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SOUTH AMERICAN AÑOLES: THE GEOGRAPHIC DIFFERENTIATION AND EVOLUTION OF THE *ANOLIS CHRYSOLEPIS* SPECIES GROUP (SAURIA, IGUANIDAE)

P. E. VANZOLINI
Museu de Zoologia, Universidade de São Paulo

ERNEST E. WILLIAMS
Museum of Comparative Zoology at Harvard College

FIRST PART: TEXT

Anolis chrysolepis brasiliensis, ssp. n., holotype.

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INTRODUCTION

Among the approaches to the problem of the origin and mode of formation of complex tropical biotas, the study of differentiation at the species and species-group level, given suitable materials and methods, can afford very rewarding results.

Many South American animals, and among them species of *Anolis,* appear to show in their patterns of differentiation the paramount importance of the history of forest and open formations in the northern two-thirds of the continent. One paper (Williams & Vanzolini, 1966) has already been published delineating such a pattern. A more detailed analysis, with proportionally more far reaching conclusions, is permitted by the widely distributed *Anolis chrysolepis* species group.

The species group previously analyzed was that of *Anolis punctatus* and its closest relative *A. transversalis.* These are members of the endemic South American *alpha* section of Etheridge (1960) (fig. 1) — old residents whose distribution is in no way an immigrant pattern. The group under study in this paper is, on the contrary, a member of Etheridge's *beta* section, which is believed to be autochthonous in Mexico-Central America and only a relatively recent, probably post Pliocene, invader of South America. It will be seen that very recent events in the evolution of the South American morphoclimatic regions have played a very important part in the determination of the present pattern of differentiation, and that some of the processes are surprised, as it were, in mid-course.

In fact, the recency of the phenomena that have resulted in the present patterns of distribution and differentiation is such that no difference due to the length of presence in the continent is found between autochthonous and immigrant groups. The general pattern we find is one of alternate differentiation of isolates in refuges and pronounced recombination following coalescence of the refuges. It must be emphasized that these alternations have been very rapid, of the order of magnitude of thousands of years and not of geological periods, as formerly believed.

There are several reasons for choosing the *chrysolepis* species group for analysis. First, it has an extremely broad latitudinal distribution in South America, from 12 degrees North to 22 South. The longitudinal distribution is also very extensive north of the Equator, encompassing all of cis-Andean South America. South of Amazonia the area of the group is narrower, but, for this same reason, extremely interesting. Furthermore, previous knowledge of the group indicated the presence of areas of marked differentiation. Finally, it was known that, through the cooperation of a number of scientific institutions in Europe and the

Americas, it would be possible to assemble enough materials for as detailed an analysis as is presently possible in South American zoology.

Another incentive for the undertaking of this study is the recent availability of some data on the Quaternary climates and plant distributions in the continent. These data are still few, scattered, hard to obtain and to interpret, but have alrealdy enough significance to permit

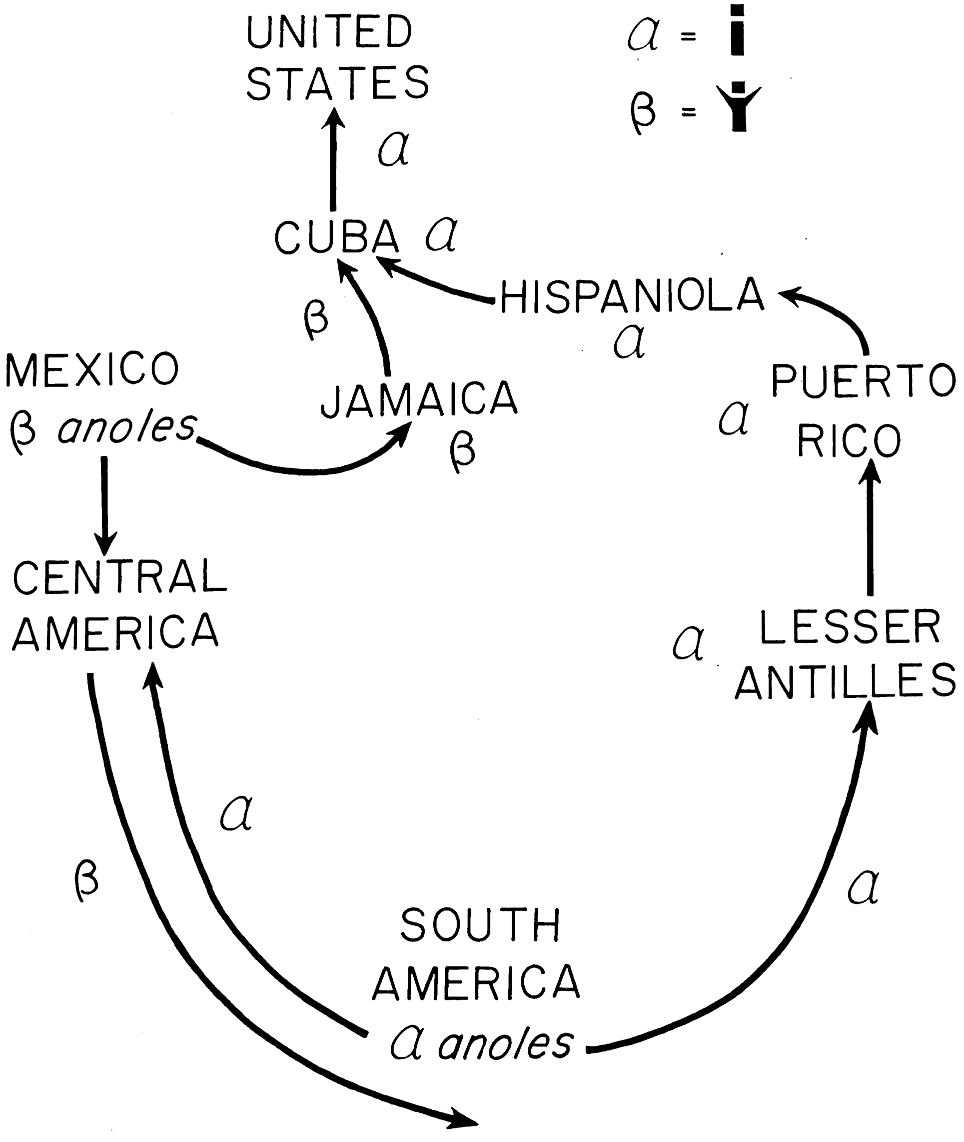


Fig. 1. Centers of origin and invasion patterns of two major groupings in *Anolis* distinguished by Etheridge (1960) on the basis of presence or absence of transverse processes on the caudal vertebrae.

a depth of analysis one order of magnitude beyond what was previously possible.

Thus a study of the *chrysolepis* species group may be expected to display a picture of the differentiation of a successful immigrant group in a large tropical continental area, and to furnish indications regarding the mechanisms operative in such evolutionary phenomena. At the same time, it will illuminate one corner of the general evolution of the genus *Anolis,* perhaps the largest and possibly the most complicated of vertebrate genera. Thus the main interests of the authors, as well as their special resources and talents, complement and interdigitate with each other, a phenomenon most desirable in co-authorsip.

THE *ANOLIS CHRYSOLEPIS* SPECIES GROUP DEFINED

Definition of any species group within *Anolis* is difficult. Numerous as the species are, the number of characters that vary are far fewer, and there is therefore a tremendous amount of parallelism and convergence. Remotely related forms, especially if geographically well separated, may be quite similar. We must therefore use geography as part of any species group definition, and we distinguish the *chrysolepis* group only against South American forms adjacent or sympatric.

Members of the *chrysolepis* species group are *beta* (Etheridge, 1960) forest anoles of moderate size (up to 80 mm snout-vent length) with short heads and narrow but "raised" digital pads. Each nasal scale is separated from the rostral by 2-3 scales. The middorsals are usually enlarged but never as large as the ventrals. The ventrals are large (38-63 counted from the level of the anterior margin of the arm to the level of the anterior end of the inguinal sulci), and strongly keeled. Lamellae under digits ii and iii of fourth toe, 12-20. Dewlap short to moderate, present in both sexes, but smaller on the female, not reaching to level of axilla, either wholly red, or wholly black, or black with a red edge. Postanals not or indistinctly enlarged.

The ventral scales of the *chrysolepis* species group are larger than those of any South American anole that does not either (1) have the dorsals as large as or larger than the ventrals, or (2) have the *Norops* condition of the digital dilations (fig. 2) or (3) both. All South American species with the dorsals as large as or larger than the ventrals are allopatric to the *chrysolepis* species group and are confined to the trans-Andean zone.

Two species with the digital dilations on phalanges ii and iii continuous with the scales under phalanx i and hence formerly called *Norops* (for a discussion of the rejection of the name *Norops* see Williams, 1963), do, however, widely overlap the range of the *chrysolepis* species group: *Anolis auratus* Daudin in Venezuela, the Guianas and Brasilian Amazonia, and *Anolis meridionalis* Boettger in Brasil south of the Amazon. These, however, are grassland forms never syntopic with the forest-dwelling *chrysolepis* species group.

Only two species have been erroneously referred to the *chrysolepis* species group, *Anolis tropidogaster* Hallowell and *Anolis meridionalis*

Boettger. The first, confined to Colombia, Panamá and western Venezuela, overlaps a *chrysolepis* group member only in the Bogotá region. The second, occurring from northern Paraguay through lowland Bolivia to Central Brasil is widely sympatric with the south-central Brasilian representatives of the *chrysolepis* species group. We present below a synonymy and comment on these two species the better to eliminate them from further discussion.

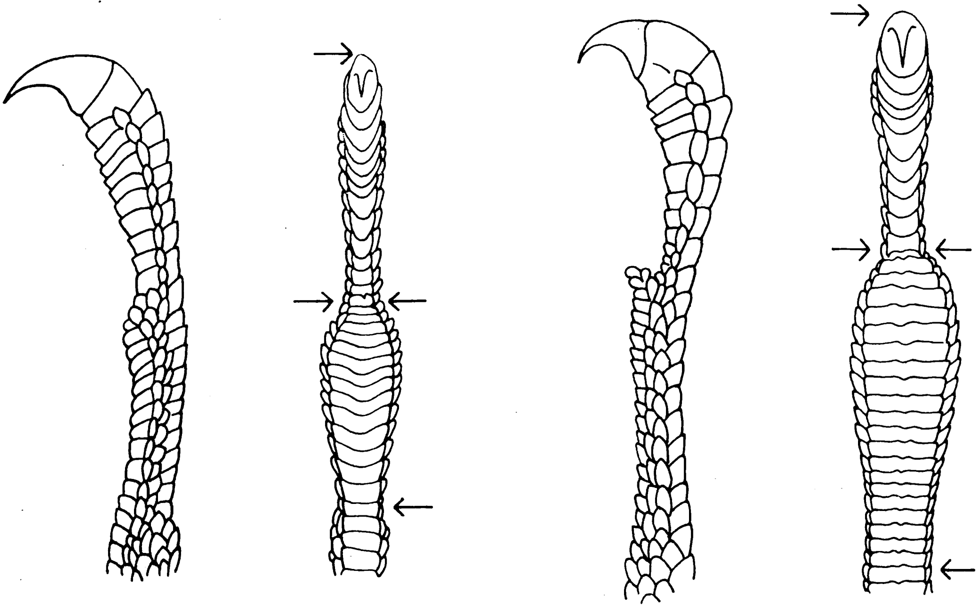


Fig. 2. The *Norops* condition of digital dilations and the more usual *Anolis* condition (After Williams, 1963).

SPECIES EXCLUDED FROM THE *CHRYSOLEPIS* GROUP

Anolis meridionalis Boettger

Anolis meridionalis Boettger, 1885: 215. "Paraguay".
Anolis holotropis Boulenger, 1895: 522. Mato Grosso, Brasil.
Norops sladeniae Boulenger, 1903: 69.Chapada, Mato Grosso, Brasil.
Anolis steinbachi Griffin, 1917: 308. Provincia del Sara, Bolivia.
Norops marmorata Amaral, 1932: 63. Jaguara, Rio Grande, Minas Gerais, Brasil.
Norops meridionalis; Schmidt, 1939: 9.
Anolis chrysolepis meridionalis; Hellmich, 1960: 22.

This species, descriptively a *Norops* as that genus has usually been defined, is only superficially similar to the other species that have usually been referred to the genus (e.g. by Schmidt, 1939). In fact

Norops as conceived by such authors as Schmidt is a composite of distantly related convergent species (Etheridge, 1960; Williams, 1963).

A. meridionalis is, however, like the other species that have been referred to *Norops,* a *beta* anole in the informal grouping of Etheridge (1960); if *meridionalis* is ever returned to the genus *Norops,* it will presumably be according to a concept which includes all the numerous *beta* anoles in this one taxon.

TABLE A

Comparison between *A. meridionalis* and adjacent *A. chrysolepis* (Tapirapés)

Character	*meridionalis*	*chrysolepis*
first phalanx of digit	*Norops* type	not *Norops* type
dewlap	black with red edge	black
ventrals, males	42 - 54	43 - 53
females	44 - 53	40 - 50
fourth toe lamellae, males	13 - 16	16 - 19
females	12 - 15	15 - 18
loreals, males	3 - 6	5 - 8
females	4 - 6	5 - 8
scales across snout, males	6 - 10	8 - 11
scales between semicirles	0 - 2	0 - 2
scales between interparietal and semicircles	1 - 2	2 - 4
snout-vent length	54 mm	65 mm
habitat	open country on grass	forest on trees and ground

Among *beta* anoles *A. meridionalis* has been demonstrated by Etheridge (1965) to be distinctive and primitive in the high number of its inscriptional ribs ("parasternalia"). This primitive feature strongly suggests that *meridionalis* represents a very early wave of invasion of *beta* anoles into South America. (See further comment below in the history of the *chrysolepis* complex in South America).

A. meridionalis is not at all close to the *chrysolepis* species group with which Hellmich (1960) has confused it. Hellmich has in fact based his concept of *meridionalis* on a southern specimen ("Laguna S. Paulo, Ostufer des Rio Parana, 16 km von Pto Tibirica" = Lagoa S. Paulo, Brasil, *q.v.* in the gazetteer) of a Central Brasilian race of *A. chrysolepis* that we describe as new in this paper. Only Hellmich's second specimen referred to *meridionalis* (from "Apa Bergland, San Luis-Centurion", Paraguay) is actually that species. The two forms confused by Hellmich differ in squamation and ecology: table A records the differences.

All type specimens of synonyms were seen by one of us (EEW) and found to be unmistakable specimens of *meridionalis*. In the case of *Anolis steinbachi* Griffin, Barbour (1934) commented that: "It would be impossible to find a more typical *A. punctatus* than the type of *A. steinbachi* for the figures of this specimen may be absolutely matched by any of our series from Buenavista in the Province of Santa Cruz, Bolivia...". This is a singularly unfortunate remark. Actual examination of the type of *steinbachi* shows a minimum of resemblance to any *A. punctatus* and specific identity with *A. meridionalis*. Even attention to the description would have revealed that Griffin described the number of lamellae under the fourth toe in *steinbachi* as half or less the number characteristic of *A. punctatus*.

