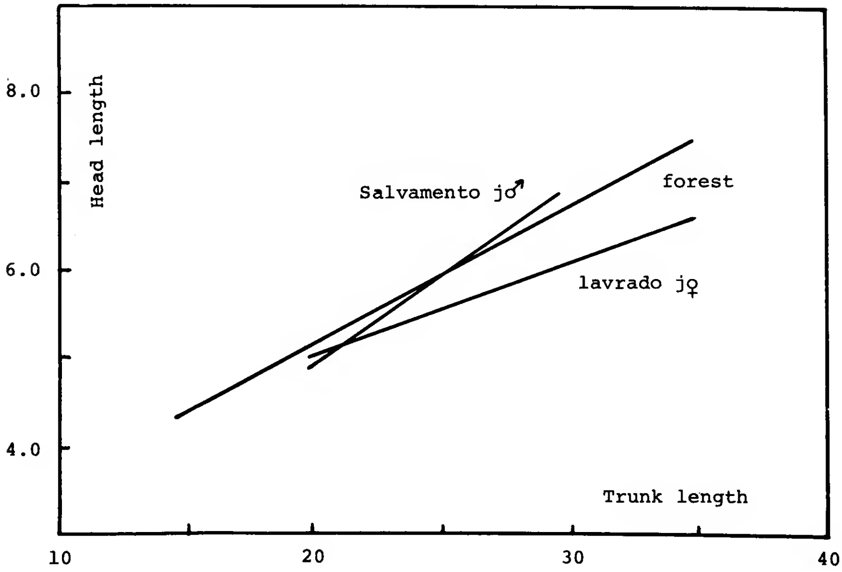


Fig. 9. Regression of head length on trunk length, forest and lavrado samples.

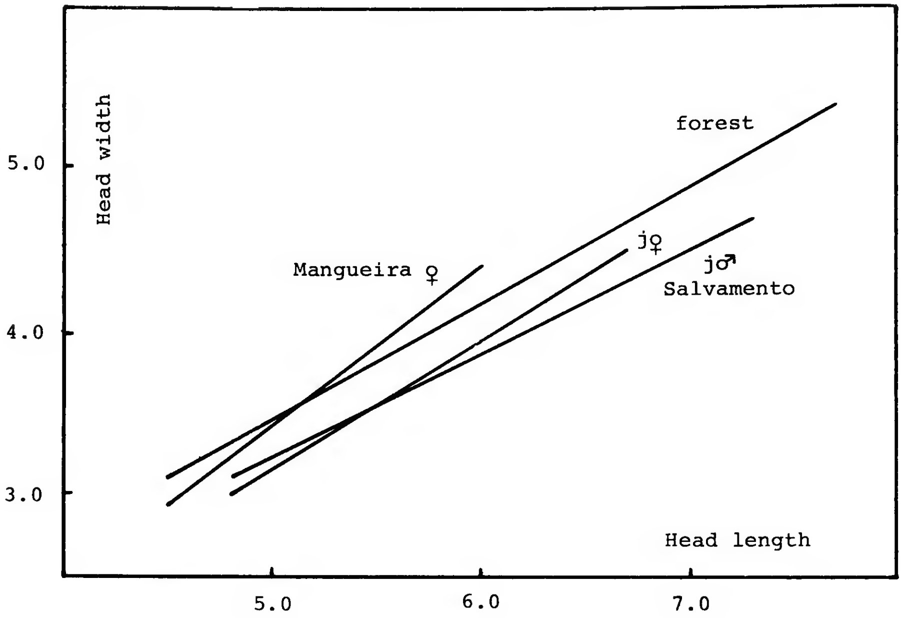


Fig. 10 Regression of head width on head length, forest and lavrado samples.

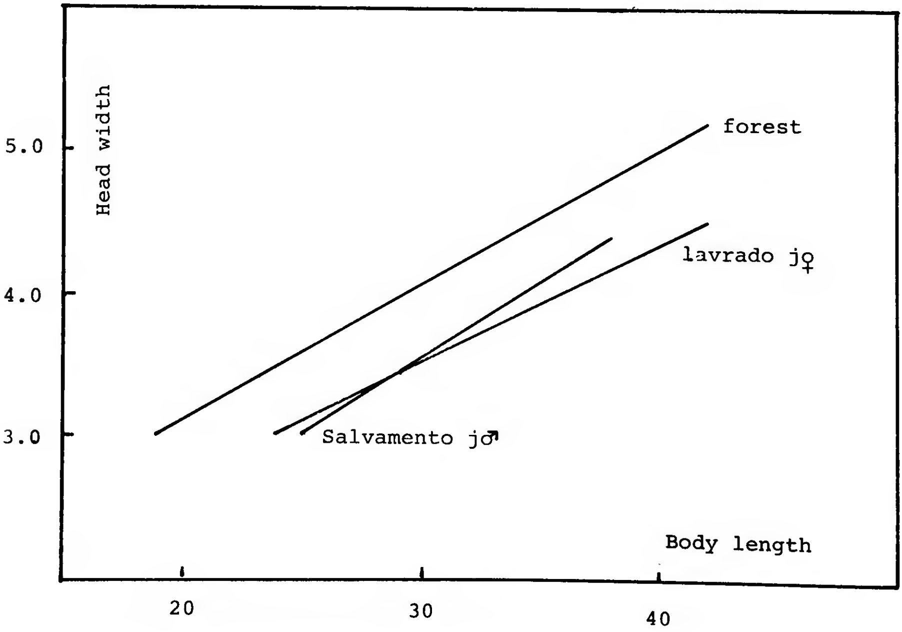


Fig. 11. Regression of head width on body length, forest and lavrado samples.

Head width x total length (Table 10, Fig. 12). In spite of the scarcity of intact tails, the regressions for this character are surprisingly good, and very interesting. The forest lizards are seen to have remarkably wider heads than the lavrado females, the lavrado males being intermediate. The differences are in the intercept.

Hind limb length x body length (Table 10, Fig. 13). This is another case in which the forest regression is much better than the lavrado ones. The forest lizards have longer legs; it is not possible to test directly the difference between Salvamento males and females, but by analogy it is possible to say that the males have longer legs than the females.

Hind limb length x total length (Table 10, Fig. 14). This regression fully confirms that of limb length on body length.

Comment on body proportions. A first point is that there is almost always a marked difference in variability between forest and lavrado lizards, the former affording much closer fits.

On the strictly morphometric side, all the regressions bearing on body attenuation and limb reduction indicate that the lavrado form, in spite of its relatively shorter tail, has progressed farther along this road.

DISCUSSION: *G. underwoodi*

Identification

The forest-dwelling parthenogenetic lizard we have been dealing with is undoubtedly *G. underwoodi*, as could be predicted from previous knowledge and is confirmed by comparison with a paratype, MZUSP 7633 (originally MCZ 55743).

There is complete agreement in pholidotic characters — but this is usual in *Gymnophthalmus*. Scale counts are: dorsals 35, ventrals 24, midbody 13, fourth toe lamellae 14, all in agreement with the Roraima sample.

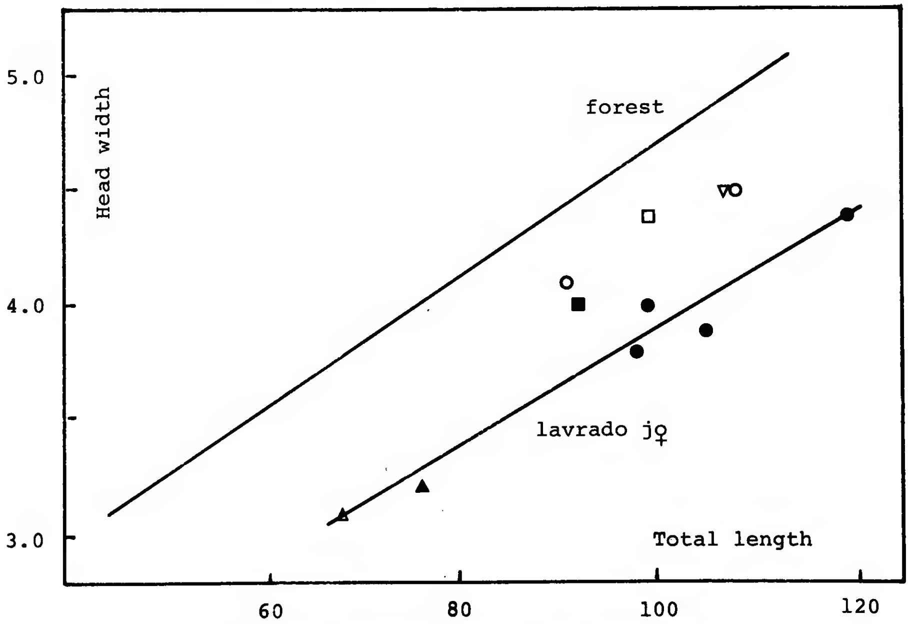


Fig. 12. Regression of head width on total length, forest and lavrado samples.

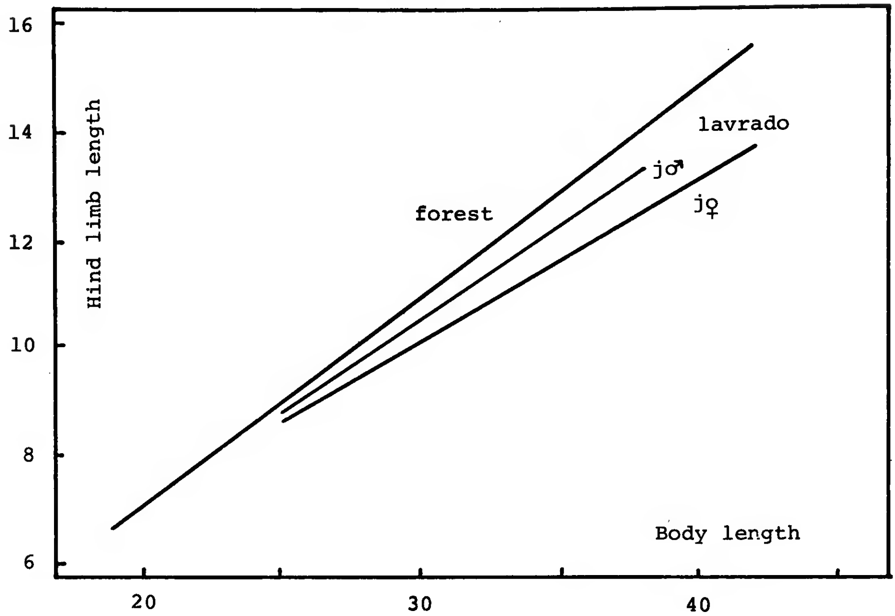


Fig. 13. Regression of hind limb length on body length, forest and lavrado samples.

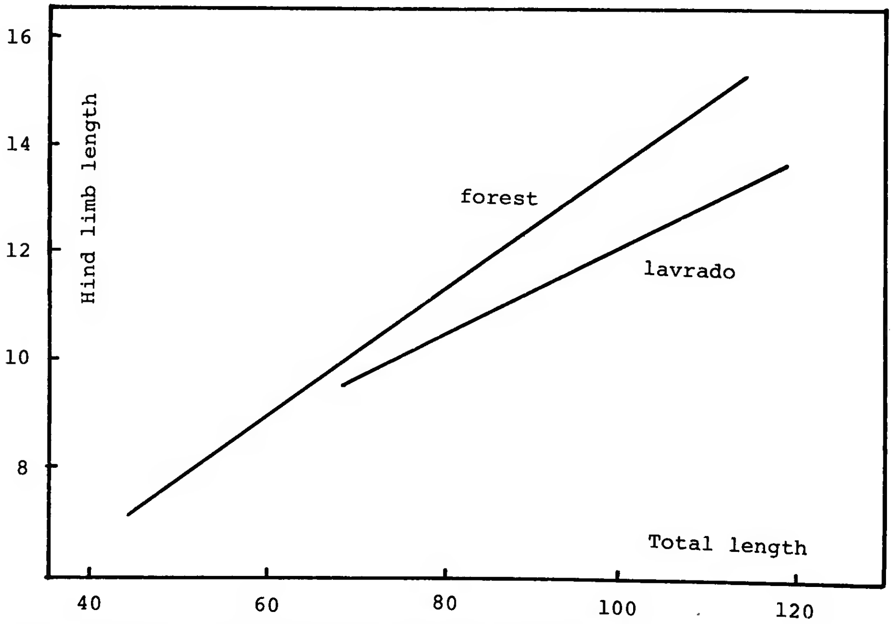


Fig. 14. Regression of hind limb length on total length, forest and lavrado samples.

The measurements (body 31mm, tail broken, head 6.0 x 4.0, hind limb 12), plotted on the respective Roraima graphs, show again good agreement. As to color pattern, the paratype has a dark lip, a dark belly, and inconspicuous dorso-lateral stripes, indistinguishable from the duller Roraima specimens.

DIFFERENTIATION

G. underwoodi, a widespread unisexual species, has not been studied from the viewpoint of geographical differentiation. A preliminary inquiry can be undertaken, with basis on the literature and on materials at hand. Thomas (1965) has data from Barbados and Trinidad, Hoogmoed (1973) from Surinam and Guyana. We have the following small samples: 11 specimens (2 males and 9 females, only the latter here analyzed) from two adjacent localities in northeastern Surinam, Langamankondre and Christiankondre: 7 specimens from localities on the middle Rio Negro: São João near Tapurucuara, Barcelos and Paricatuba; 3 specimens from the Santarém region (Alter do Chão and Taperinha).

Meristic characters. Table 11 shows the statistics of the scale counts, complemented by the Roraima data, transcribed from Table 8.

Table 11. *Gymnophthalmus underwoodi:* scale counts, geographical variation

		N	R	$\bar{x}$	s	V	I($\bar{x}$)
Dorsals							
Thomas 1965	Barbados	33	31 -34	32.7 ± 0.13	0.76	2.3	32.4 - 33.0
	Trinidad	18	31 - 34	32.2 0.19	0.79	2.4	32.4 - 32.6
Hoogmoed 1973	Suriman	32	29 - 35	33.3 0.20	1.12	3.4	32.9 - 33.7
	Guyana	9	32 - 34	32.7 0.24	0.71	2.2	32.1 - 33.2
MZUSP	Surimam	9	31 - 38	33.2 0.73	2.17	6.5	31.6 - 34.9
	Roraima	59	30 - 37	33.1 0.24	1.85	5.6	32.6 - 33.5
	Rio Negro	8	32 - 36	34.6 0.57	1.60	4.6	33.2 - 38.6
Ventrals							
Thomas 1965	Barbados	33	21 - 23	22.2 0.12	0.68	3.1	21.9 - 22.4
	Trinidad	17	21 - 24	22.4 0.19	0.79	3.5	22.0 - 22.8
Hoogmoed 1973	Surinam	32	22 - 26	23.5 0.19	1.05	4.5	23.1 - 23.9
	Guyana	8	20 - 26	22.9 0.79	2.23	9.8	21.0 - 24.7
MZUSP	Surinam	9	21 - 28	24.2 0.66	1.99	8.2	22.7 - 25.7
	Roraima	63	20 - 26	22.7 0.19	1.48	6.5	22.4 - 23.1
	Rio Negro	6	22 - 25	23.5 0.50	1.22	5.2	22.2 - 27.4
Lemallae							
Hoogmoed 1973	Surinam	31	16 - 19	17.0 0.13	0.71	4.2	16.8 - 17.3
	Guyana	9	15 - 17	16.7 0.24	0.71	4.2	16.1 17.2
MZUSP	Surinam	9	15 - 17	16.1 0.31	0.93	5.8	15.4 - 16.8
	Roraima	64	15 - 18	16.7 0.12	0.95	5.7	16.4 - 16.9
	Rio Negro	8	15 - 17	16.3 0.31	0.89	5.5	15.5 - 17.0

Two scale counts are available for all materials, dorsals and ventrals. Analysis of variance indicates heterogeneity of the means of both characters. Table 12 shows that in the case of dorsals this is due to the high values on the Rio Negro; in the case of ventrals the pattern is complex and makes no geographical sense.