Anolis tropidogaster Hallowell

Anolis tropidogaster Hallowell, 1856: 224. "Colombia".
Anolis stigmosus Bocourt, 1869: 43. Rio Magdalena, Colombia.
Anolis gaigei Ruthven, 1916: 6. San Lorenzo, Santa Marta Mts., Colombia, alt. 2700 ft.
Anolis incompertus nicefori Barbour, 1932: 100. Humbo, Department of Boyacá, Colombia.
Anolis nicefori; Dunn, 1944: 74.

Since the type of *tropidogaster* Hallowell is (*fide* Barbour, 1934) now only a skeleton, the ascription of this name to the species currently so denominated is an act of faith. There appears, however, to be no good reason to disturb settled usage.

This species, like *meridionalis*, has been confused with the *chrysolepis* species group, perhaps with slightly more reason. In terms of external characters, it might well represent a stock ancestral to *chrysolepis*: it has smaller ventrals, less enlarged middorsals and a more primitive nasal-rostral relationship (fig. 3). However, the evidence of

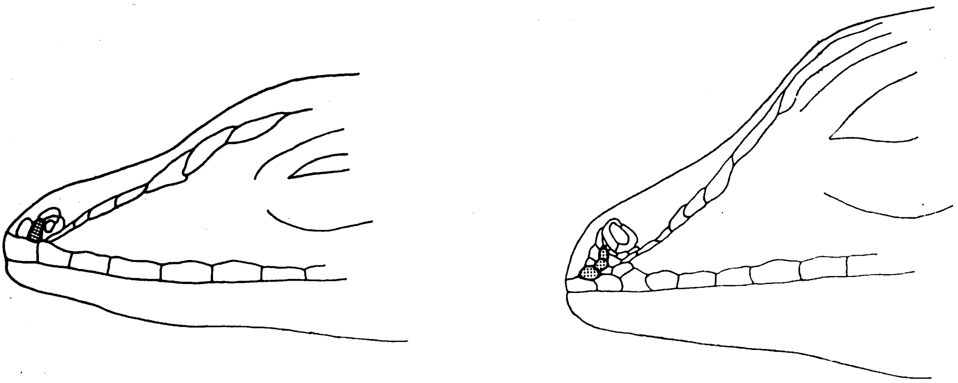


Fig. 3. Left: *Anolis tropidogaster*, prenasal scale in contact with rostral. Right: *Anolis chrysolepis*, prenasal scale separated from rostral by one or more scales.

chromosomes (Gorman, 1968) suggests greater specialization than occurs in *chrysolepis*. Some elements of high specialization in *tropidogaster* do not, of course, preclude origin from a common stock with *chrysolepis*, but they do make immediacy of relationship less credible.

The ranges of *tropidogaster* and of the *chrysolepis* species group overlap only in limited areas of eastern Colombia and western Venezuela. This virtual allopatry permitted Barbour (1932) to describe a *chrysolepis* group member as *Anolis incompertus incompertus* from the vicinity of Villavicencio and *tropidogaster* as *A. incompertus nicefori* from Boyacá. The diagnostic differences are listed in table B.

The types of all synonyms of *tropidogaster* have been seen by Williams.

TABLE B

Comparison of *A. tropidogaster* with adjacent *A. chrysolepis* (Villavicencio)

Character	*tropidogaster*	*chrysolepis*
nasal scale and rostral	in contact	separated by 1 - 2 scales
ventrals, males	60 - 82	44 - 50
females	56 - 74	40 - 48
fourth toe lamellae, males	14 - 19	16 - 18
females	14 - 18	14 - 19
loreals, males	5 - 8	5 - 8
females	6 - 8	5 - 8
scales across snout, males	10 - 15	9 - 12
females	11 - 14	9 - 14
scales between semicircles	2 - 4	1 - 2
scales between interparietal and semicircles	2 - 4	1 - 3
snout-vent length, males	52 mm	60 mm
females	60 mm	63 mm

GEOGRAPHIC VARIATION: A PHILOSOPHY OF STUDY AND THE SUBSPECIES PROBLEM

The *Anolis chrysolepis* complex is an exceptionally favorable subject for the study of geographic variation. We know of no other species of *Anolis*, no South American iguanid and, perhaps, no other South American lizard that provides equally favorable opportunities.

We are persuaded also that the method we have here adopted is the preferred, indeed necessary, method for the extraction of maximally useful information on geographic variation wherever found. This method is, of course, an elaboration of methods long used by one of us (Vanzolini, 1951, 1953) in the analysis of South American lizards.

It is our fundamental idea to study the geographical differentiation of each character separately, first comparing strategically selected major samples and then analyzing variation along transects between these major samples. At a further stage regularities are looked for among patterns obtained for the individual characters. This approach is a consequence of a general model of geographic differentiation we have adopted. This model, which derives from the consideration of some previous favorable and well-analyzed cases (*Amphisbaena fuliginosa,* Vanzolini, 1951) recognizes areas of character stability and areas of transition. Thus if a number of characters, statistically independent *within* samples, show agreement as to the areas of stability, we take it to mean that well-integrated genomes have evolved within these areas. It will, it is true, be repeatedly shown below that the ranges of the several characters that we regard as defining areas of stability are *not* coterminous (*cf.* Wilson & Brown, 1953). But we do not believe that the expectation of coterminous ranges is a plausible one, and certainly we do not regard the lack of coterminous ranges as any argument against the reality of the areas that we describe. It is on the contrary to be expected, more often than not, that the coadjusted character complexes built up in isolation would suffer some disorganization when they meet the similarly coadjusted character complexes of other areas. Whenever such disorganization occurs, the several characters or character states may be expected to have independent fates under the competing influences of local selection and gene flow. Thus what we look for as a result of our analysis is a superposition of polygons of roughly similar but not identical shape and surface; the area of maximum overlap of these figures we call a "core area", after the geomorphological concept. The location and peculiarities of the core areas and the features of the transition belts are our clues to the history of the differentiation of the group. They offer a much firmer basis for analysis than the alternative method of looking for differences between so-called "populations" — differences which will always be found if enough statistical analysis is done. The latter course usually leads to the recognition of a number of subspecies that contribute little to the understanding of the evolutionary patterns.

Given the importance we attach to core areas and transition belts, we believe that they should be exhaustively analysed and abundantly documented. This has led in the present paper to a very large number of tables, graphs and maps — but we think all of them are essential to the delineation of the general patterns of differentiation.

That as one result of our study of geographic variation in *Anolis chrysolepis* we have chosen to employ the subspecific category is no essential part of the basic study. We regard subspecific names as a convenient summary of the broader aspects of our conclusions. We hope by these names to call attention to the largest and best demarcated centers of differentiation, at which *plesiospecies,* those evolutionary units that almost achieved species grade, came into existence.

We have not neglected to point out the multiple levels of differentiation below those that we choose to recognize nomenclatorially. We are quite conscious that these might be multiplied indefinitely by further collection and investigation. We regard these levels of differentiation as interesting not just for themselves, but for their possible contribution to our knowledge of the sources and modes of intraspecies variation. However, we regard that level of differentiation closest to species difference, and indicative, perhaps, of past or future potential species formation, as of highest intrinsic interest and alone worth naming in the formal system. We are aware that our expressed preferences diverge from current standards and practices, and we admit an element also of arbitrary choice, based on our own estimate of convenience and utility, in the exact number of forms that we recognize. We have had, in fact, to make a break within a continuum and set an arbitrary level below which we will not formally name. Our effort here is to preserve something of the utility of subspecies but with the explicit philosophy that the number recognized should be minimal.

For us the issue of subspecies recognition is an unimportant one. We have expressed our views and defended our position. Having made this limited contribution to a dispute more voluminous than illuminating, we pass on to more interesting topics, insisting only that geographic variation, properly studied, is a worthy topic of scientific investigation.

SPECIMENS STUDIED

Of *chrysolepis* proper we have used in the study of geographical differentiation 761 specimens (391 males and 370 females) from 177 localities. Many other specimens were examined but not included in the analysis because the localities were too imprecise or, in a few cases, impossible to identify.

Besides the *chrysolepis* specimens we used 9 males and 11 females of *Anolis bombiceps* from 11 localities; 20 males and 15 females of *Anolis tropidogaster* from 9 localities; and 13 males and 14 females cf *Anolis meridionalis* from 11 localities.

This brings up the number of specimens to 843 and of localities to 208 (there are two cases of syntopy).

The specimens used are listed below.

Abbreviations

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia
BM	British Museum (Natural History)
CM	Carnegie Museum, Pittsburgh
FM	Federico Medem private collection
FMNH	Field Museum of Natural History, Chicago
LS	Instituto La Salle, Bogotá
JRT	J. R. Tamsitt private collection
LACM	Los Angeles County Museum
LM	Rijksmuseum van Naturlijke Historie, Leiden
MCZ	Museum of Comparative Zoology, Cambridge, Mass.
MG	Museu Paraense "Emilio Goeldi", Belém, Pará
MJP	Museu de Historia Natural "Javier Prado", Lima

MNRJ	Museu Nacional, Rio de Janeiro
MP	Muséum National d'Histoire Naturelle, Paris
MVZ	Museum of Vertebrate Zoology, University of California at Berkeley
MZUSP	Museu de Zoologia da Universidade de São Paulo (formerly Departamento de Zoologia da Secretaria da Agricultura)
NMB	Naturhistorisches Museum Basel
SM	Senckenberg Museum und Naturforschung Institut, Frankfurt a. Main
UIMNH	University of Illinois Museum of Natural History
UKMNH	University of Kansas Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum, Washington
ZMB	Zoologisches Museum Berlin
ZSM	Zoologische Staatsammlung München

Anolis chrysolepis

(Maps A to F)

Brasil

Roraima: Alto Rio Catrimani, MNRJ 1626, 3321.

Amazonas: Serra da Neblina, MCZ 86763; Boca do Rio Tucano, MCZ 86762; Tapurucuara, MG 1750; Estirão do Equador MG 901; Benjamin Constant, MNRJ 3323-29, MZUSP 9145; Paraná do Jacaré, MNRJ 1621; Reserva Ducke, MCZ 92682, SMF 60985-87, MZUSP 8350, 8356, 10906, 11920; Maués, AMNH 98403-04; Manjuru, AMNH 98398; Rio Juruá, MCZ 65580, MZUSP 400, 405, 700, 3014; Itapiranga, MZUSP 16908-16; S. Sebastião do Uatumã, MZUSP 17439.

Pará: Aldeia dos Índios Tiriós, MG 1702, 1704, MZUSP 13134, 13141, FMNH 84580; Cachimbo, MZUSP 3714-16, 3725, 3989-90; Belém, FMNH 83580.

Amapá: Serra do Navio, FMNH 83581-83, MG 1700-01, MCZ 79146-50, 85009; Porto Platon, MCZ 85010; Alto Rio Maracá, MG 817-25, 829-30, 1687-88.

Maranhão: 40 km S Loreto, AMNH 98483.

Acre: Alto Purus, MZUSP 2513-14.

Rondônia: Mutum-Paranã, MZUSP 3718-19.

Mato Grosso: Barra do Tapirapés, MG 1705-08, MCZ 98284-89, AMNH 87913, 93155-66, MZUSP 9744, 10075-86, 10319, 12327-28, 12974-81, 12983-85.

Goiás: Porangatu, MG 1699; Aruanã, MZUSP 4660; Cana Brava, MZUSP 4378-79.

Minas Gerais: Uberlândia, MZUSP 4635.

São Paulo: Lagoa S. Paulo, ZSM 251/1933; Itapura, MZUSP 551; Araçatuba, MZUSP, 4365; Ribeirão Azul, CM 949; Bueno de Andrade, MZUSP 4384; Ibarra, MZUSP 4487; Vista Alegre do Alto, MZUSP 4383.

Colombia

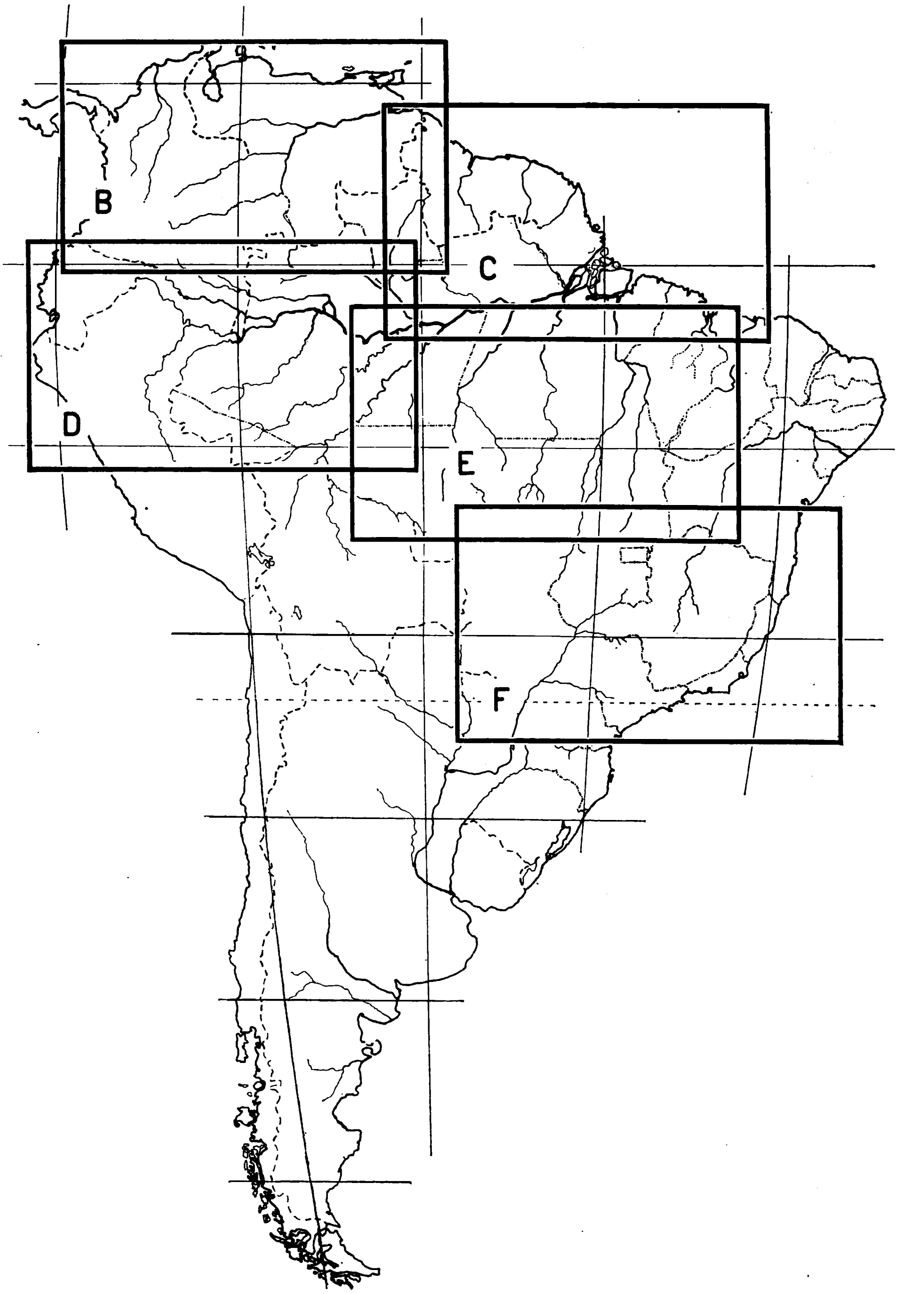
Cundinamarca: E base Cordillera de Bogotá, ANSP 24288; Bogotá, UMMZ 120748, MCZ 19304-05.