Counts of fourth toe lamellae are available for Hoogmoed's materials, additionally to our own. Analysis of variance indicates heterogeneity, and Kramer's test has a curious result: there are two extreme groups, and two intermediate ones. One of the extreme groups is Hoogmoed's Surinam sample, the other our Surinam plus Rio Negro. That the two Surinam samples differ significantly can only mean that there has been a difference in the process of counting. The difference between the means is 0,92 scales, practically 1, which most probably means that Hoogmoed systematically included in his counts one more scale (basal or distal), than we did. It seems clear that there is no real geographic differentiation in the number of fourth toe lamellae.

Table 12. *Gymnophthalmus underwoodi:* homogeneity of means of scale counts (Kramer's test)

Dorsals

Rio Negro	Surinam Hoogmoed	Surinam MZUSP	Roraima	Barbados	Guyana	Trinidad
34.63	33.31	33.22	33.05	32.73	32.67	32.17
	—	—	—	—	—	
		—	—	—	—	—

Ventrals

Surinam MZUSP	Rio Negro	Surinam Hoogmoed	Guyana	Roraima	Trinidad	Barbados
24.22	23.50	23.49	22.88	22.73	22.35	22.18
	—	—	—			
		—	—	—	—	
			—	—	—	—

Fourth toe lamellae

Surinam Hoogmoed	Guyana	Roraima	Rio Negro	Surinam MZUSP
17.03	16.67	16.66	16.25	16.11
—	—	—		
	—	—	—	—

Means that do not differ significantly are underlined.

Table 13. *Gymnophthalmus underwoodi:* body proportions, geographic variation

	N	R(x)	R(y)	b	a	F	r^2
Tail length x Body length							
Roraima	23	20-42	24-72	2.06±0.098	-15.7±3.18	432.969***	0.9573
Hoogmoed, Surinam	11	26-42	46-78	1.88±0.156	-4.5±5.65	144.977***	0.9415
Head length x Trunk length							
Roraima	66	14.5-34.8	4.5-7.5	0.16±0.0047	2.0±0.13	1096.428***	0.9448
Hoogmoed, Surinam	31	20.2-34.9	5.8-8.4	0.17±0.010	2.3±0.30	273.939***	0.9043
Guyana	9	15.5-32.5	4.5-7.5	0.19±0.018	1.8±0.49	111.192***	0.9408
MZUSP, Surinam	9	24.8-32.8	5.7-7.2	0.15-0.045	2.1±1.31	10.696*	0.6044
Rio Negro	7	18.4-31.8	4.6-7.2	0.15±0.025	2.0±0.62	35.387**	0.8762
Head width x Head length							
Roraima	67	4.5-7.7	3.0-5.5	0.72±0.020	-0.2±0.12	1319.388***	0.9530
Hoogmoed, Surinam	32	5.8-8.4	3.7-5.5	0.61±0.059	0.2±0.43	106.889***	0.7805
Guyana	9	4.5-7.5	3.0-5.3	0.65±0.156	0.0±1.008	13.949**	0.4826
MZUSP, Surinam	9	5.7-7.2	3.0-5.3	0.79±0.153	-0.7±0.98	26.675**	0.7921
Rio Negro	7	4.6-7.2	3.5-4.9	0.59±0.057	0.7±0.32	104.278***	0.9543
Head width x Body length							
Roraima	67	19-42	3.0-5.5	0.10±0.0040	1.1±0.13	589.682***	0.9007
Hoogmoed, Surinam	32	26-44	3.7-5.5	0.092±0.0085	1.3±0.31	118.423***	0.7979
Guyana	9	20-40	3.0-5.3	0.11±0.011	0.8±0.38	96.885***	0.9326
MZUSP, Surinam	9	31-40	3.7-4.9	0.12±0.0296	0.1±1.05	16.132**	0.6974
Rio Negro	7	23-39	3.5-4.9	0.093±0.0070	1.3±0.21	176.472***	0.9725
Hind limb length x Body length							
Roraima	68	19-42	6-16	0.38±0.016	-0.6±0.54	549.733***	0.8928
MZUSP, Surinam	9	31-40	10-14	0.49±0.079	-5.3±2.80	38.844***	0.8473
Rio Negro	7	23-39	9-15	0.38±0.037	0.2±1.09	109.755	0.9564

Body proportions. Not much can be done about the geographical variation of body proportions in *G. underwoodi*; data are scarce. The only author to publish measurements, Hoogmoed, did not measure the hind limb. Additionally, our sample from Surinam and Hoogmoed's from Guyana lack complete tails. Finally, Hoogmoed's and our cephalic measurements are not comparable. Both his and our Surinam samples show excellent fits, which indicates that measuring procedure was consistent in each case. However, the differences between them are excessive, clearly indicating some difference in procedure. Accordingly, comparisons involving head proportions shall be performed only on materials measured by the same persons.

The regression of tail length on body length can be studied in MZUSP Roraima and Hoogmoed Surinam. The two regression lines (Fig. 15) are statistically parallel, but the intercepts differ: Surinam has longer tails.

With regard to the regression of head length on trunk length (Fig. 16), Hoogmoed's two samples are in close agreement; so are MZUSP Roraima and Surinam. The Rio Negro sample and the specimens from the Santarém area differ from the other MZUSP samples in having shorter heads.

The regression of head width on head length (Fig. 17) shows no geographic variation, i.e, all the MZUSP samples (Roraima, Surinam and Rio Negro, plus the Santarém area specimens) agree among themselves, and so do Hoogmoed's Surinam and Guyana samples.

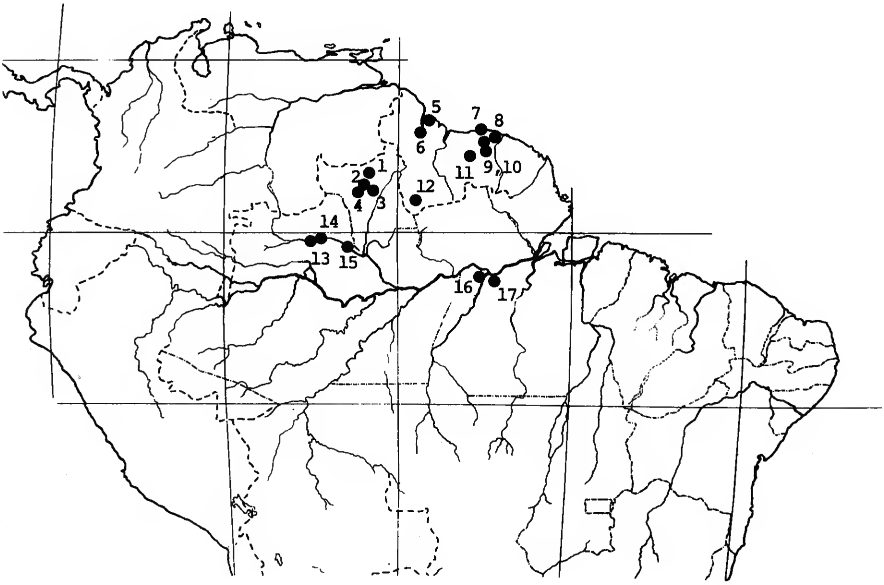


Fig. 15. Localities of *Gymnophthalmus underwoodi* involved in the geographic analysis: 1, Ilha de Maracá. 2, Cachoeira do Paredão. 3, Apiaú. 4, Cachoeira do Cajubim. 5, Georgetown. 6, Penal Settlement, Mazaruni. 7, Paramaribo. 8, Langamankondre and Christiankondre. 9, Wageningen and Moengo. 10, Brokopondo. 11, Voltzberg and Raleigh Cataracts. 12, Marudi. 13, São João and Paricatuba. 14, Tapera. 15, Barcelos. 16, Alter do Chão. 17, Taperinha. (Localities 5-7, 9-12, from Hoogmoed, 1973).

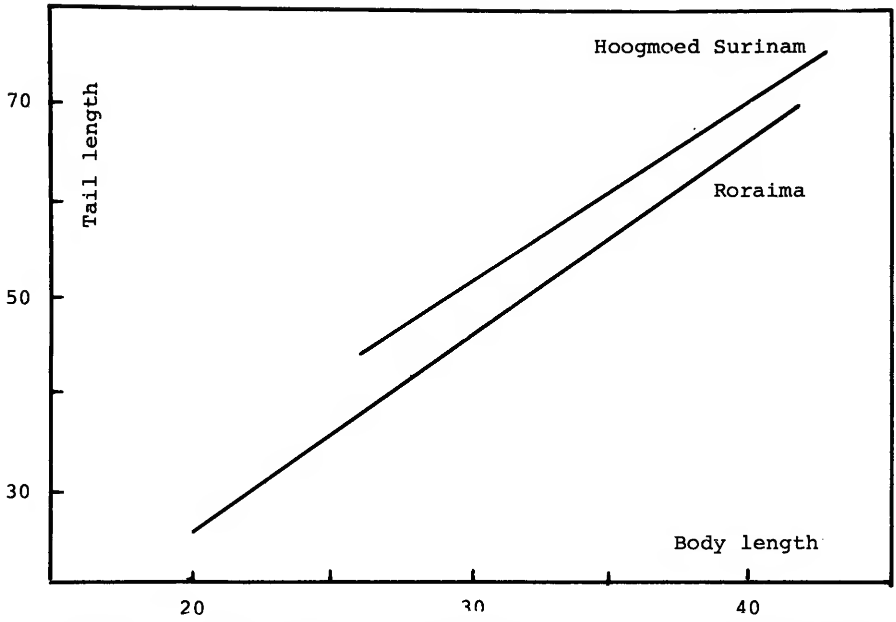


Fig. 16. *Gymnophthalmus underwoodi*: regression of tail length on body length, Roraima and Surinam (Hoogmoed) samples.

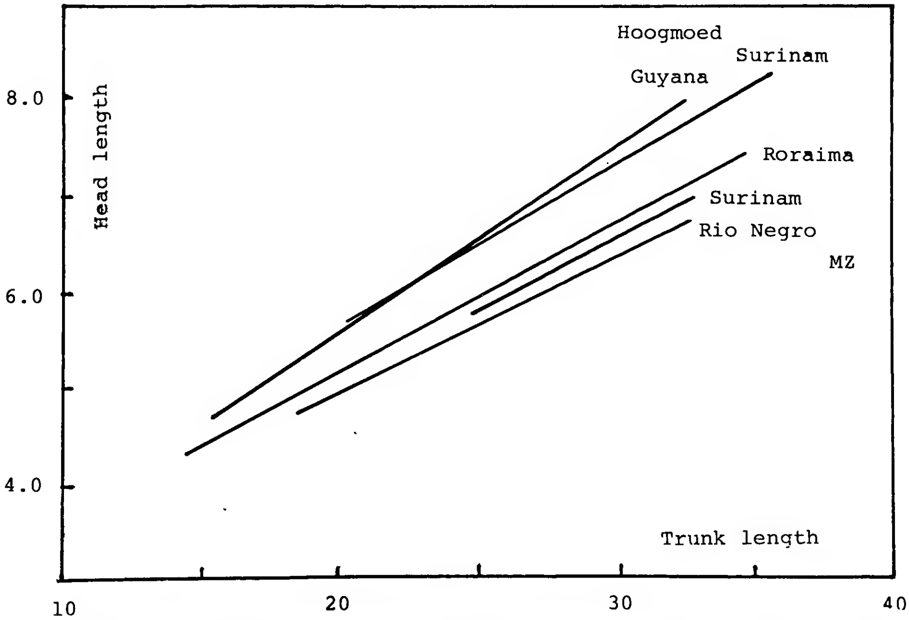


Fig. 17. *Gymnophthalmus underwoodi*: regression of head length on trunk length, geographic differentiation.

Head width on body length (in the circumstances the only measure of attenuation) shows a different pattern (Fig. 18). Hoogmoed's Surinam sample has narrower heads than his Guyana one. The difference between MZUSP Roraima and Surinam is larger still (Surinam specimens being again more slender) and the Santarém area lizards are the slimmest of all.

Finally, the regression of hind limb length on body length (Fig. 19), studied in the MZUSP samples, shows considerable geographic variation, Rio Negro having the longest limbs and Surinam the shortest. The specimens from the Santarém area have still shorter limbs.

Conclusion. It is apparent that the variation of *G. underwoodi* over an area of about one million square kilometers (very thinly sampled, it is true) shows very moderate geographic differentiation; especially, no manifest pattern is discernible.

THE LAVRADO FORM

We find that the bisexual lizard found in Roraima differs significantly in every respect, color pattern, meristic characters, body proportions and ecology, from sympatric *Gymnophthalmus underwoodi*. We proceed to describe it as a new species.

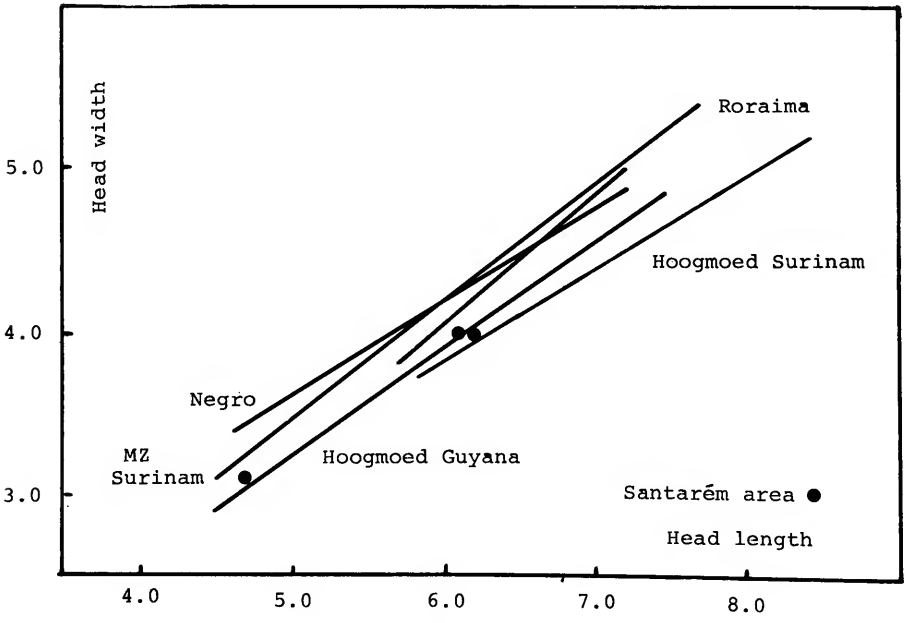


Fig. 18. *Gymnophthalmus underwoodi*: regression of head length on trunk length, geographic differentiation.

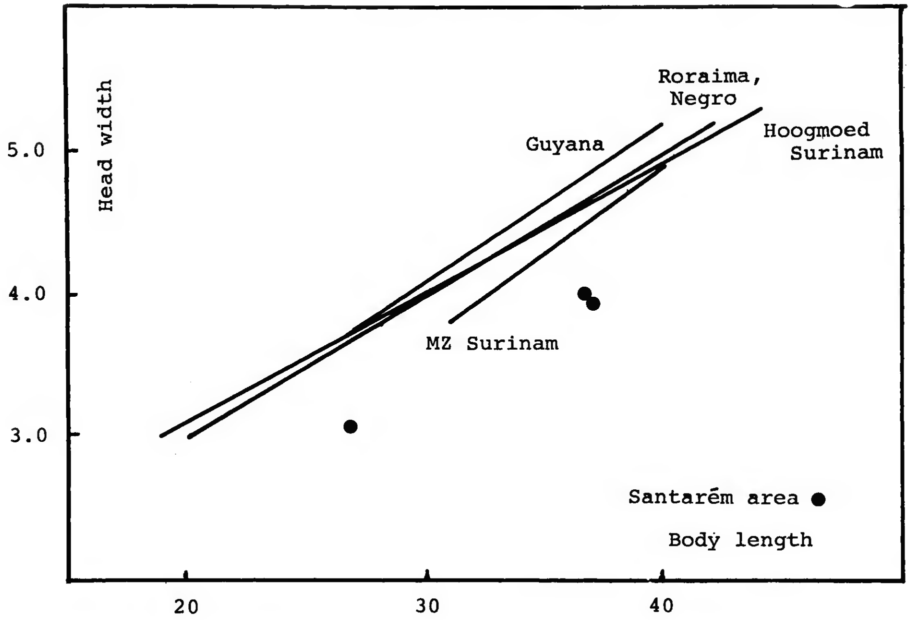


Fig. 19. *Gymnophthalmus underwoodi*: regression of head width on body length, geographic differentiation.