Meta: Villavicencio, UMMZ 78288 (2 exs.); FMNH 30790; MCZ 19231-33, 32309-10 (paratypes of *incompertus*), 32312-15 (paratypes of *incompertus*), 32317 (paratype of *incompertus*), 32319 (paratype of *incompertus*), 71416-19, 74319, 77465-69, 100005, 100407-09, 100967-69, FM s/n (6 exs.); Acacias MCZ 74318; Hacienda La Guardia, 5 km NE Villavicencio, UMMZ 126625; Restrepo, MCZ 42192; Puerto Lopez, AMNH 98405, 98407, MCZ 77474; Apiay, UKMNH 110582-83; Finca Guadualito, Rio Güejar, area of Serrania La Macarena, FM s/n (2 exs.); Finca El Diamante, region of Rosaleño, FM s/n.

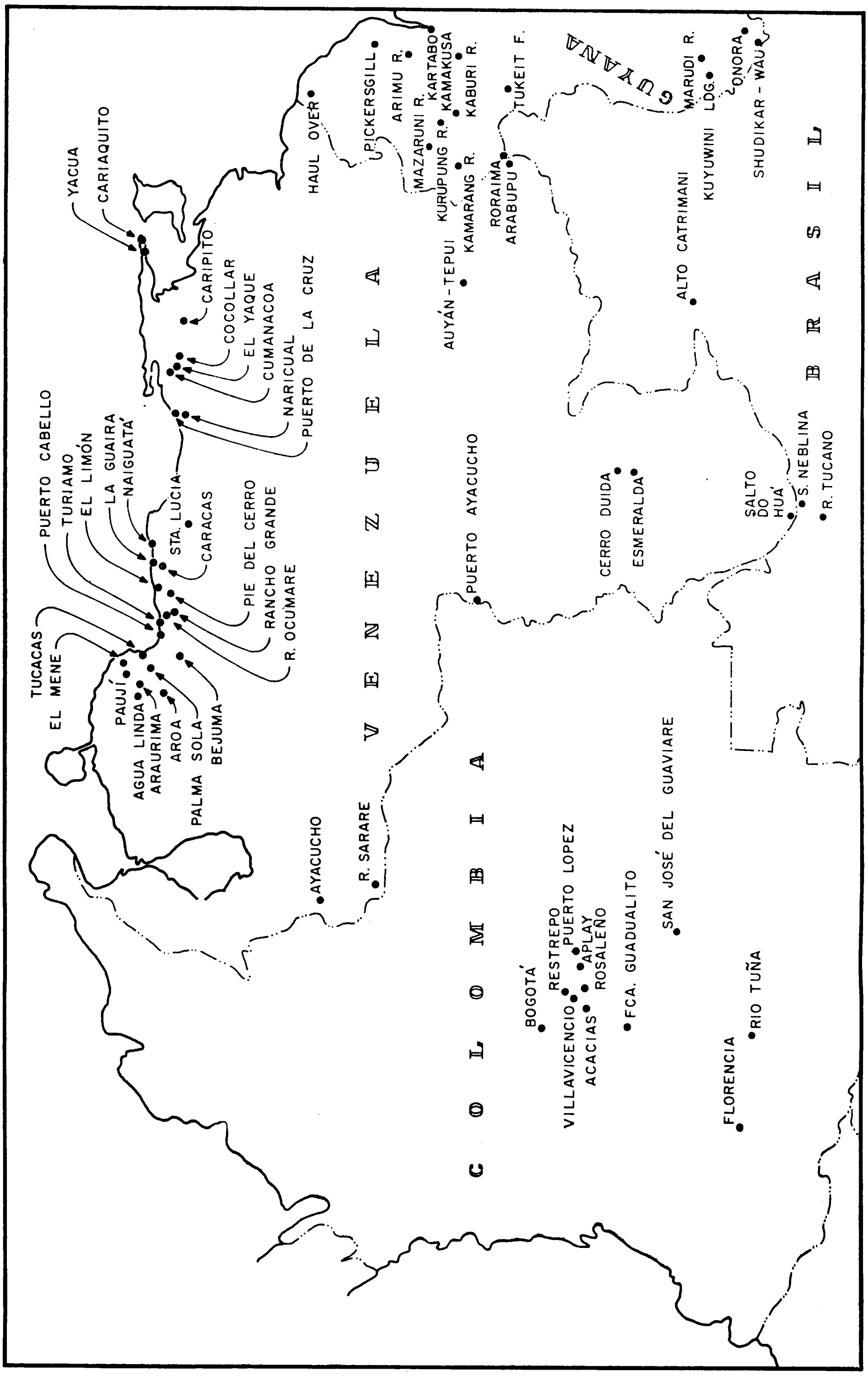
Caquetá: Rio Tuña, MCZ 92683; Florencia, MCZ 61164-66.

Vaupés: San José del Guaviare, FMNH 75690.

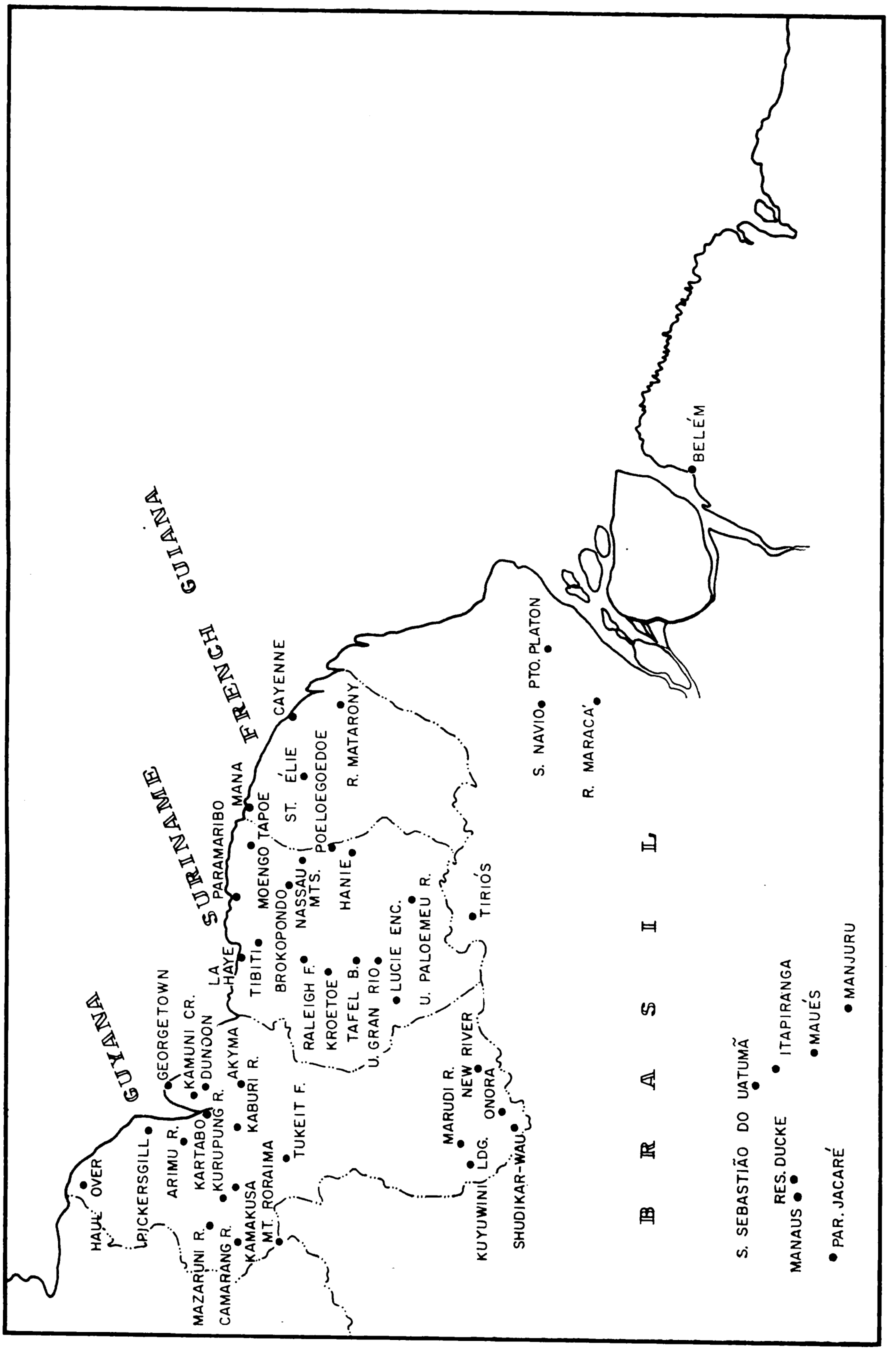
Vichada: Santa Teresita, AMNH 99659.



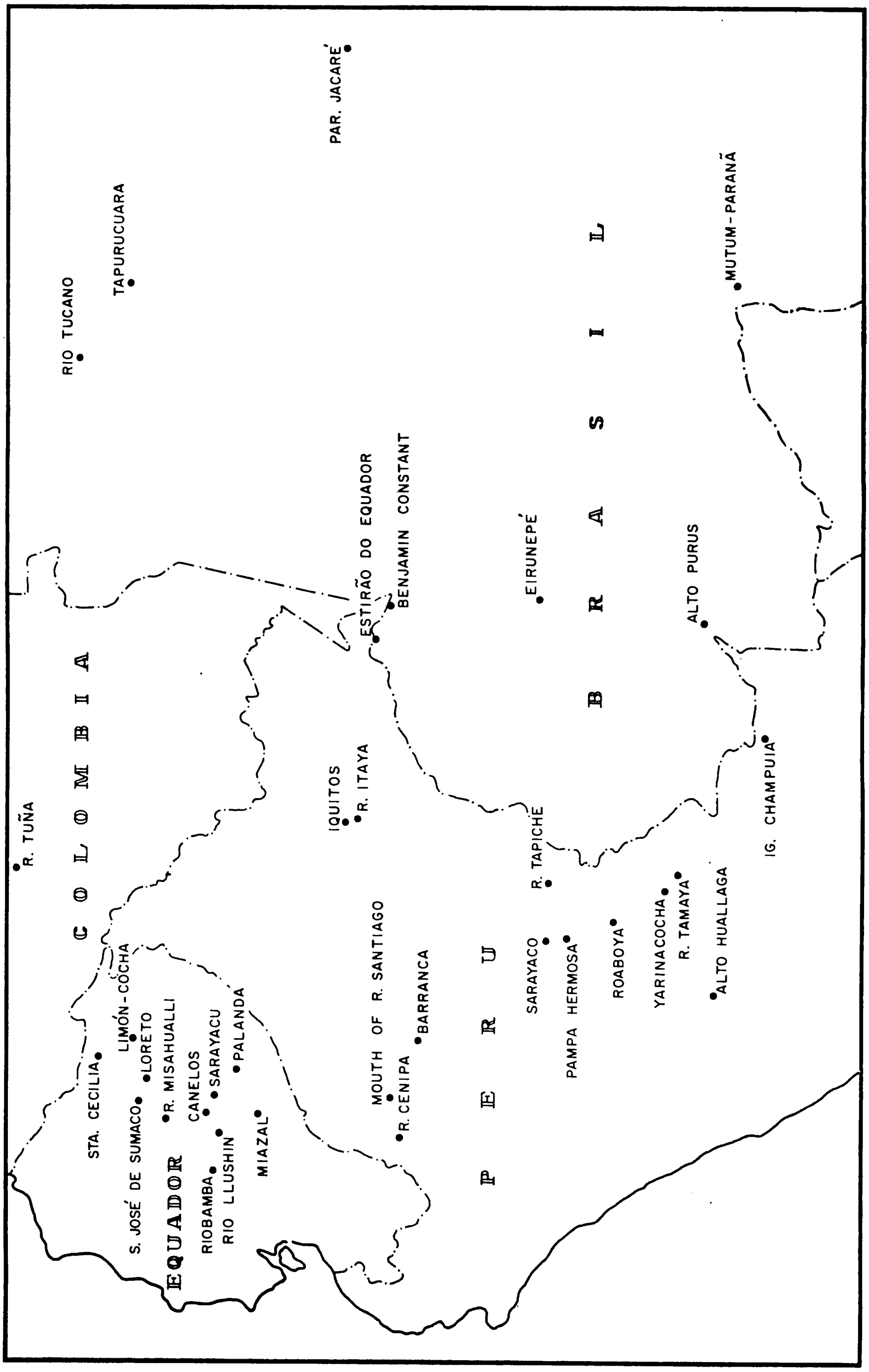
Map A. Key to maps B to F.



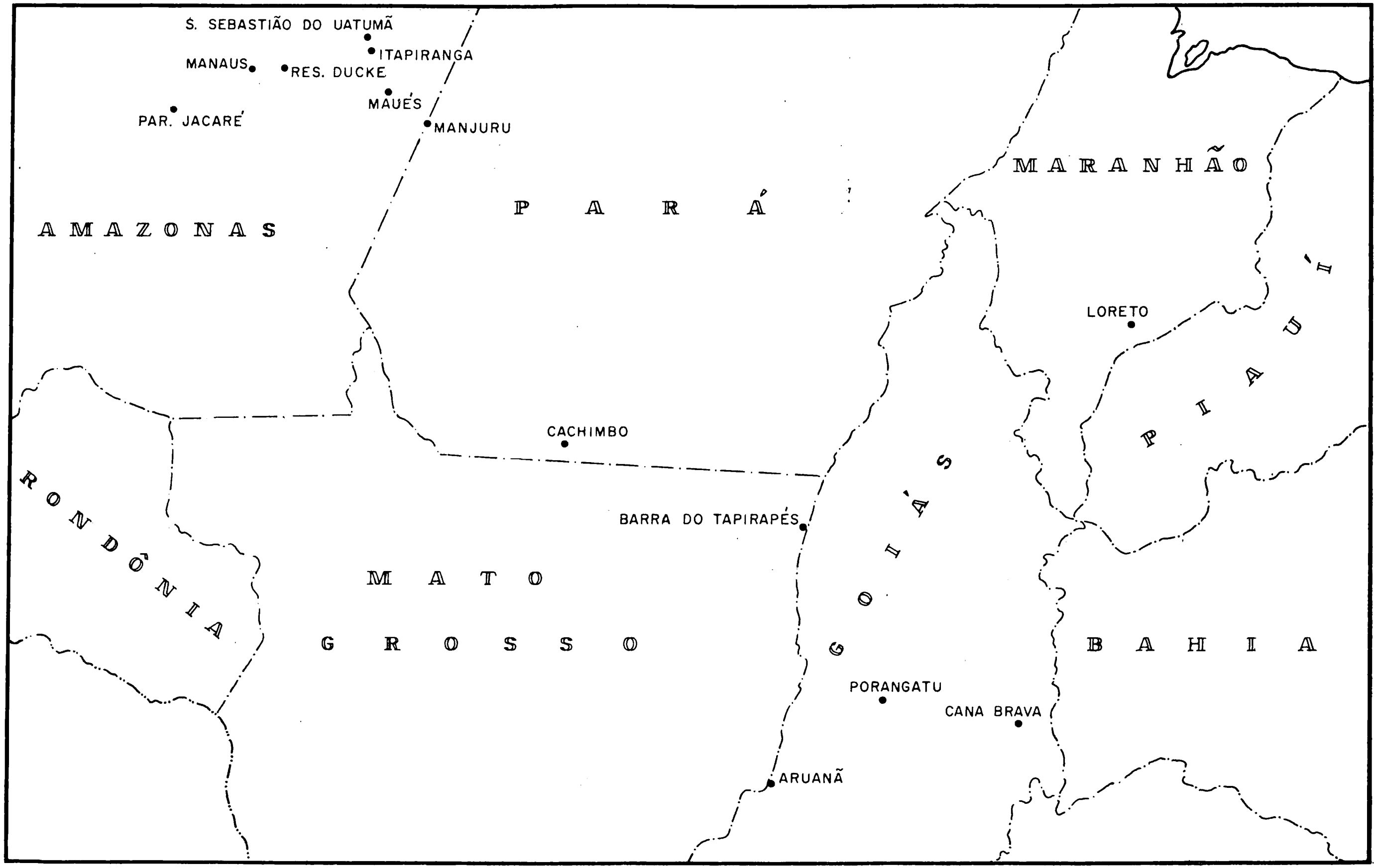
Map B. Localities of *Anolis chrysolepis*; area B of Map A.