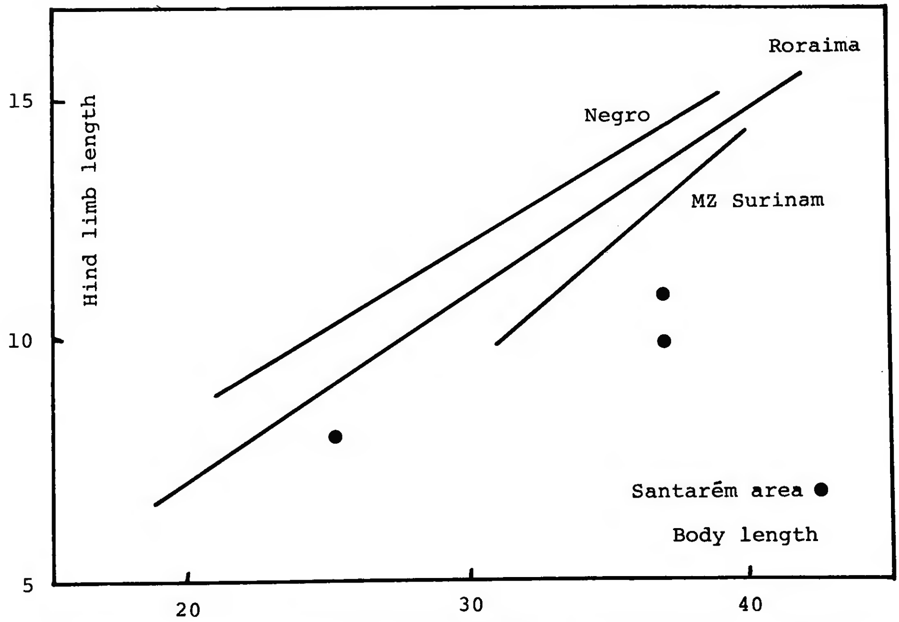
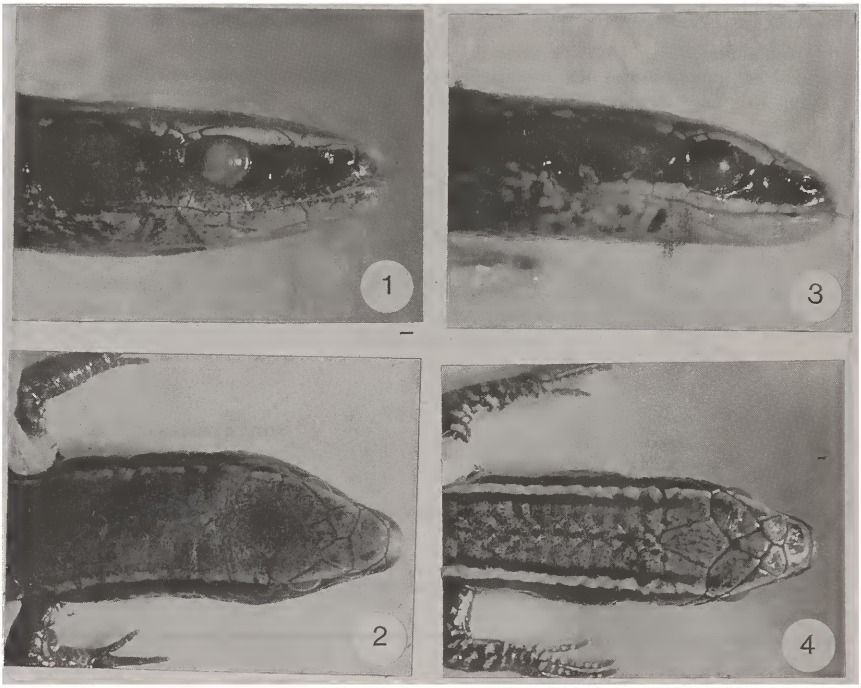


Fig. 20. *Gymnophthalmus underwoodi*: regression of hind limb length on body length, geographic differentiation.



Photos 1 and 2. *Gymnophthalmus underwoodi,* Ilha de Maracá.
Photos 3 and 4. *Gymnophthalmus leucomystax*, sp.n., holotype.

Gymnophthalmus leucomystax, sp.n.

Holotype: MZUSP 69301, Fazenda Salvamento, Rr, 23 September 1988, C.M. Carvalho coll., female.

Paratypes, all from the type locality. Males: 69302-303, 69307-309, 69311-312, 69314, 69316, 69319-321, 69324, 69327, 69335, 69340-341, 69346, 23 September 1988, C.M. Carvalho; 69351, 69354, 69638, 16 December 1988, P. E. Vanzolini & C. M. Carvalho, 69411, 11 December 1988, C.M.Carvalho. Females: 69304-306, 69310, 69313, 69315, 69318, 69322-323, 69325-326, 69328-334, 69336-339, 69342-345, 69347-349, 23 September 1988, C. M. Carvalho; 69352-353, 69355-356, 16 December 1988, P.E.Vanzolini & C. M. Carvalho; 69410, 11 December 1988, C. M. Carvalho; 69413, 23 September 1988, C. M. Carvalho; 69637, 16 December 1988, C. M. Carvalho; 69639, 69645-647, 13 March 1989, C.M. Carvalho. Unsexed young: 69317, 23 Setember 1988, C.M. Carvalho; 69640-644, 13 March 1988, C. M. Carvalho.

DIAGNOSIS

All scales smooth. Scales around midbody 13; dorsals to the level of the posterior margins of the thighs 30-37; ventrals 21-28; fourth toe lamellae 14-19. Upper lip entirely white or with a white bar. A pair of white, black bordered dorso-lateral stripes, extending from the supraocular region to the base of the tail, very vivid on the shoulder; ventral parts white to light tan, with a greenish metallic tinge.

ETYMOLOGY

Since the generic name is Greek and the first character to call attention to the individuality of the species was the white upper lip, leucomystax, "white moustache", in apposition, seems unavoidable.

DESCRIPTION (TABLES 6,8-10, FIGS. 7-14)

Body elongate, head flat, not distinct from the body, limbs moderately reduced, tail in the young about as long as the body, in the adult much longer. Four fingers, in the following order of increasing length: II-IV subequal, III a little longer, almost as long as IV. Five toes, I, II, III, V, IV.

Rostral broad, well visible from above, in contact with the first upper labial, with the nasal and with the frontonasal, which is large, irregularly heptagonal. Prefrontals small, slightly irregular, in contact on the midline. Frontal small, irregularly diamond-shaped, the posterior sides about twice as long as long as the anterior. A very large supraocular, meeting the prefrontal, the frontal, the interparietal, the parietal, the uppermost anterior temporal and the superciliaries. Interparietal the largest scale on the top of the head, diamond-shaped, with rounded posterior angle, meeting the frontal (briefly), the supraoculars, the parietal and the first row of dorsals. Parietals trapezoid, large, broadly separated by the interparietal, extending over the temporal edge. One post-parietal, small, subtriangular, also placed on the temporal edge.

Nasal entire, small, longer than high, almost fully occupied by the nostril; in contact with the rostral, the frontonasal, the loreal and the first upper labial. Loreal small, irregularly polygonal, in contact with the nasal, the frontonasal, the prefrontal, the anterior superciliary, the first (narrowly) and the second supralabials, and a small round preocular, which meets the second and third labials below and the subocular behind. The ring of scales around the eye comprises: the anterior superciliary, which is very large, triangular, broadly extending on the upper surface of the head, where its angle fits between the prefrontal and the supraocular; a second superciliary, minute, followed by two small scales on the posterior margin of the orbit; one very large subocular, with widened ends, at times divided in the middle, where it is narrowed. Five or six supralabials, first and fourth a little longer than the others, second to fifth following the outline of the orbit, the last similar to the temporal. Temporal rounded, smooth, imbricate, four or five between eye and ear. Ear opening small, with major axis dipping to the front, margins smooth.