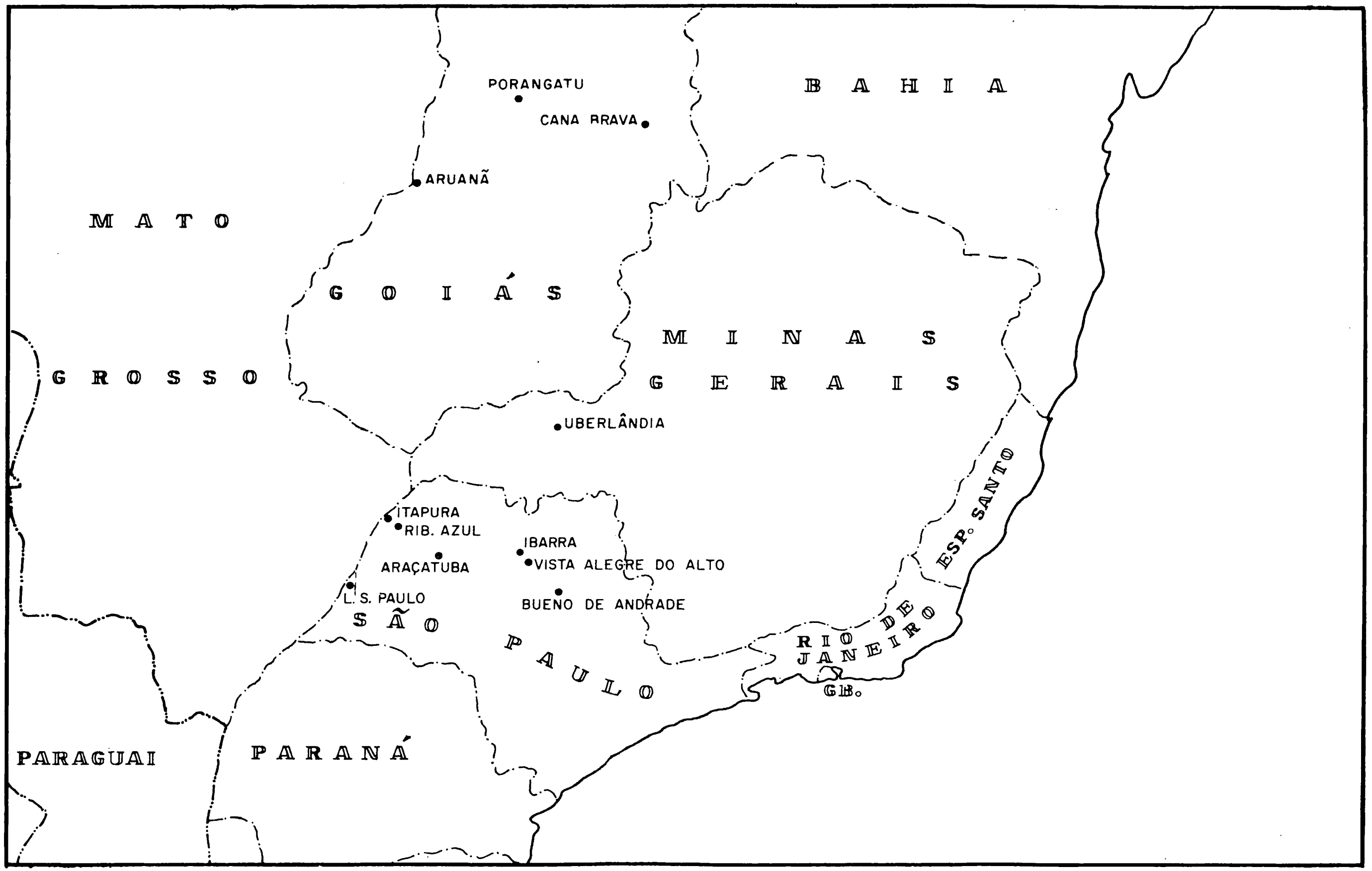
Map C. Localities of *Anolis chrysolepis;* area C of Map A.



Map D. Localities of *Anolis chrysolepis;* area D of Map A.



Map E. Localities of *Anolis chrysolepis*; area E of Map A.



Map F. Localities of *Anolis chrysolepis;* area F of Map A.

Ecuador

Napo-Pastaza: Santa Cecilia, UKMNH 105326-37, 109698-23, MCZ 92601-08; Limón Cocha, UKMNH 98929-38, 107050-52, UIMNH 54353, 54363, 54532-36, 64272, 64297-304, 64314-15, 64355, 64416-25, 65979-80, MCZ 85097-101, 92609-12; San José, AMNH 28866-67, 28884-87; Loreto, USNM 163994; Rio Bobonaza, entre Sarayacu y Canelos, MZUSP 11367-68; Sarayacu, MCZ 37709; Churoayacu nr. Sarayacu, Rio Bobonaza, USNM 163996; Palanda, Rio Bobonaza, USNM 163995; Rio Misahualli, USNM 163991-93; Miazal, USNM 163998-4001.

Santiago-Zamora: Rio Llushin, USNM 163997.

Chimborazo: Riobamba, AMNH 23327, MCZ 29290.

Not placed: Tuvula, AMNH 38676-81; Dureno, UKMNH 105325.

Guyana

Haul Over, Aruau River, UMMZ 83752-53; Pickersgill, Pomeroon River, UMMZ 82852 (2 exs.), 82853; Georgetown, UMMZ 46445, AMNH 8564-66, 17693-94; MCZ 8080; Demerara Falls, BM 1946, 8.8.58 (syntype of *nummifer*); Dunoon, UMMZ 55995-56005, 70053-55, 70062-64; Aremu River, UMMZ 70051; Kaburi, 30 mi Bartica, MCZ 81306-07, 81502; Akyma, Demerara River, AMNH 38565, 38571; Kamuni Creek, Demerara River, UMMZ 83630; Kartabo, CM 4241-42, 5367, AMNH 15142, 21310, 21313, 21322, 32277, 46448-50; near Kartabo, AMNH 98322-23, 98326, 98332-33, 98342, 98347, 98354-55, 98357, 98360, 98362-69, 98371-72, 98375, 98394-95; Kamakusa, AMNH 25072-73, 25078a, 25081, 25120-27, 25131, 25135; Upper Mazaruni River, UMMZ 85223, 85225; Tukheit Hill, below Kaieteur Falls, UMMZ 63051-52; Kurupung, Upper Mazaruni Distr., UMMZ 83631; Branch of Kurupung River, UMMZ 85226; Machreba Falls, Kurupung River, UMMZ 85227 (2 exs.); Machripa Falls, Kurupung River, UMMZ 83632; Kuyuwini Landing, AMNH 79963; Marudi, AMNH 61383; Onora, MCZ 65350, AMNH 61251, 61253; New River, BM 1939. 1.1.69; Shudikar-wau, AMNH 61492-95, 65348-49; Kamarang River, UMMZ 85224 (2 exs.).

Surinam

La Haye, LM 2812; Tibiti, LM 11638-39; Paramaribo, ZMB 25982 (2 exs.); Kroetoe, LM 11660; Moengo Tapoe, LM 11636 (2 exs.), 11637, 11665; Coppename River, BM 1946. 4.2.81; Nassau Mts., LM 11640-54, 11655 (2 exs.), 11656, 11657 (2 exs.), 11658-59, 11661 (2 exs.), 11662; Upper Paloemeu, LM s/n; Brokopondo, LM s/n; Poeloegoedoe, LM 11663; Raleigh Falls, Upper Coppename, LM s/n; foot Tafelberg, LM 11664; Upper Gran Rio, LM 4857; Hanie, LM 447; Lucie encampment, LM 11666.

French Guiana

Sophie, S St. Élie gold pit, MCZ 77548; Cayenne, MP 2459, 5243, LM 2828; Mana, MP 2436 (syntype of *chrysolepis*); lower Matarony, LACM 42093-100, 42105-107, 42109-110. No further data, MP 2439 (syntype of *chrysolepis*).

Peru

Loreto: Barranca, AMNH 57076, Mouth of Rio Santiago, AMNH 57071, 57075, 57371, 56810, 56819-22, 56834-35; Rio Itaya, Iquitos, AMNH 56831; Iquitos, FMNH 45512; Yarinacocha, FMNH 45519, 56038, 56065-67; Pedrera, prov. Ucayali, FMNH 45513; Lower Rio Cushabatay, AMNH 56804-06, 56826-28; Pampa Hermosa, AMNH 56486-89, 56811-13, 56815-16, 56832-33, 56838, 56841-44, 57077, MCZ 57369, 57372; Brasil-Peru frontier, Rio Tapiche region, AMNH 56840; Rio Tamaya, MCZ 57374, AMNH 56824-25, 57084; Roaboya, AMNH 56809, MCZ 57373; Igarapé Champuia, Alto Curanja, Alto Purus, MZUSP 3323-25, MCZ 65581.

Amazonas: Manayacu, Rio Cenipa, AMNH 57072; Rio Cenipa, AMNH 57073.

Huanuco: Upper Huallaga R. valley, AMNH 57070.

Trinidad

San Rafael, FMNH 49832-33; Tucker Valley, USNM 119077; Mt. St. Benedict, St. George Co., CM 8003; Port of Spain, AMNH 6567; Mayaro, AMNH 72829; Moruga, MCZ 31495; Nariva Swamp, MCZ 42983, 60800; Toco, MCZ 10746-47; Guayaguyam, NHMB 7771-72; Churchill-Roosevelt Hwy, AMNH 72827, 72830-33; Palmist Estate, 3 km S San Fernando, MCZ 81303-05, 81501, 85011-18; 3 mi S San Fernando, MCZ 81302; La Seiva, MCZ 8998-9000; no further data, AMNH 6569, NHMB 8644-46, 9002-09, USNM 17729, 20414.

Venezuela

Falcón: Caño Tigre, Agua Linda, NHMB 9994-95; Riecito, Acosta Distr., MCZ 49050; Pauji, Acosta Distr., MCZ 48723-24, 49035-37; El Mene d'Acosta, NHMB 9239, 9251, 9563, 9917-23, 9925-26, 9997-98, 12868, 13890; Palma Sola, UMMZ 55966, 55974, 55977-78, 55984; Riecito-Araurima area, NHMB 13614; Tucacas, UMMZ 55979

Yaracuy: Boquerón, UMMZ 55976, 55989; Aroa, UMMZ 55972.

Carabobo: Bejuma, UMMZ 55968-69; San Esteban, UMMZ 55967, 55982, 55985; Puerto Cabello ZMB 498, LM 674 (5 exs.), 3001; between San Esteban and Puerto Cabello, BM 1913. 9.10.1; Las Cuiguas, San Esteban, UMMZ 55970-71, 55987.

Aragua: Pie del Cerro (La Victoria), CM 7402, 7416; along Rio Ocumare, UMMZ 124296; Rancho Grande, AMNH 98309; Rancho Grande-Ocumare road, 3.9 km S of fork to Turiamo, UMMZ 124300-01; Rancho Grande-Turiamo road, ca. 1700 ft, UMMZ 124297; La Cumbre, UMMZ 124295; Hda Sta. Theresa, FMNH 128908.

Distrito Federal: Caracas, UMMZ 124302, ZMB 529 (type of *planiceps*), 4251, MP 2460; La Guaira, USNM 22522-25, 27818; El Limón, CM 7349, USNM 121180; Puerto La Cruz, CM 7318, 7320, 7335, 7338, USNM 121181; El Valle, USNM 128905-07.

Miranda: Santa Lucia, 11 km ENE of Quebrada Siquire, CM 7443, 7460; Los Canales, Naiguatá, CM 22781.

Anzoátegui: Puerto La Cruz, MCZ 48782; Vallée du Naricual, MP 85 (6 exs.).

Sucre: San Rafael, nr. Cumanacoa, CM 7830, 7838, 7851, 7853, 7858-59, 7862, 7864, MCZ 48781; Cumanacoa CM 7938; Cuchivano, AMNH 29325; Cocollar, FMNH 17801; El Yaque nr. Turumiquire, CM 7970-71, 7974; Hacienda Mirasol, nr. Latal, CM 7959; Yacua, MCZ 43856-58, 43860; Cariaquito, ANSP 18277 (type of *nitens bondi*).

Monagas: Caripito, AMNH 98310-21.

Táchira: Ayacucho, MCZ 84073.

Apure: Sarare, MP 03-174 (4 exs.).

Bolivar: Arabupu, Mt. Roraima, AMNH 36329, 38684-86; Glycon Swamp, Mt. Roraima, AMNH 38683; Auyán-Tepui Plateau, 2200 m, AMNH 61013.

Amazonas: 6 mi. N Esmeralda, AMNH 36656; 10 mi. N Esmeralda, AMNH 36657; Vegas Falls, 20 mi N Esmeralda, 4600 ft, AMNH 36648; Rio Pescada, Mt. Duida region, AMNH 36639; Summit Brook, Mt. Duida Region, 6300 ft, AMNH 36646; nr. Salto do Huá, Brasil-Venezuela border, USNM 83574; Puerto Ayacucho, MCZ 58328.

Without locality data or with erroneous data: BM 1946. 8.8.55 (type of *scypheus*); BM 1946.8.8.51 ("Grenada", type of *turmalis*).

Anolis bombiceps

(Map I)

Brasil

Amazonas: Igarapé Belém, MZUSP 13026-27.

Colombia

Amazonas: Leticia, JRT 103; Puerto Nariño, ILS 3.

Ecuador

Napo-Pastaza: Rio Bufeo, MCZ 96802; Rio Shiona-yacu, MCZ 96803; Puerto Napo, MCZ 87248; Conambo, MZUSP 13140.

Peru

Loreto: Estirón, Rio Ampiyacu, MZUSP 13135-39; Rio Itaya, AMNH 56215, 56830, 57074; 1 day canoe trip from mouth of Rio Nanay, AMNH 56845; San Regis, MJP 0131 A-B.