Symphysial broadly trapezoid, narrower in front, wider than the rostral, reaching almost the midle of the first supralabial. One very large post-symphysial, with irregularly curves and angled sides. Two pairs of mentals, in full contact with each other on the middle and with the infralabials on the sides; their median sutures form a zigzag. Anterior gulars band-like, oblique, alternating (stepped) on the midline, well imbricate, becoming narrower toward the rear. Eleven or twelve scales between the mentals and the interbrachial row. No collar. Interbrachial row with five scales, the median one by far the largest, irregularly diamond-shaped.

Dorsal scales rounded, imbricate, keelless, finely shagreened, quincuncially arranged, those on the midline distinctly narrower in front, becoming broader posteriorly. Thirty one to thirty six scales between the interparietal and the level of the posterior margins of the thighs. Flank scales similar to the dorsals. Ventrals broader, well imbricate, each scale with 4-6 large pits near the hind edge. There are between the interbrachials and the anal flap 21-25 ventrals in males, 23-28 in females. Anal plate inconspicuous, with a medium-sized central scale and three marginals, of which the central is narrower than the laterals.

Dorsal scales of the forelimb similar to those on the trunk, but smaller. Posterior antebrachials large; carpals as antebrachials, passing abruptly into the convex scales of the single dorsal row of the fingers. Ventral scales of the upper arm small, irregular, becoming larger and more regular on the forearm. An ill-defined granular flexure zone on the wrist. Palm with large prominent granules, in five to seven very irregular transverse rows. Infradigital lamellae proximally bluntly tubercular, becoming flatter distally; eleven to fourteen lamellae under finger IV.

Scales on the front half of the dorsal aspect of the thigh similar to the trunk dorsals, merging gradually behind into a band of granules which is in abrupt contact with the ventral scales; these resemble the anterior dorsals. Male whith well defined femoral pores, 3-6 on each thigh, with prominent yellow plugs, increasing in diameter towards the midline, the two rows separated by one scale on the middle. Scales of the crus uniform, flat, rounded, imbricate. Tarsals almost as large as the crurals, similar to them in shape. No flexure bands. One single row of dorsal scales on the toes, some of the distal ones irregularly elongate. Plantar surface with prominent granules, roughly arranged in longitudinal rows more or less aligned with the toes. Ventral lamellae of the first phalanx produced, forming a distinct serration, which disappears distally. Twelve to eighteen lamellae under the fourth toe.

The scales of the intact tail are in direct continuation with those of the trunk, naturally diminishing gradually in size. Those of the regenerated tail are narrow, elongate, sub-hexagonal, with a sharp median keel.

The dorsal parts are fundamentaly olive gray, with a greenish metallic sheen in the live animal. The top of the head has a brownish cast and the tail gets darker distally. There is over all the back some degree of dark mottling. On the head the melanophores are assembled in patches on all scales, except the rostral. On the anterior part of the trunk they are particularly condensed on the vertebral scale row, forming a streak that varies in definition and length, but seldom surpasses the level of the shoulder.

The condensed patches of mottling on the head scales are the beginning of a black line that becomes continuous on the parietal region and runs onto the tail, blacker and more definite in front, becoming progressively less dense from about midbody. This dark band is the upper border of the white stripe that was discussed in the initial characterization of the species, and which begins on the rostral, runs along the canthal, superciliary and temporal edges, becomes, as repeatedly stressed, very vivid on the neck and shoulder, then progressively loses contrast, acquires a greenish tinge and disappears on the tail.

The sides of the body are dark, beginning on the rostral, continuing on the flanks and extending on the tail. The upper edge of this lateral belt is darker and limits ventrally the white stripe. It is still evident after the dorsal border has vanished. The upper lip, as described, is white; there is, in sequence, an irregular light stripe, crossing the ear, progressively losing definition and acquiring mottling, to disappear on the anterior quarter of the flank. There is a series of dark spots on the infralabials, continued posteriorly, behind the level of the ear, as a heavily mottled band that limits ventrally the light flank stripe.

The ventral parts are light, with a greenish-bluish tinge, and a variable amount of mottling posteriorly. This mottling gets much denser on the tail, that is almost black ventrally. The ventral aspect of the limbs resembles the belly, but is invaded to a variable extent by the darker dorsal color. The palmar and plantar areas are particolored, brown and light gray.

COMPARISONS

The geographic distribution of *Gymnophthalmus*, as currently understood, is complex. For exemple, *G. underwoodi* provenly occurs on islands and on the continent; *speciosus* is questionably distributed over Central America and large extents of South America; *multiscutatus* is shown by preliminary analysis to vary geographically. This general pattern compels us to compare *leucomystax* with all described forms. Comparison with G. *underwoodi* is of course the mainspring of this work, and we hope it has already been satisfactorily done. As to the remainder, we adopt the following order: (i) *speciosus*, which is said to occur in the Venezuela llanos, an adjacent and ecologically related dominion (ii) *multiscutatus*, the next nearest neighbor; (iii) *rubricauda*; (iv) the purely insular forms.

Cunha's (1981) specimens from Coronel Motta, Roraima, a lavrado locality, are doubtless *leucomystax*.

Gymnophthalmus speciosus (Hallowell, 1861)

The distribution of this species in South America, in fact its very presence, is a vexatious problem. Three subspecies are recognized in Central America, from the isthmus of Tehuantepec southward, the nominal one extending into northerm South America (Peters and Donoso-Barros, 1986). Almost all South American records are flat, uncommented statements, the only critical one being Thomas's (1965), who, as already mentioned, preferred to cite the form within quotation marks.

The question is not simple, and not to be solved within the scope of this paper. We cannot avoid addressing it, however, albeit in a limited and tentative way, given the record of *G. s. speciosus* by Staton and Dixon (1977), from the Venezuelan llanos, an area of extreme relevance to us.

We have before us: (1) MZUSP 70246-70247 (formerly USNM 167212 B-C), from San Salvador, El Salvador, originally identified simply as *speciosus* but, given (Mertens, 1952) the cephalic scutellation and the locality, to be rather called *speciosus birdi*; considering the triviality of the subspecific differences mentioned by Mertens (1952) we see no objection to using these specimens to represent the species. (2) ZMB 1361-1363, from "Caracas", Moritz coll., the Lichtenstein (1856) specimens. (3) MZUSP 64962-64967, from Mantecal, estado Apure, Venezuela (07°33'N, 69º09'W), in the llanos, closely corresponding to Staton and Dixon's (1977) record.

Even taking into account the insufficiency of these materials, and additionally the age of the Berlin specimens, there are still unescapable differences among then. The Venezuelan samples agree between themselves and widely differ from the Salvadoran one in number of dorsal scales (respectively 32-37 and 45-48), in number of ventral scales (22-27, 29-26), and in head length (longer heads relative to trunk length in Venezuela).

The "Caracas" specimens seem to differ from the llanos ones in scales around midbody (15-17 against 13-14) and fourth toe lamellae (12-14, 14-17).

Concerning color pattern, the ZMB specimens are very faded, but whatever coloration remains tends to be reddish. The El Salvador and Mantecal samples differ significantly. The background of both Central American examples is sombre; dorsally, the scales are dusky, with slightly lighter edges; there is in front (neck and shoulders) an indistinct dorso-lateral line formed by the coalescence of adjacent light edges. The ventral parts are also dark, but less so than the back; the light edges of the scales tend to form a reticulate pattern, lighter and better defined on the belly than on the chest. The tail is very definitely red, with sooty markings dorsally on the base. This color pattern closely agrees with Hallowell's description. Taylor (1956), however, describes, for Costa Rican examples, a brighter pattern, not unlike that to be described next.

The Mantecal specimens show, as said, a much more vivid pattern. The middle of the back is gray with mottling that tends to form three longitudinal, rather indistinct streaks. There is one definite longitudinal line, from the rostral through the canthus and the superciliary edge down the back, passing well above the ear and the limbs, and disappearing on the tail. This stripe is formed, on the body, by particolored white (above) and black scales. The flanks are darker than the back, rather densely mottled. Each belly scale is dark gray in front, lighter behind, the whole assuming an irregularly barred appearance. The tail is gray in five specimens, red in one; dorsally it shows ill-defined cross-bars made of alternate dark and light spots. The sides of the tail are conspicuously white-spotted; the middle of the ventral surface is a smudgy light gray.

It seems clear to us that it would be unreasonable to assemble these materials under one subspecific name. Since there are no unaccounted for synonyms in the literature, the Venezuelan specimens seem to belong to a new form, but we think it would be premature to describe one without a better geographic coverage and without samples adequate, in number of specimens and quality of preservation, to bring the analysis to the level made possible by the Roraima materials. It would be very useful, too, to have a better understanding of the Central American forms. Anyway, it becomes imperative at present to verify whether the llanos populations should not be included in *leucomystax.*

Of the four scale counts investigated, three, dorsals, ventrals and lamellae, show a same pattern, one much to be expected: Mantecal has a narrower range of counts, included within that of *leucomystax*. The exception is scales around midbody. All *leucomystax* have 13; three specimens from Mantecal have 13, the other three have 14. The probability of this difference in frequencies being due to random causes (Fisher's exact test) is less than 0,0004.

Differences in body proportions were verified graphically, by plotting the Mantecal values on the corresponding *leucomystax* graphs. Llanos materials at hand are not adequate for analysis of regression, but in several cases (e.g., head length x trunk length, head width x body length, hind limb length x body length) there are differences that cannot be overlooked.

Finally, there is very good resemblance in color pattern, but again some differences, the three main ones being: (i) the longitudinal stripe of the Apure specimens in never as vivid as in *leucomystax;* (ii) their belly is always dark bluish gray, with reticulations formed by light scale edges; (iii) in two specimens the tail has a very definite red tinge.

Differences such as these might be expected from a geographically differentiated population, or from an intergrading one between well-defined subspecies. Of course, intensive geographic samplig and molecular techniques may reveal yet another sibling species. This is a far as we are prepared to go in the present context.

Gymnophthalmus multiscutatus Amaral, 1933

We have before us abundant materials of this species (156 specimens, including the type) from many localities in northeastern Brasil. The present comparison was based initially, in more detail than here reported, on samples from the caatingas and agreste of Pernambuco (Vanzolini, 1974), and then checked against the remainder of the materials.

G. multiscutatus, in spite of occurring in an ecologically well defined area, not very large by continental standards (ca. 800,000 sq km) is not a simple lizard at all. It has been known (Vitt, 1982) to present strong dimorphism in body shape; additionaly the present investigation evinced marked, complex and hitherto unsuspected geographic differentition within relatively short distances. Thus, in spite of the relevance of the form to any speciation scenario, comparison at this time must be restricted to diagnostic features, with the only object of validating and placing into perspective the new species.

There are some pholidotic differences. The supraocular of *leucomystax* is much larger, and is entire, while that of *multiscutatus* is smaller, less oblique and transversely split behind. The anterior superciliary of *leucomystax* appears on the dorsal aspect of the head, insinuated between the supraocular and the prefrontal, which does not happen in *multiscutatus*. Ventrally, the postsymphysial of *multiscutatus* is transversely, and the next scale is longitudinally, divided.

The body scales of *multiscutatus* are relatively narrower, which reflects on the scale counts. Dorsal scales, longitudinally counted, vary from 30 to 38 in *leucomystax*, from 31 to 40 in *multiscutatus*; ventrals vary from 21 to 28 in both forms. Scales around midbody, however, differ diagnostically: all *leucomystax* so far have 13 scales, while *multiscutatus* has 14 to 19, with the mode at 16. Fourth toe lamellae and femoral pores have similar ranges in both forms.

A detailed comparison of body proportions is not desirable at present, as it would need a deeper study of *multiscutatus*. It is safe to say, however, that the latter has a relatively shorter tail and that head proportions are about the same in the two species.

The importance of color pattern to the systematics of *Gymnophthalmus* has already been mentioned. In the present comparison we must deal again with hue and pattern.

G. multiscutatus has overall a rich reddish brown hue, turning to red on the tail; *leucomystax*, as described, is generally a bronze olive, with a dusky tail.

G. multiscutatus has two pattern morphs. One, that can be called "striped", shows light longitudinal, narrow but very definite light stripes. Those of the outermost pair start under the ear, run over the insertion of the arm and end at the groin. Those of the next pair start on the upper lip, pass over the ear, run along the flank, touching the insertion of the thigh, and disappear on the tail. Each stripe of the next pair runs over the canthus, the superciliary edge and the side of the back onto the tail. Finally, a median pair of light lines starts on the rostral and frontonasal as a single streak which, on the frons, splits in two, which run along the back, separated by two scales, become fused again on the sacrum and disappear on the tail. The area between the two median lines is slightly lighter than the remainder of the back and flank which, besides being darker, shows a variable but always conspicuous amount of mottling. It is a vivid and rather pretty pattern.

What can be called the "plain" morph lacks the median pair of stripes, or shows only a shadow of it, but the pattern on the sides is still much more complex and vivid than that of *leucomystax.*

The two morphs of *multiscutatus* are equally distributed between the sexes and among size classes. Their scale counts do not differ significantly.

Gymnophthalmus rubricauda Boulenger, 1902

We have one specimen of this form, from a locality (Fazenda Canaã, at 20°20'S, 52°02'W) in the Brasilian state of Mato Grosso do Sul, which is far from the type locality, Cruz del Eje, in Córdoba, Argentina (30°44'S, 64°48'W); the specimen, however, agrees exactly with Boulenger's description and drawing. There are many differences between this form and *leucomystax,* as could be expected. The main ones are: prefrontals separated on the midline (meeting in *leucomystax*); 16 scales around midbody (13); 5 pairs of longitudinal lines over a dark brown or black background (on each side: one streak from axilla to groin; one from the lip through the ear and over the limbs to the tail; one from the canthus through the superciliary edge to the tail; one starting as a single streak on the snout and bifurcating on the frontonasal; and finally one starting as a single streak on the interparietal, splitting at level of the 4th-5th dorsal scale and reuniting again on the tail). Our specimen is presumably a female, as it has no pores; Boulenger's type had eight pores on each side, the highest count we have eucountered in the genus, *leucomystax* having at most six.

The Lesser Antillean forms

We base this set of comparisons on the literature, especially on Thomas (1965), and on five ZMB specimens, four *lineatus* from Bonaire and one *pleii* from Martinique. There are several statistical differences between these forms and *leucomystax*: we shall cite only fully diagnostic ones.

G. pleii (the three subspecies) has from a few to many rows of keeled dorsal scales; scales around midbody vary from 17 to 19, against the 13 of *leucomystax.* The same count for *G. lineatus* is 15-17.

As to color pattern, in *pleii* (Thomas, 1965) the dorso-lateral light stripe reaches at most midflank; the hind limb is characteristically reddish. The belly is dark. In *lineatus* (ZMB specimens), the upper light stripe is rather broad and varies in definition, looking duller at midflank, but definitely continues for a short length on the tail, which is red. The lower ("quadrilineatus") ligth stripe is narrow, and extends from axilla to groin. The belly is creamy, the throat from light to dark gray.

CONCLUSION

We hope it has become evident how rich in interesting problems are the systematics and ecology of *Gymnophthalmus* in northernmost Amazonia and certainly elsewhere if properly investigated.

It has been possible, at this stage, to establish the presence of two sympatric species in Roraima, to characterize them morphologically, and little else. The problems raised are not intrinsically intractable, but, at all levels, they demand much more information than available at present.

As of now, it is possible to draw the following outline. The systematics of the microteiids at the generic level is far from stabilized; furthermore, many new species await description. These qualifications do not forbid, however, a semi-quantitative appraisal of the broad geography of the group; the data are, in fact, unequivocal.