Anolis meridionalis

Bolívia

Beni: Reyes, UMMZ 57704; Rio Mamoré, ca 23 km W San Javier, AMNH 98413-16; Rio Mamoré, ca 10 km W San Pedro, AMNH 98417-25; Rio Mamoré, ca 12°26'S, AMNH 98427.

Santa Cruz: Buena Vista, UMMZ 60591, 60607 (3 exs.), 60626; Rio Surutu, UMMZ 63807; Provincia del Sara, CM 985 (paratype of *steinbachi*).

Brasil

Mato Grosso: Chapada, BM 1946.8.8.44 (syntype of *Norops sladeniae*), UMMZ 61757.

Goiás: Goiânia, MG 1685.

Distrito Federal: Brasília, USNM 148771.

São Paulo: S. José dos Campos, AMNH 88319.

Anolis tropidogaster

Panamá

Saboga, MCZ 12372-74, 12377, 12379, 12381, 12384-85, 12387, 12391-93.

Colombia

Santander: El Centro, MCZ 74361-62.

Chocó: Andagoya, MCZ 32301-02 (types of *albi*).

Boyacá: Otanche, Muzo distr., MCZ 74365-67; Humbo, Muzo distr., MCZ 32322-23 (types of *incompertus nicefori*), 74363-64.

Cundinamarca: Sasaima, MCZ 34324; La Mesa, MCZ 46423-24, UMMZ 90624 (2 exs.).

Venezuela

Táchira: La Fria, UMMZ 55973, 55975, 55981, 55983, 55988; San Felix, UMMZ 55980, 55986.

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METHODS

THE BASIC APPROACH

We have analyzed the geographic differentiation of the *chrysolepis* group by first considering separately the differentiation of 11 numerical characters and two qualitative characters over the whole territory of the group, and afterward comparing the resulting patterns. The sexes were studied separately, since preliminary analysis of first category major samples (see below) showed widespread occurrence of sexual dimorphism. In each case of its occurrence the latter was considered as an additional character, and its distribution analyzed. In the few cases where sexual differences were not statistically significant in the major samples, the geographical analysis was nevertheless done separately for each sex, as experience showed that otherwise some differences in general pattern would be lost.

The investigation of each character was begun by the joint consideration of 13 "major samples" and carried forward by the analysis of "transects" — series of localities more or less linearly arranged between major samples. In this manner a two dimensional differentiation pattern of each character was obtained.

The organization of the major samples and transects was decided initially only on the basis of the materials available and of the geometry of a map of the area of study. The results of a first analysis were then used to adapt the methods to permit better clarification of the patterns perceived. For example, the evidence (in fact known beforehand but not taken into consideration in the first study) of the existence of a well differentiated form, previously believed to be a well set-off species, in the area from Surinam to eastern Pará, led to a preliminary arrangement of the Guianan and Guiano-Brasilian transects, and to their subsequent modification in order to show to better advantage the phenomena of transition between these populations and adjacent ones.

This sort of feedback and even bias in the analysis is not only unavoidable but highly desirable in studies of geographical differentiation in South America. If we had a perfect network of localities, each one represented by good samples — with statistically sufficient numbers of males and females, and with all age classes equally represented — a system of isophenes would emerge from the analysis, which might even be computerized.

In fact, the available collections are, as is usual with museum collections, not made for a specific purpose, an irregular and patchy representation of the group range, and the study must begin by the setting of preliminary hypotheses, to be tested. In our case the hypothesis is, in all instances, that differences between the major samples correspond to geographic patterns and not to mosaics, and this hypothesis must be tested by adaptations of the analysis to the materials available, to the numbers of specimens and their position on the map, in other words, by the consideration of transects.

After the 11 initial quantitative characters are analyzed below, and their joint distribution described in "interim summaries", and after we have discussed the unquantifiable character of size of middorsal scales compared with size of arm scales, we have added to the discussion a further, and very important character, dewlap color. We delay citation of this character until this point because the test of the meaning of dewlap color in two crucial cases depends upon knowledge of everything else.

It will be clear that our presentation of the evidence does not reflect the evolution of our analysis. It is instead the presentation of a case, with, however, due insistence on primary evidence (hence the very high number of tables, graphs and maps) and only thereafter on what constitutes interpretation, impression and guess. Our results might have been asserted as conclusions from the very beginning, but we have preferred to develop our case more elaborately for didactic and esthetic reasons.

MAJOR SAMPLES

We call major samples those that have a "reasonable" number of males and females and that fulfill some requisites of geographical and morphological homogeneity. "Reasonable number" was defined operationally: we have used samples with as few as 5 specimens, in cases in which we believe that information on the locality was important enough to offset the disadvantages of the lesser precision of the comparisons.

The geographical criteria embrace 3 orders of stringency: (i) one single, well-defined locality; (ii) an ecologically homogeneous group of close-set localites; (iii) a group of not so close, but still ecologically homogeneous localities. The three groups of course overlap.

The first type of sample is ideal for the purposes of this study, as it permits the establishment of criteria of variability, the study of dependence between size (treated as representing age) and morphological characters, and an evaluation of sexual dimorphism. Whatever its variability, a sample of this type is basic for our work.

However, the concept of a single locality in the interior of South America is not simple and unambiguous. Large samples are usually collected during some more or less long stay in a place, which is well defined by the notes of the collector. On the other hand, many specimens are brought in by natives, and this transforms the single point locality into an area, roughly circular in drier regions and elongate (along rivers) in the rain forest. In the latter case experience shows that the actual collecting area may extend about 50 km each way along the stream.

This is certainly not a serious drawback, in terms of the scale of the present work, or even of the population dynamics of common animals. However, this to a marked extent bridges the gap between the first and second categories of major samples. The locality "Barra do Tapirapés" may well encompass an area of the same order of magnitude as that comprised by the samples Villavicencio, which includes Villavicencio proper, and at least San Martin, Restrepo and Acacias, or Pampa Hermosa, which includes the lower Rio Cushabatay.

Given the differences often observed between adjacent first category samples (e.g. Limón Cocha and Santa Cecilia), major samples of the second category should only be assembled after careful statistical testing of homogeneity of all characters under analysis. Once they are found in agreement with the good single locality samples, they may be used for the same purposes.

Major samples of the third category have been assembled for tactical reasons, not primarily for the study of variability, sexual differences or associations of characters. They aim at representing critical geographical areas. Thus, samples from Anzoátegui, Sucre and Monagas (Caripito) in Venezuela are individually considered in the analysis of the North Venezuelan transect, but taken together as "NE Venezuela" they serve as a starting point for the consideration of the Guianan areas. When the component subsamples agree very closely with regard to a certain character, their ensemble obviously affords a better inductive basis for geographical comparisons, but the other data which do not show this close agreement should be taken with caution.

In the study of body proportions it has sometimes happened that a given sample has too few juveniles or large adults, or too few specimens of one sex; or, in the case of tail length, that not enough unbroken tails are available. In such cases samples have been combined, after testing for homogeneity.

The major samples adopted in this work are:

Category	Code	Name and Localities	Males	Females
First	ESS	Essequibo: Kartabo and surrounding area	18	19
	DUN	Dunoon	7	10
	NAS	Nassau Mountains	11	14
	SCE	Santa Cecilia	17	19
	LCO	Limón Cocha	31	32
	TAP	Barra do Tapirapés: plus Porto Velho	26	24
Second	TRI	Trinidad: several localities	26	23
	VIL	Villavicencio: plus Acacias, Restrepo, San Martin	22	17
	PHE	Pampa Hermosa: plus Lower Rio Cushabatay	17	9
Third	FAL	Falcón: Agua Linda, Araurima, Aroa, Boquerón, El Mene d'Acosta, Palma Sola, Paují, Riecito, Tucacas	21	13
	NEV	Northeastern Venezuela: Puerto de la Cruz (Anzoátegui), Naricual, "Sucre" (see North Venezuelan transect, below), Caripito	17	18
	WBG	Western Guyana: Kamarang, Kurupung, Machripa Falls, Upper Mazaruni	11	13
	APA	Amapá: Alto Rio Maracá, Serra do Navio, Porto Platon	12	18

THE TRANSECTS (MAP G)

As stated above, we call "transects" series of localities more or less linearly arranged between, and including, major samples. Localities situated close together were in some cases combined, after testing for homogeneity in all characters. In several instances alternative combinations could have been made, and some were tried, but are not reported here, as they would not add to the results of the analysis or to the clarity of the presentation.

Localities which do not fit exactly any of the transects adopted are called "laterals", and considered together with the nearest transect.

Of course many localities are part of (or lateral to) more than one transect or included in one transect and lateral to another.

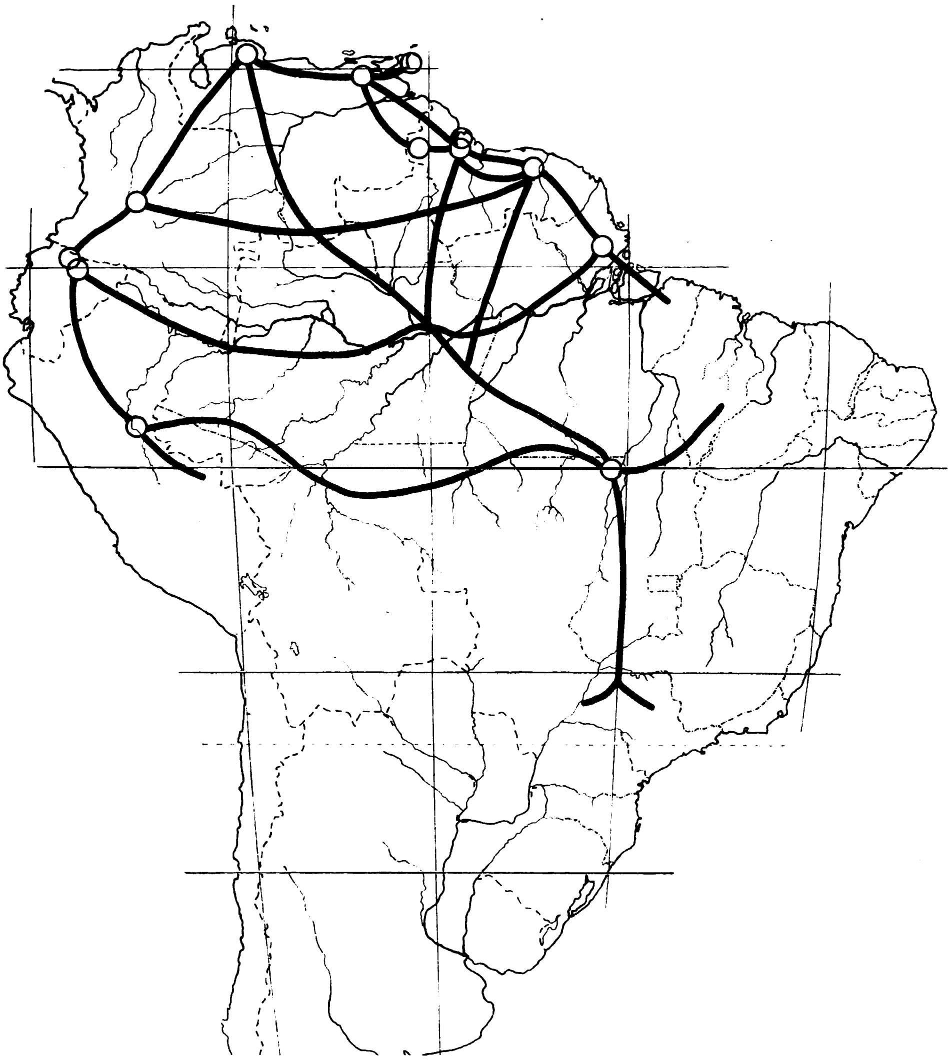
In the analysis the transects are usually cited in the original order, which was initially designed to bring out first the features of the better differentiated areas, especially the eastern Guianas, and only later the less differentiated areas. However, on occasion, and depending upon the intrinsic logic of the case, the order has been altered, or transects combined or altogether omitted.

Two localities (Brokopondo, Surinam, one female, and Tukeit Hills, Guyana, two females) were inadvertently omitted in the analysis; since it was later seen that they would not have added any relevant information, the oversight was not corrected.

North Venezuelan transect. This is a fairly linear series of 24 localities between Falcón and Trinidad:

Code	Localities	Males	Females
FAL	FALCÓN	21	13
Bej	Bejuma	1	1
Car	Carabobo (San Esteban, Las Quiguas, Puerto Cabello)	8	6
Rgd	Rancho Grande area	—	6
Pdc	Pie del Cerro	2	—
Dif	Distrito Federal (Caracas, El Valle, El Limón, La Guaira, Los Canales, Puerto de la Cruz, Santa Lucia)	13	9
Anz	Anzoátegui (Puerto de la Cruz, Naricual)	5	2
Suc	Sucre (Cocollar, Cuchivano, El Yaque, Latal, San Rafael)	4	12
Cap	Caripito	3	4
Yac	Yacua	3	1
TRI	TRINIDAD	26	23

First Guianan transect. This aims at analyzing variation along the coast. It is also a fairly linear series of 12 localities, plus 4 major samples, the first of which is a composite (NE Venezuela).



Map G. *Anolis chrysolepis;* transects.

Code	Localities	Males	Females
NEV	NE VENEZUELA	17	18
Hov	Haul Over	—	2
Pic	Pickersgill	—	3
Geo	Georgetown: plus Kamuni Creek	2	6
DUN	DUNOON	7	10
Lhy	La Haye	—	1

Tib	Tibiti	1	1
Par	Paramaribo	1	1
Mtp	Moengo Tapoe	3	1
NAS	NASSAU	11	14
Man	Mana	1	—
Sel	St. Élie	1	—
Cay	Cayenne	2	1
Mat	Lower Matarony	5	8
APA	AMAPÁ	9	16
Bel	Belém	1	—

Second Guianan transect. This transect includes 8 localities and 5 major samples and is parallel to the first, but situated more to the interior. It includes Dunoon, in order to show differences between it and the neighboring Essequibo sample.

There are 3 lateral localities: Auyán-Tepui and Roraima, which should be compared with the westernmost localities, and Lucie, to be considered between Guyanan and Surinamese localities.

Code	Localities	Males	Females
NEV	NE VENEZUELA	17	18
WBG	WESTERN GUYANA	11	13
Ari	Arimu River	—	1
ESS	ESSEQUIBO	18	19
DU	DUNOON	7	10
Aky	Akyma	1	1
Kro	Kroetoe: plus Raleigh Falls	2	—
Tfb	Tafel Berg: plus Upper Gran Rio	—	2
NAS	NASSAU	11	14
Poe	Poeloegoedoe: plus Hanie	2	—
Laterals			
Auy	Auyán Tepui	1	—
Ror	Roraima	2	4
Luc	Lucie	1	—

Western transect. This is a long arc (26 localities, 5 major samples) parallel to the Andes (with one upland locality in Colombia, Bogotá, and one in Equador, Riobamba). In the southern end it bends eastward, to reach the Ucayali valley and cross to the upper Purus. In Ecuador the course of this transect is not very orderly. There are also several lateral localities: (1) Puerto Lopez and (2) San José del Guaviare, which should be considered between Villavicencio and South Colombia; (3) Riobamba and (4) Rio Llushin, with Bobonaza; (5) Rio Tapiche and (6) Alto Huallaga, with the southernmost localities.

Code	Localities	Males	Females
FAL	FALCÓN	21	13
Cvb	Colombia-Venezuela border: Sarare, Ayacucho, Santa Librada	6	1
Bog	Bogotá	3	—
VIL	VILLAVICENCIO	22	17
Sco	South Colombia: Florencia, Rio Tuña	3	1
SCE	SANTA CECILIA	17	19
LCO	LIMÓN COCHA	31	32
Sum	Sumaco: San José, Loreto	4	3
Mis	Rio Misahualli	2	1
Bob	Bobonaza: Palanda, Sarayacu, Canelos	1	4
Mia	Miazal	2	2
Mar	Marañon: Manayacu, Rio Cenipa, Mouth of Rio Santiago, Barranca	8	5
PHE	PAMPA HERMOSA	17	9
Roa	Roaboya	—	2
Yar	Yarinacocha	3	2
Tam	Rio Tamaya	3	1
Pur	Purus: Igarapé Champuia, Alto Purus	3	3
Laterals			
Plp	Puerto Lopez	2	1
Sjg	San José del Guaviare	1	—
Rbb	Riobamba	1	1
Rll	Rio Llushin	—	1
Rta	Rio Tapiche	1	—
Uhu	Alto Huallaga	—	1

Colombo-Guianan transect. This transect of 7 localities and 2 major samples links Villavicencio with the Guianas and aims at analyzing the localities in southern Venezuela and southern Guyana. The latter were initially individually considered, but are here presented as a single sample, "Southern Guyana". There are two lateral samples: (1) the localities on the Brasil-Venezuelan border, to be considered with Duida; (2) Alto Catrimani, between Duida and Southern Guyana.

Code	Localities	Males	Females
VIL	VILLAVICENCIO	22	17
Plp	Puerto Lopez	2	1
Dui	Duida: Mt. Duida, Esmeralda	4	1
SBG	Southern Guyana: Kuyuwini Landing, Shudikar-wau, Onora, New River	6	6
Luc	Lucie	1	—
NAS	NASSAU	11	14

Laterals

Brv	Brasil-Venezuela border: Salto do Huá, Serra da Neblina, Rio Tucano	—	3
Cat	Alto Catrimani	1	1

Guiano-Brasilian transects. These two transects aim at analyzing the differentiation between the Guianas and the Central Brasilian areas, represented by Tapirapés. The first transect (4 localities) goes from Essequibo through Southern Guyana to Tapirapés. The second transect (7 localities), from Surinam to Tapirapés, joins the first on the right margin of the Amazonas (Maués). Dunoon has been added to the first transect in cases where this sample differs markedly from Essequibo. Manaus is a lateral locality to the second transect.

Code	Localities	Males	Females
	First transect		
ESS	ESSEQUIBO	18	19
SBG	Southern Guyana: Kuyuwini Landing, Shudikar-wau, Onora, New River	6	6
Ita	Itapiranga: plus S. Sebastião do Uatumã	6	4
Mau	Manaus	5	3
Mes	Maués: plus Manjuru	—	3
Cax	Cachimbo	5	1
TAP	TAPIRAPÉS	26	24
	Second transect		
NAS	NASSAU	11	14
Poe	Poeloegoedoe: plus Hanie	2	—
Pal	Upper Paloemeu	—	1
Tir	Tiriós	1	3
Mes	Maués: plus Manjuru	—	3
Cax	Cachimbo	5	1
TAP	TAPIRAPÉS	26	24
	Laterals		
Mau	Manaus	5	3
Ita	Itapiranga	6	4

Venezuelo-Brasilian transect. This is a long transect, with 20 localities and 2 major samples, intended to complete the north-south analysis and to prolong it beyond Tapirapés to the southern limits of the group. There is only one lateral locality, Aruanã.

Code	Localities	Males	Females
FAL	FALCÓN	21	13
Pay	Puerto Ayacucho	—	1

Dui	Duida: Mt. Duida, Esmeralda	4	1
Brv	Brasil-Venezuela border: Salto do Huá, Serra da Neblina, Rio Tucano	—	3
Tpu	Tapurucuara	—	1
Mau	Manaus	5	3
Ita	Itapiranga: plus S. Sebastião do Uatumã	5	4
Mes	Maués: plus Manjuru	—	3
Cax	Cachimbo	5	1
TAP	TAPIRAPÉS	26	24
Pgt	Porangatu	1	—
Cbr	Cana Brava	4	3
Ube	Uberlandia	1	—
Spa	S. Paulo: Ibarra, Vista Alegre do Alto, Bueno de Andrade, Ribeirão Azul, Araçatuba, Itapura, Lagoa S. Paulo	4	3
Lateral			
Aru	Aruanã	1	—

Napo-Brasilian transect. This sequence of 9 localities and 3 major samples is intended to show relationships in the area between the Ecuadorian and eastern Guianan samples, especially in the upper and middle Amazonas. The transect includes both Santa Cecilia and Limón Cocha, because at times these two samples diverge in spite of being geographically very close.

Code	Localities	Males	Females
SCE	SANTA CECILIA	17	19
LCO	LIMÓN COCHA	31	32
Iqi	Iquitos: plus Rio Itaya	1	1
Jav	Javari: Benjamin Constant, Estirão do Equador	5	4
Pja	Paraná do Jacaré	1	—
Mau	Manaus	5	3
Ita	Itapiranga: plus S. Sebastião do Uatumã	5	4
Mes	Maués: plus Manjuru	—	3
APA	AMAPÁ	12	18
Bel	Belém	1	—

Ucayalo-Brasilian transect. This transect, from Pampa Hermosa to Central Brasil and Maranhão, aims at analyzing relationships in southern Amazonia. There are 5 localities and 2 major samples.

Code	Localities	Males	Females
PHE	PAMPA HERMOSA	17	9
Rta	Rio Tapiche	1	—
Jur	Rio Juruá	3	2

Mup	Mutum-Paranã	2	—
Cax	Cachimbo	5	1
TAP	TAPIRAPÉS	26	24
Lor	Loreto (Maranhão)	—	1

THE CHARACTERS STUDIED

The choice of characters to analyze was oriented by previous experience with *Anolis* and by the peculiarities of the group under study. Obviously we tried to consider a large number of characters, in order to obtain as detailed as possible a picture of geographic differentiation.

After preliminary trials we decided to use 6 scale counts, 4 measurements, one qualitative scale character and one color character. Additionally, sexual dimorphism for each character was also considered.

The scale counts used were:

1. Number of loreal rows at the level of the second canthal.

2. Number of scales along a line joining the two second canthals. In cases of doubt the smallest count was adopted.

3. Minimum number of scales between two supraorbital semicircles.

4. Minimum number of scales between the interparietal scale and the supraorbital semicircles, regardless of side or position.

5. Number of lamellae under phalanges ii and iii of the fourth toe.

6. Number of ventrals between the level of the anterior insertion of the arm and the anterior end of the inguinal sulcus. The latter corresponds to the ridge of the adductor muscles and so to the middle of the thigh. This may seem a hazardous count in iguanids, but actually in well preserved specimens a consistency within 1-2 scales can easily be reached, after a certain experience is acquired. Specimens of which consistent counts could not be obtained were discarded with regard to this character.

Of all scale counts numerous checks were made.

The measurements used, all to the nearest millimeter, were:

7. Body length (rostro-anal) measured along the ventral side with a steel ruler.

8. Tail length, measured with the same ruler. The intact tip of the tail in this group of *Anolis* is very characteristic, so that this is a reliable measurement.

9. Head length, from the rostral to the anterior edge of the ear opening, measured with dividers.

10. Length of tibia, from the middle of the knee joint to the middle of the tibio-tarsal joint, measured with dividers.

11. Subtracting head length from body length we obtained trunk length, against which head length was plotted.

A qualitative scale character studied was the relationship in size between the middorsal scales and those of the dorsal aspect of the upper arm. This character has only two states: either the arm scales are much larger than the dorsals or about equal in size to them. It is quite an unambiguous character.

One obvious character, qualitative or semiquantitative, we considered but in the end did not use in the primary analysis: size and number of rows of enlarged middorsal scales. We found ourselves unable to make this character unambiguous and repeatable. It is, however, useful as a supplementary qualitative character in the identification of certain races or species once these have been recognized on other grounds.

A final qualitative character was the color of the dewlap, which was dealt with only after all the other characters had been analysed, as explained above under "The basic approach".

A CHARACTER DISCARDED: BODY PATTERNS

We have left body color wholly outside our discussion of geographic variation in the *chrysolepis* complex. We have done so because (1) body pattern is extremely variable within populations; (2) by far the greater part of our material was not seen by us in life, and we have no means of estimating the vagaries of preservation; (3) though there are a few constant elements, the elaboration upon these are so diverse as not to be readily separable into categories. We have therefore selected for illustration a few of the the striking patterns, without claiming that these are characteristic of the subspecies or local population that they represent, insisting only that they are part of the spectrum of pattern variation possible to the species.

STATISTICAL METHODS

All numerical comparisons contained in this work were initially made by simple inspection of tables and graphs. Statistical analysis was used in doubtful cases and in those in which there was interest in more accurate comparisons of variability or of magnitude of effects, beyond the simple decision on presence or absence of differences.

The statistical methods employed are all simple and routine, and can be found in Mather (1947) and Siegel (1956), with exception of the analysis of variance, which was performed according to Kramer (1956). Of course, the methods were those found more appropriate to the nature of each variate or pair of variates.

From the chapter on characters studied it will be seen that we had:

1. Quantitative discontinuous variates (scale counts): loreals, scales across snout, scales between supraorbital semicircles, scales between supraorbital semicircles and the interparietal, ventrals, fourth toe lamellae.

2. Quantitative continuous variates (measurements): body length, head length, tail length, length of tibia.

3. Qualitative characters: size of arm scales, dewlap color, sex dimorphism.

Data of the first group were treated in either of two ways. If the distribution was symmetrical and had a range of 5 or more unreduced classes, standard parametrical tests were used (t, F, analysis of variance). In the absence of any one of these two requirements, comparisons were made either by means of a chi-square test or of a test based on the binomial distribution.

In several cases (fourth toe lamellae, ventral scales) some samples were treated by parametric data and others not, following the criteria explained above. We feel this is legitimate because there is no reason to believe that any given character has the same frequency distribution in all the localities. In fact, such differences in shape of distribution may furnish valuable clues to the study of differentiation.

Body length could not be statistically treated. The theory of extremes (Gumbel, 1958; Silva-Leme, 1954), which would be the adequate tool, has no methods for unspecified distributions.

Body proportions were treated by means of regression analysis. In practically all cases straight lines gave such excellent fits that no further analysis was necessary. In cases where inspection showed the inadequacy of linear regression, or when (as in a very few instances) the correlation coefficient was low, the usual anamorphoses were tried (second degree, arith-log, log-log). Regression lines were systematically compared by analysis of variance. In addition, visual comparison was always made, using the value of the dependent variate corresponding to fully adult body size.

The purely qualitative characters received no statistical treatment.

In a preliminary stage of the analysis, we plotted all meristic characters against body length. The presence of significant correlations would mean that the character undergoes ontogenetic change. A broader range of the character at smaller body lengths would mean that its states have different survival values, i.e., that juveniles showing extreme values of the character do not reach adulthood. In either case we would be prevented from using as a unit samples composed of juveniles and adults. Neither case was found to occur.

We checked for correlations between characters. This was done for two purposes. First, as a preliminary step, we wanted to eliminate from the analysis any character strongly correlated with any other in all samples. Then we wanted to study the geographical distribution of the correlations; this is the subject of a section to be presented below. The correlations between pairs of meristic characters and between pairs of measurements were made by routine regression methods. Correlations between body proportions and meristic characters were studied by taking the deviation of each measurement from the regression line against the natural value of the meristic character. When 3 or more characters were associated two by two, multiple regression analysis was performed to eliminate spurious (indirect) correlations.

In the analysis of transects frequent reference is made to "breaks" in the sequence. Some of these are indicated by significant differences between two adjacent adequate samples. In many cases, however, a small number of specimens or even a single specimen is responsible for the statement. This has been done when the lone specimen, geographically situated between two adequate samples, agrees quite closely with one and is obviously outside the range of the other (e.g., in Table 3, the Tibiti specimen).

In looking for clinal variation we used only graphic methods. Either the range of the sample or the range plus the mean and t times its standard deviation were plotted against latitude or longitude of the sample or its distance from a given origin, and a decision reached, by inspection, on the presence or absence of regression. The features of the regression were not found relevant in the present context. Lateral samples were included in the sequence, according to their latitude or longitude.

MAPS

In all cases we attempt to summarize the pattern of differentiation discerned by means of maps. Emphasis has been placed on the existence of areas of stability and transition in the values of characters, not on the values themselves. Simple hatching indicates areas of character stability, and overlap of hatchings areas of transition; arrows indicate the definite presence of clines and point in the direction of higher values of the variate. Stippling identifies areas of complex variation.

THE PRESENTATION OF TABLES, GRAPHS AND MAPS

The large number of tables, graphs and maps precludes their inclusion in the text. We have preferred to present individually, as an appendix, those that illustrate the analyses of individual characters. They are numbered and bound in a separate fascicle, so that they can be laid open to the side of the text, for easier reference. Tabular materials and illustrations used in the discussions are included in the text and lettered consecutively.

DATA

FOURTH TOE LAMELLAE

Males

Table 1 brings together all the major samples. It is easy to see that the samples between Falcón and Dunoon are homogeneous, with range 14-19 and mean between 16 and 17, while much lower values are found in Surinam and Amapá, and much higher in the west.

North Venezuelan transect (Table 2). Along this transect there is some irregular variation but the two pockets of low values (Carabobo and Sucre) are well within the general range.

Guianan transects (Tables 3 and 4). The samples to the east of Dunoon agree in having low values (range 12-16, means around 14) and obviously differ significantly from the western samples. There are two sharp breaks, respectively between Dunoon and La Haye and between Akyma and Kroetoe.

Western transect (Table 5, Graph 1). Table 1 shows that the number of lamellae of the major samples increases from north to south (Villavicencio to Pampa Hermosa), but that there is a sharp difference between the neighboring localities of Santa Cecilia and Limón Cocha. In table 5 one finds a suggestion of clinal variation, except for the southernmost sample, Purus, which is obviously quite off the trend. Graph 1 shows that there is regression of the number of lamellae on latitude, and that the distribution is compatible with the idea of a cline. However, this is not a very good cline, as indicated by the sharp difference between Santa Cecilia and Limón Cocha.

The localities outside the main line of the transect (laterals) agree well with the latitudinal scheme.

Colombo-Guianan transect (Table 6). It is quite clear that Southern Guyana is intermediate between the northeastern low count area and more westerly populations with higher numbers of lamellae. The Duida sample, however, seems to have higher values than Villavicencio; among the samples in Table 1 it would fit better with Santa Cecilia or Limón Cocha. The only relevant lateral sample (Catrimani) has an undiagnostic count of 17.

Guiano-Brasilian transects (Tables 7 and 8). The first transect shows again that Southern Guyana is markedly influenced by the low count area. The Manaus values are undiagnostic, but Cachimbo seems to be lower than Tapirapés.

Along the line from Nassau to Tapirapés (Table 8), Tiriós and Upper Paloemeu agree closely with Nassau, and Itapiranga is intermediate with the higher values to the south.