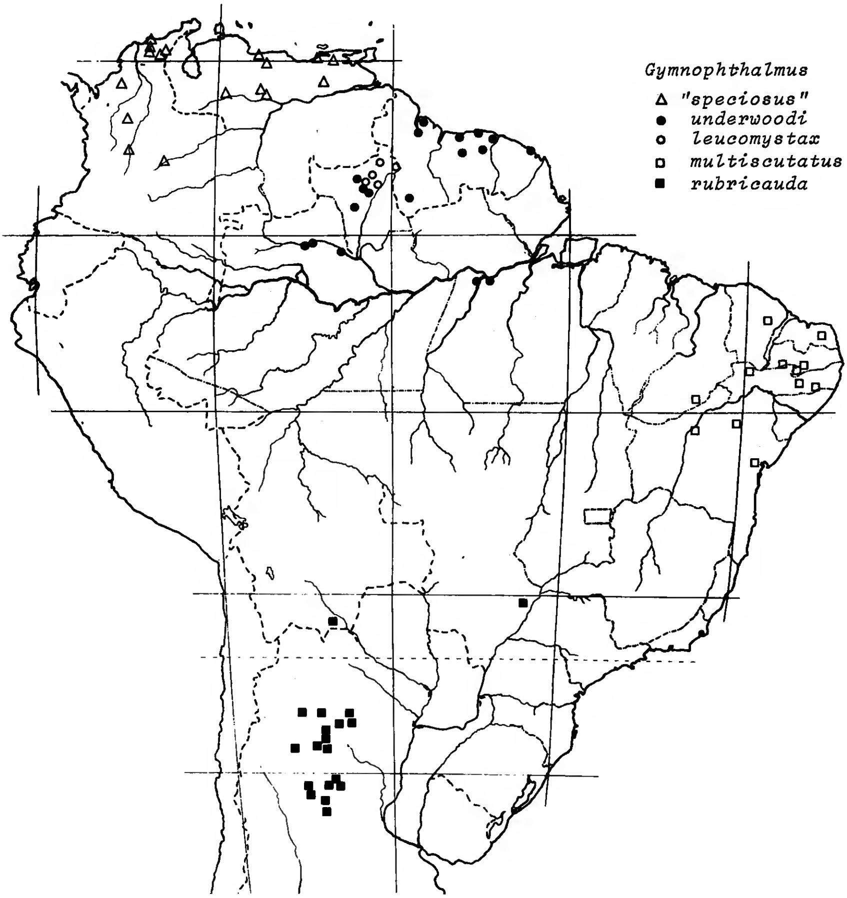


Fig. 21. Approximate distribution of the species of *Gymnophthalmus* in continental South America. Data from the MZUSP collection and from Ruthven (1922), Burt and Burt (1931), Mertens (1933), Dunn (1944), Schmidt and Inger (1951), Thomas (1965), Test, Sexton and Heatwole (1966), Donoso Barros (1968), Gallardo (1969), Medem (1969), Hoogmoed (1973), Gasc (1975, 1976, 1981), Hulse (1977), Staton and Dixon (1977), Gasc and Lescure (1981), Gallardo, Tio-Vallejo and Miranda (1985).

Twenty-seven microteiid genera are currently accepted, all occurring in the Neotropical region. Of these, twenty genera are restricted to South America, none to Central America. The seven shared genera differ in extension to the north: three reach Panama, three get to Costa Rica and one, our own *Gymnophthalmus*, goes as far north as Guatemala and southernmost Mexico.

We have counted in the literature 106 species considered as valid, of which three are endemic to Central America. Three species are known from the Lesser Antilles, of which two (one is *G. underwoodi*) also occur on the continent. There is no doubt that the group as a whole and the genera individually are autochtonous to South America.

Fig. 21 shows the *Gymnophthalmus* localities we have been able to identify in continental South America. The following patterns emerge:

1. With the exception of the pair *underwoodi-leucomystax*, the species are allopatric.
2. With the exception of *underwoodi*, they inhabit open formations. Especially interesting is the bipolar distribution of *multiscutatus* and *rubricauda* in the NE-SW belt of open formations that crosses South America from the caatingas to the Chaco (Vanzolini, 1988).
3. The only hylaean species, *underwoodi*, is limited to Central Amazonia, from the right bank of the Amazon to the Caribbean shores, but no farther east than 54°, west than 64°. This is not an artifact, as there has been intensive collecting in several areas where the genus has been found (Crump, 1978; Cunha et al., 1985; Dixon and Soini, 1986).

On the basis of these patterns, we believe *Gymnophthalmus* to have originated in the open formations of Central Brasil. The bipolar differentiation of *multiscutatus* and *rubricauda* has parallels, such as the gekkonid *Phyllopezus* (Vanzolini, 1953; Hellmich, 1960). The spread of the genus northward is certainly one more instance of distributions determined by contraction and spreading of forested areas consequent to climatic cycles (review in Blondel, 1986). Present evidence clearly implicates Haffer's belt of low rainfall as a major route. It is in this respect that relationships between cerrados and lavrados, stressed above, acquire special importance, in that they indicate past spatial continuity.

It would be tempting to nominate *leucomystax* as the extant representative of the immigrant stock, but we already know that there is still much to learn about *Gymnophthalmus* in Amazonia. Some questions that may be raised in the context are:

First, and of course a most intriguing one, is that of the origin of *underwoodi*. As a parthenogen, it may be a hybrid. If so, who are the parents? If not, by which mechanism was parthenogenesis attained? In either case, how were the morphological peculiarities (especially tail color) and the sylvan habit acquired? Was there a "vanishing refuge" episode (Vanzolini & Williams, 1981) or one of sympatric or parapatric speciation? These are questions that morphological and chronological analyses cannot solve, only propose: fortunately, the animals are common, and materials are available for cytogenetic and biochemical studies, which are under way (Martins, in prep.)

Another engaging problem is that of the identity and distribution of the red-tailed forms north of the hylaea. The matter of tail color, and the correlated one of tail-waving behavior, has been experimentally studied in scincids by Cooper and Vitt (1985), who concluded that it is related to predation avoidance. Laurie Vitt has kindly brought to our attention some unpublished observations of his on analogous behavior in the microtiids *Micrablepharus maximiliani* and *Pantodactylus albostrigatus*, studied in the cerrados of Central Brasil. We also have preliminary observations on a not yet identified red-tailed form ("speciosus" group) in Roraima. There is no doubt that there are a dark-tailed and a red-tailed suites of *Gymnophthalmus*, probably with distinctive behaviors, but taxonomic, distributional and ecological information on them is still meagre. For instance, what is called *G. speciosus* in Venezuela may well be something else: what about the Colombian populations? Additionally, as said, we have materials of one other (in fact, possibly two) species of red-tailed *Gymnophthalmus* from Roraima and northern Pará, but not yet in sufficient numbers for adequate morphological analysis, much less for a geographical study; these would be, on their turn, basic for cytogenetic and biochemical investigations. To inquire into the origin of parthenogenesis, for example, one needs at least a catalog of putative parents, an idea of their present and past distributions, and adequate experimental materials.

In the circumstances, we are proceeding with field work; besides whatever further taxonomy that may be needed , materials will continue to be forwarded to geneticists and molecular biologists. We are confident the returns will be ample.

Note added in proof.

Since this paper was delivered for publication two articles have appeared which have direct relevance to it, although they imply in no change to our conclusions. One is: C.J. Cole, H.C. Dessauer, C.R. Townsend and M.G. Arnold, 1990, "Unisexual lizards of the genus *Gymnophthalmus* (Reptilia: Teiidae) in the Neotropics: genetics, origin and systematics", Amer. Mus. Novit. 2994; the other J.M. Martins, 1991, "An electrophoretic study of two sibling species of the genus *Gymnophthalmus* and its bearing on the origin of parthenogenetic *G. underwoodi* (Sauria: Teiidae)", Rev. Brasil. Gen. 14. The lizard referred to in Martins's work as *"Gymnopthalmus* sp.n." is *G. leucomystax*. In the same context, we agree that (as in fact our statistical analysis shows) more than one clone goes under the name *G. underwoodi*. What status to give them is still a moot question. As to the Novitates paper, we must only repeat that the specimens that have been called *G. speciosus* in Venezuela certainly do not belong to this Central American species. They represent a new species that should be described whenever good South and Central American samples are available.

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