Venezuelo-Brasilian transect (Table 9). This transect is somewhat confusing. The difference between Falcón and Tapirapés is statistically significant, but the intervening localities do not offer a clear pattern. It is easy to see that Cachimbo has lower values than Tapirapés, agreeing with Falcón, while Manaus, to the north, goes better with Tapirapés than with Falcón. Itapiranga has an unassignable skew distribution. This area can be considered as one of complex intergradation, better understood after we consider the next transect.

The southern samples agree quite well with Tapirapés in having higher values than the Venezuelan area.

Napo-Brasilian transect (Table 10). There are indications of a break between Iquitos and the Brasilian border. The Javarí sample resembles the northern samples. Manaus and Itapiranga show transition towards the lower values in the eastern Guianas.

Ucayalo-Brasilian transect (Table 11). Immediately east of the Ucayali, as already seen above, there is a sharp break toward lower count populations. In fact, all values along this line are very low, and would fit better the Venezuelo-Guyanan samples.

Summary (Map 1). The general picture is then:

1. A well defined area, including Surinam, French Guiana, Amapá and northeastern Pará, with the lowest counts: range 12-15, means around 14.
2. A narrow belt, from northwestern Venezuela to the upper Ucayali, showing a cline: from range 14-19(means 16.3) in the north to 16-21 (mean 18.7) in the south, the highest values for the species.
3. An area of intermediate values (16-19, mean around 17.5) from northern Mato Grosso south to S. Paulo.
4. An area also of intermediate values (but lower than 3 above), in Venezuela, Trinidad and Guyana: ranges 14-19, means between 16 and 17.
5. The picture in the region between areas 3 and 4 above, essentially the Amazonas valley, is not completely clear, but seems to be one of broad, non-clinal, intergradation.

Females

Table 12 does not show immediately much pattern, except for very low values in Nassau and Amapá, and very high ones along the Western transect.

North Venezuelan and Guianan transects (Tables 13 to 15). In Venezuela and Guyana there is much local variation. There is a pocket of low counts in Carabobo (Table 13), as in the males. Essequibo and Dunoon differ sharply, as was the case with Santa Cecilia and Limón Cocha for the males. Several distributions are markedly asymmetrical, such as Falcón, Essequibo and Nassau (Tables 13 and 15). In general, ranges are from 14 to 18, and modes 15 or 16.

Nassau and Amapá have the lowest values of all, and agree between themselves. The first Guianan transect (Table 14) shows a break between Dunoon and Tibiti, the intervening specimen (La Haye) being intermediate. The second Guianan transect (Table 15) shows the break between Dunoon and Tafel Berg, the specimen from Akyma being intermediate but more on the Guyanan side.

Western transect (Table 16 and Graph 1). This table suggests the presence of a cline from Falcón to the Marañon (Graph 1): a regression line may be traced across the distributions plotted against latitude. Pampa Hermosa is decidedly off the cline, but the neighboring localities of Roaboya and Yarinacocha resume the trend of increase southwards (Graph 1). The Rio Tamaya specimen agrees with Pampa Hermosa and the Purus ones have again low values, as in the males.

Colombo-Guianan transect (Table 17). This transect shows conclusively that Southern Guyana belongs with Nassau and Amapá in the low count area, while Duida, the Brasil-Venezuela border and Catrimani belong to the high count area.

Guiano-Brasilian transect (Tables 18 and 19). The first transect confirms that Southern Guyana really belongs with Nassau and Amapá.

Itapiranga may be said to agree both with Guyana and Tapirapés. The other middle Amazonian localities (Manaus, Maués-Manjuru, and Cachimbo) have values too low both for Guyana and Tapirapés, and may be considered intermediate between the low counts of the northeast and the areas to the south and west.

The second transect shows that, as in the males, Tiriós and Upper Paloemeu are definitely inside the low count area; it also makes quite evident the complex transitional character of the middle Amazonian localities.

Venezuelo-Brasilian transect (Table 20). High values are seen in the Venezuela-Brasil border more compatible with the western samples, intermediate values in Itapiranga and low ones in Manaus, Maués-Manjuru and Cachimbo. This demonstrates conclusively that the influence of the low count area reaches the middle Amazonas, and that there is no clinal or other regularity in the transition between the northern (Venezuelan) and southern (Central Brasilian) areas. South from Tapirapés the localities are homogeneous.

Napo-Brasilian transect (Table 21). The western Amazonian localities (Javarí and Iquitos) agree with the centro-Amazonian ones in being intermediate between low and high count areas.

Ucayalo-Brasilian transect (Table 22). Pampa Hermosa agrees well with Tapirapés, as do Rio Juruá, between them, and Loreto, at the eastern extreme of the range. Cachimbo is off, under the influence of the low counts.

Summary (Map 2). We may define:

1. One area of low counts (12-15, means around 13.5) including Surinam, French Guiana, Amapá, Northern Pará and southern Guyana.
2. A broad area of intermediate counts (15-18, means between 16.5 and 17.0) from S. Paulo to Tapirapés on the north and Pampa Hermosa on the northwest.
3. A clinal area from western Venezuela (15-17, mean 15.5) to the Marañon (ranges 16-20, means above 17.5).
4. A highly variable area in Venezuela and Guyana with ranges 14 to 18 and means from 15.5 to 16.7.
5. Intergradation is obvious between the low count area and the southern one. The situation in the Upper Amazonas is not clear, but broadly intermediate values seem to be the rule.

Sex differences

Three samples (Table 23) show statistically significant sexual differences. These are Limón Cocha, Pampa Hermosa and Tapirapés. However in all other samples the male mean is higher, even if only slightly so. We cannot find any regularities in the geographical distribution of the significant differences.

Combined pattern

A comparision of maps 1 and 2 shows very striking both similarities and differences between the male and female patterns of differentiation.

There are four cases of similar differentiation in the two sexes: (1) the best differentiated area, with the lowest counts in both sexes, extending from the Guyana-Surinam border east to Belém and south to the north of Pará; (2) the clinal belt from northwestern Venezuela to Peru, where the highest values occur; (3) the Venezuelo-Guyanan area, with third-ranking values, and (4) the Brasilian area, second-ranking, from Tapirapés to S. Paulo.

It appears that the sexes have some degree of independent variation. This is indicated by the case of Pampa Hermosa, whose males are at the upper end of a cline, but whose females are considerably below the neighboring samples. We have also the case of Essequibo and Dunoon, in which the male difference does not reach significance level (chi square 7.228 for 4 degrees of freedom), while the females differ at the .01 level (chi square 11.412 for 3 degrees of freedom).

LOREALS

Males

Table 24 shows that there are two groups of samples: (1) those from Santa Cecilia to Pampa Hermosa, with higher values (mode 7), (2) Villavicencio, intermediate, and (3) the remainder of the range, essentially homogeneous, with lower counts (mode 6). The differences are mainly due to the shifting upwards of the upper extremes and modes.

Western transect (Table 25). Variation along the Western transect is broadly clinal, but the regression is very imperfect.

Given the homogeneity of the general territory (confirmed by inspection of the transect), we must consider the West-East transects, to verify the relationships of the clinal area.

Colombo-Guianan transect (Table 26). The area of low counts begins immediately to the east of Villavicencio.

Napo-Brasilian transect (Table 27). The data are not very clear, but there seems to be a gradual transition, the influence of high counts reaching Itapiranga.

Ucayalo-Brasilian transect (Table 28). Again there is a suggestion that the influence of the high counts reaches mid- continental longitudes (Cachimbo).

Summary (Map 3). We have only two units: the clinal western area with high counts (5-9, mode 7), extending along the Amazonas, and the remainder of the range, with low counts (5-8, mode 6). Apparently there is an area of intergradation in Central Amazonia.

Females

Table 29 shows much local variation. However, statistical analysis shows that the samples for Falcón to Amapá are essentially homogeneous, not even the difference between the two samples with extreme values (Falcón and Western Guyana) being significant. Tapirapés belongs with this assemblage.

Western transect (Table 30). On the other hand, Limón Cocha clearly differs from both Falcón and Tapirapés. The variation from Falcón to Limón Cocha is clinal but the populations to the south have lower values, approaching again Villavicencio levels. We must then examine the West-East transects.

Colombo-Guianan transect (Table 31). Puerto Lopez, Duida, the Brasil-Venezuela border and Catrimani, taken together, indicate the presence of an area of complex transition. Southern Guyana is clearly on the low count side.

Napo-Brasilian transect (Table 32). The transition here is evident, the influence of the high counts reaching Manaus and Itapiranga but not Maués.

Ucayalo-Brasilian transect (Table 33). Except for the fact that Loreto agrees well with Tapirapés, this transect adds no information.

Venezuelo-Brasilian transect (Table 34). This transect confirms that in Western Amazonia the influence of the high count area is marked. In the southernmost end of the range there seems to be a reversal of the trend, with high values in S. Paulo.

Summary (Map 4). The general pattern is then:

1. One western clinal area of high values (range 5-9, mode 7), increasing southwards, with climax in northern Ecuador, but still with high values to the south.
2. Low values in the remainder of the range (5-8, mode 6).
3. An intergradation belt extending from the longitude of the upper to that of the middle Amazonas.

Sex differences

No sample afforded significant sex differences (Table 35). However, it was nevertheless thought better to analyze the sexes separately, since the single sex samples were adequate, and confirmation of general results from separate analyses very desirable. It turned out that a very interesting difference between the individual sex patterns would have been lost if we had mixed the sexes from the beginning: the fact that the western cline has its climax in Pampa Hermosa in the males and in Limón Cocha in the females.

Combined pattern

The two sexes have fundamentally the same pattern, with two differences. One is that, as mentioned above, the western female cline stops 7 degrees of latitude north of the termination of the male cline. The other is that the influence of the high counts extends further east in the female than in the males.

SCALES ACROSS THE SNOUT

Males

Inspection of Table 36 does not suggest much, except that there is local variation, and we move on to the transects.

North Venezuelan transect (Table 37). Falcón is lower than the samples to the east, as far as Trinidad, which agree very well among themselves. There is, however, no sharp break, the gap being bridged by the samples from Bejuma to Pie del Cerro.

Guianan transects (Tables 38 and 39). There are differences between the eastern and western halves of the area. Along the first transect there is a large difference between Dunoon and Paramaribo. Along the second transect the break is between Dunoon and Kroetoe. However, Dunoon shows some tendency to higher counts. The lateral localities fit the pattern.

Western transect (Table 40). Initially there is a very clear break between Falcón and Villavicencio, with the samples from the Colombia-Venezuela border bridging the gap. Falcón is thus seen as a pocket of low values, with higher counts on both sides. From Villavicencio to Santa Cecilia there is no major variation, but Limón Cocha and the southernmost samples have very high values. The distributions are very irregular, especially that of Limón Cocha, which is practically bimodal. The laterals agree with the general scheme.

Colombo-Guianan transect (Table 41). Puerto Lopez and Duida are lower than Villavicencio, and must be considered as fitting better the Venezuelan distribution. Southern Guyana is intermediate between low and high counts, and is midway between Villavicencio (or Dunoon) and Nassau. Catrimani fits better with the low count distributions.

Guiano-Brasilian transect (Tables 42 and 43). The first transect shows good agreement among all samples except Southern Guyana, which has higher counts, as already seen.

The second transect shows that the Amazonian samples (including Tiriós in northernmost Pará) are on the low count side, the high count area being strictly north of the Tumuc-Humac range.

Venezuelo-Brasilian transect (Table 44). There is very good agreement along the entire transect.

Napo-Brasilian transect (Table 45). This transect indicates that the eastern and western areas of high counts are separated in the middle by a low count area, typical of which is Itapiranga, as seen above. The western Amazonian samples (Iquitos, Javarí, and Paraná do Jacaré) agree very well with Limón Cocha, not with Santa Cecilia, which has more moderate values.

Ucayalo-Brasilian transect (Table 46). It is noticeable that Rio Tapiche agrees closely with Pampa Hermosa, but the Brasilian localities, Rio Juruá and Mutum-Paranã, are intermediate between the high values to the west and the low ones at Cachimbo and Tapirapés.

Summary (Map 5). The situation may be thus described:

1. One northeastern area with high counts (range 10-14, means around 10.5) including Surinam, French Guiana and Amapá.
2. One second area, with comparable means but lower range (9-12) from Villavicencio to Santa Cecilia.
3. Immediately to the south of this one, and entering the Amazon valley to the Solimões, an area of very high counts (9-17, mean between 12 and 13).
4. The remainder of the range is an area of low counts (range 7-12, means between 9 and 10).

Females

Table 47 shows that more than half (7) of the female samples are so asymmetrical that it is worthless to cite a confidence interval for the mean. This also influences the variability of the average, as single extreme observations may markedly distort the arithmetic mean.

It is easy to see, however, that there are two areas of high counts, Nassau-Amapá on one side, the Western transect on the other.

North Venezuelan transect (Table 48). In spite of the variability, it is clear that the samples in this area are fundamentally homogeneous.

Guianan transects (Tables 49 and 50). A break between high and low counts occurs to the north between La Haye and Tibiti, inland between Akyma and Tafel Berg.

Western transect (Table 51). There are two breaks: one between the Colombia-Venezuela border and Villavicencio and the other, much sharper, between the Marañon and Pampa Hermosa. The localities to the south of Pampa Hermosa have relatively lower values, intermediate to those on the north, so that locality really constitutes a pocket of very high counts. The laterals agree with the general scheme.

Colombo-Guianan transect (Table 52). The eastern area (Nassau) has higher values than the western (Villavicencio). Of the intervening localities, Puerto Lopez, Duida, and the Brasil-Venezuela border are intermediate between Villavicencio and the low count Venezuela-Guyanan area, as represented by Southern Guyana; Catrimani is on the Guyanan side.

Guiano-Brasilian transects (Tables 53 and 54). The Central Brasilian sample (Tapirapés) has lower values than the Guyanan ones, but the intervening samples do not bridge the gap. On the contrary, they show high values transitional to those of Surinam; it is clear that the influence of the area of high counts gets to the right bank of the Amazonas, as shown by Maués; the samples on the left bank have much lower values.

Venezuelo-Brasilian transects (Table 55). This one confirms the first Guiano-Brasilian transect: Tapirapés is lower than the Venezuelan and Guyanan samples, whose influence gets to the Amazonas (Maués) as does that of the high counts area to the northeast. South of Tapirapés there seems to be an increase in number of scales, but too few localities are represented.

Napo-Brasilian transect (Table 56). The Javarí agrees with the western values, as does the Maués region, and all agree with Amapá. Only Manaus and Itapiranga disagree, as already seen.

Ucayalo-Brasilian transect (Table 57). A very sharp break is evident between the Juruá, which agrees with Pampa Hermosa, and Cachimbo, which agrees with Tapirapés, as does Loreto.

Summary (Map 6). In general we have:

1. One area of low counts in Venezuela (north of Mt Duida) and Guyana (ranges 7-12, means around 10).
2. One area of low counts from Cachimbo and Loreto south to S. Paulo (ranges 8-12, means around 9).
3. One vast, diversified area of high counts in the remainder of the range, with three main subdivisions: (1) Villavicencio to the Marañon (ranges 9-14, means between 11 and 12); (2) Surinam, French Guiana and Amapá (range 10-15, means between 11 and 13). Except for a southern tongue of the Guyano-Venezuelan low count area, Amazonia has high counts. (3) A pocket of very high values (range 12-19, mean about 15) centering in Pampa Hermosa, and making its influence felt from the Huallaga to the Juruá.

Sex differences

In 6 samples (Table 58) there are significant differences between the sexes: Falcón, Essequibo, Nassau, Villavicencio, Santa Cecilia, and Pampa Hermosa. In 5 cases the female counts are higher. No geographical regularities are seen.

Combined pattern

The following similarities between the male and female patterns of differentiation are rather striking: (1) there are two areas of high counts, one eastern and one western, and two areas of low counts, one northern and one southern; (2) the western area of high counts is further subdivided, higher counts to the south.

The main differences are: (1) in the males the low count areas coalesce in the middle Amazonas, while in the females the same area shows high counts; (2) the break between the northern and southern portions of the western high count area is north of Limón Cocha in the males and south of the Marañon in the females — that is, each sex in Limón Cocha belongs to a different group.

SCALES BETWEEN SUPRAORBITAL SEMICIRCLES

Males

From Table 59 it is evident that there are 3 groups of samples: (1) from Villavicencio to Amapá, range 1-3, mode 2; (2) Tapirapés, 0-3, mode 1; (3) southern samples of the Western transect, with high values and a suggestion of a cline. Inside the first area there is a low pocket in Western Guyana.

Western transect (Table 60, Graph 2). It is quite obvious that there is clinal variation from Southern Colombia to Rio Tamaya — then a sudden break between the Ucayali and the Purus.

Guiano-Brasilian transects (Tables 61, 62). The first transect shows that the transition between Essequibo and Tapirapés is clearly gradual across the middle Amazonas (Itapiranga, Manaus and Cachimbo). The second transect adds that Tiriós is on the Guianan side.

Venezuelo-Brasilian transect (Table 63). This also shows a gradual transition from the northern samples to Tapirapés. However, there is marked heterogeneity to the south: the samples in Minas Gerais (Uberlândia) and S. Paulo have higher values than Tapirapés.

Napo-Brasilian transect (Table 64). This transect shows a break between the Javarí and the middle Amazonas.

Ucayalo-Brasilian transect (Table 65). Along this line the transition is more gradual, as shown by Rio Juruá, Mutum-Paranã and Cachimbo.

Summary (Map 7). The general pattern is:

1. One low count area (range 0-2, mode 1) centering around Tapirapés — probably followed to the south by an area of higher counts.
2. One area of intermediate counts (range 0-3, mode 2) including all the northern part of the territory, from Villavicencio to Amapá.
3. A clinal area of high counts, from southwestern Colombia to Pampa Hermosa and east to the Javarí (range 2-4, no clear mode, but median 5).
4. All these areas intergrade in the middle Amazonas.

Females

Table 66 indicates the following grouping of the samples: (1) Tapirapés, with the lowest values; (2) Pampa Hermosa, with the highest; (3) Nassau, plus Amapá, with the second highest counts; (4) all other samples.

Guianan transects (Tables 67 and 68). In the first transect one notices, between Haul Over and Dunoon, much variability, but always within the range 1-3. Between Dunoon and Nassau values are intermediate. Matarony agrees perfectly with Nassau, while Amapá is lower, but the difference is not statistically significant.

Along the second transect there is a break between Dunoon and Tafel Berg, the latter agreeing completely with Nassau.

Western transect (Table 69). A break is quite evident between the Marañon and Pampa Hermosa. Values to Yarinacocha are still high, the two remaining samples (Rio Tamaya and Purus) are on the low count side.

Colombo-Guianan transect (Table 70). All samples involved in this transect agree with the lower count samples, not with Nassau.

Guiano-Brasilian transects (Tables 71 and 72). The transition between Guyanan and Surinamese high values on one side and Central Brasilian low ones on the other is perfectly gradual — even Paloemeu and Tiriós are intermediate.

Venezuelo-Brasilian transect (Table 73). The transition from higher values in the north to lower ones in Tapirapés is irregular. The southern samples (Cana Brava and S. Paulo) show higher values than Tapirapés.

Napo-Brasilian transect (Table 74). The western samples are on the high side; Javarí exceeds Limón Cocha, approaching Pampa Hermosa. The eastern samples (from Manaus to Maués) agree with Amapá.

Ucayalo-Brasilian transect (Table 75). Rio Juruá is a little lower than Pampa Hermosa. Cachimbo is in close agreement with Tapirapés.

Summary (Map. 8). The over-all pattern is:

1. One area of very low values (0-2, mode 1) centering in Tapirapés, problaby followed to the south by higher counts.
2. One area of very high values (2-6, mode 4), around Pampa Hermosa.
3. One area of high values (1-4, mode 2-3) from Surinam to Amapá.
4. One area of low values (0-3, mode 2) from Guyana west to western Venezuela and then south to the Marañon.
5. All areas intergrade in Brasilian Amazonia.

Sex differences

In no case significant sex differences were found (Table 76). However, for the same reasons as with the loreals, it was decided to analyze the sexes separately.

Combined pattern

The most important resemblances between the two patterns are: (1) there are three differentiated areas in common, and their ranks are the same (the lowest counts around Tapirapés, intermediate ones from Villavicencio to Guyana, the highest ones around Pampa Hermosa); (2) Western Guyana is a low pocket in both cases; (3) the southernmost Brasilian samples have higher counts than Tapirapés.

The main differences are: (1) the differentiation of a medium-high area in the northeast only in the females; (2) the disappearance, in the females, of the lower part of the western cline which exists in the males, leaving Pampa Hermosa abruptly separated from the northern localities.

SCALES BETWEEN INTERPARIETAL AND SUPRAORBITAL SEMICIRCLES

Males

Table 77 indicates the presence of two sharply set-off groups of samples: (1) from Villavicencio to Dunoon, plus Tapirapés, with low values (1-3, mode 2); (2) Limón Cocha and Santa Cecilia, with very high values (2-6, mode 4). Nassau and Amapá seem to have higher values than the samples to the west, but the differences are not statistically significant. Pampa Hermosa seems to occupy an intermediate position, that can be better understood through the study of the suitable transects.

Western transect (Table 78). This table shows a quick transition in Southern Colombia from the general level (Villavicencio) to the higher one of Santa Cecilia and Limón Cocha. This high level prevails to the south to the Marañon. Pampa Hermosa and samples south (excepted the Purus) have lower values, but not quite as low as the general area.

Napo-Brasilian transect (Table 79). This transect indicates that the influence of the high counts reaches the Paraná do Jacaré to the east.

Ucayalo-Brasilian transect (Table 80). This sequence shows clearly that Pampa Hermosa, seen in Table 78 to have significantly lower values than the Ecuadorian area, is really intermediate between the latter and the general low count area, the intergradation belt being not very broad (reaching only the Juruá).

The transects within the low count area indicate essential homogeneity.

Summary (Map 9). We have then:

1. One area of high counts (range 2-6, mode 4) from northern Ecuador to the Marañon.

2. Low counts (range 1-4, mode 2-3) in the remainder of the territory.

3. Intergradation occurs from the longitude of the Ucayali to that of the Juruá, from the latitude of the Upper Amazonas to that of the Upper Purus.

Females

Analysis of Table 81 shows 4 groups of samples: (1) Santa Cecilia, Limón Cocha and Pampa Hermosa, with high values (5 or more, mode 3-4) (2) immediately below (up to 4, mode 3) Nassau and Amapá; (3) with lowest rank all samples from Falcón to Essequibo and Dunoon (highest value 3, mode 2); (4) Tapirapés and Villavicencio are intermediate between groups 2 and 3, not differing significantly from either.

Western transect (Table 82). The break between the northern part (to Southern Colombia) and the southern, high count area, is sudden. The high values extend to the Purus. The lateral samples in the table agree quite well with their neighbors in the transect. One specimen from Pampa Hermosa has the highest value found for the species, 9 scales.

Napo-Brasilian and Ucayalo-Brasilian transects (Tables 83 and 84). The influence of high counts reaches the Javarí and, less strongly, the Juruá.

Summary (Map 10). We have:

1. One area of high counts (2-9, mode 3-4) from northern Ecuador to Pampa Hermosa.
2. The remainder of the area is characterized by lower counts (1-4, mode 2-3); there is a break between Guyana and Surinam, but the remaining of the range is broadly intergrading.
3. The intergradation belt between the western high count area and the others is narrow.

Sex differences

Table 85 shows only two significant differences between males and females: Santa Cecilia and Pampa Hermosa. If we examine (Table 86) the data for these samples plus Limón Cocha, it becomes evident that the difference in Santa Cecilia is of the same magnitude as in Limón Cocha, and that the high chi square reflects rather the uneven distribution in the low classes than the over-all position of the sample. Pampa Hermosa, on the contrary, has very low male values, compared with the other samples, and this is the cause of the significance of the difference.

Combined pattern

In both sexes we have a high count area in the West and a remaining low count area, inside which the indications of differentiation do not reach the level of significance. Since all the sex differences are inside the first area, the discussion must be divided into two parts: (1) the comparison of the high count and low count areas and (2) a new analysis of the general area for the sexes combined.

High count areas. In the females, the high count area extends from northern Ecuador to the Upper Purus; in the males it stops at the intermediate between this southern area and that which extends from Falcón to Villavicencio, which is homogeneous. Pampa Hermosa an samples south have slightly lower counts than Ecuador.

Colombo-Guianan transect (Table 106). The counts of the only Duida female and of the border specimens may give the impression of clinal transition between Villavicencio and Nassau. However, the specimen from Catrimani has 43 ventrals, and indicates that there is a break between populations at its longitude and that of Southern Guyana.

Guiano-Brasilian transects (Tables 107 and 108). Itapiranga and Manaus tend toward lower counts. The second transect shows, furthermore, that Paloemeu is in close agreement with Nassau, but that the transition zone reaches from Tiriós in the north to Maués in the south.

Venezuelo-Brasilian transect (Table 109). There is good agreement between Falcón and Tapirapés. However, the influence of the high count areas is seen in all intermediate localities, except again Manaus. South of Tapirapés there is no variation.

Napo-Brasilian transect (Table 110). Iquitos and the Javarí are in complete agreement with the high count Ecuadorian samples. They agree quite well with Amapá, but the intervening localities (Manaus, Itapiranga, and Maués) have values too low to be called intermediate.

Ucayalo-Brasilian transect (Table 111). There is overlap, but a decided difference, between Pampa Hermosa and Tapirapés. The former could be considered intermediate between the latter and Limón Cocha, but the Juruá specimens have values too high for that.

Summary (Map 12). The general picture is:

1. One area of very high counts (range 50-62, means around 55) including (in part) Surinam, French Guiana, Amapá and northeastern Pará.
2. Another area of high counts (47 to 60, means between 50 and 55) from southwestern Colombia to the Marañon; this area may be considered as extending south to Pampa Hermosa and east to the Juruá, with more moderate values.
3. One area of very low counts (40-52, means below 45) in Brasil, from Tapirapés and Loreto south.
4. Another area of very low counts (40-48, means around 43) from Caracas in the east to Villavicencio in the southwest.
5. An area of intermediate counts (38-52, means around 45) including eastern Venezuela and Trinidad.
6. The remainder of the range presents intermediate values (ranges 43-56, means between 45 and 50).

Sex differences (Table 112)

In all samples the males have more ventrals than the females. In 7 samples the difference is significant. In the 4 in which it is not it is possible to say in the case of Santa Cecilia that high female values are responsible for the non-significance: the male mean is practically identical to that of Limón Cocha, but the female is 1.3 scales higher.

Combined picture

The male and female patterns are much alike. In both cases there are one eastern and one western areas of high counts, and one northwestern and one southern areas of low counts, the center of the range showing intermediate values. The main difference is the break east of the Distrito Federal in Venezuela, found only in the females.

TAIL LENGTH

Males

The basic data on the regression of tail length on body length in the major samples are shown in Table 113. In Table 114 values of the estimated tail length at 65 mm body length are ranked. The distribution of the ranks in Map 13, and the observation of the differences, indicate a definite geographical pattern.

The highest value is found in Villavicencio (162.3 mm). Next, ranks 2 to 7, come the Venezuelan and Guyanan samples and Tapirapés, between 151.9 and 158.5 mm. A third group, ranks 8 to 10, includes the southern samples of the Western transect, Santa Cecilia to Pampa Hermosa (140.8 to 146.3). Finally, Nassau and Amapá rank 11 and 12, with the shortest tails (132.7 and 130.5 mm).

North Venezuelan transect (Graph 4). The graph shows that the lines of this transect are obviously parallel. They are also very close; however, the fit of each individually is so good (the smallest correlation coefficient is .95) that their regression constants must be compared. Falcón differs significantly from both NE Venezuela and Trinidad, which agree between themselves.

Plotting the smaller samples on this graph shows (as was to be expected) it is impossible to assign them to one line or the other.

Guianan transect (Graph 5). Both Guianan transects are presented together, as there are not many specimens with whole tails. Essequibo is omitted because it coincides exactly with Western Guyana, which has a wider range. Dunoon, which has a very short range, also overlaps perfectly the other samples.

There is need to check statistically the significance of the differences between Western Guyana and NE Venezuela. The regression coefficients do not differ significantly; as to the distance between the lines, the result is close to but does not reach the level of significance. If we combine the samples Western Guyana and Essequibo and repeat the test against NE Venezuela, we see that the difference is definitely not significant.

Assignment of the small samples is unambiguous: Georgetown, Roraima, Akyma and Auyán-Tepui are on the Guyanan side; the Surinam and French Guiana samples agree with Nassau.

Western transect (Graphs 6 to 9). Villavicencio (Graph 7) is obviously a pocket of long tails, the regression line being significantly above both Falcón and the samples to the south. The latter three do not differ significantly; they are in fact extremely close. Plotting the intermediate northern localities (Graph 8) one sees that the samples of the Colombia-Venezuela border are on the Falcón side or intermediate. Bogotá fits exactly Villavicencio, as does the lateral locality, Puerto Lopez.

Going south (Graph 8) we see that the South Colombia sample is intermediate between Villavicencio and Limón Cocha. The Ecuadorian localities all fit well Limón Cocha (except for a very long-bodied and long-tailed specimen from the Marañon).

The southern samples (Graph 9) fit very well with the local major samples. The slightly longer tails of Rio Tamaya are within the variation of the excellent Limón Cocha regression (r .986).

Colombo-Guianan transect (Graph 10). Up to Duida tails are as long as in Villavicencio, those of Southern Guyana somewhat larger than Nassau. Including Western Guyana in the graph, it becomes apparent that both Southern Guyana and Catrimani are intermediate between, on one side, Villavicencio and Venezuelo-Guyanan values, and, on the other the short Nassau tails. Lucie belongs with Nassau.

Guiano-Brasilian transects (Graph 11). The difference between Tapirapés and Nassau is significant, in spite of the extreme variability of Tapirapés. Western Guyana and Tapirapés converge, so differences could only be found in young specimens. Manaus and Itapiranga agree closely with Western Guyana, their smaller specimens differing decidedly from Tapirapés. Cachimbo agrees with Tapirapés, and Tiriós and Poeloegoedoe clearly with Nassau. Southern Guyana, which has been shown to be intermediate, is omitted, to avoid cluttering up the graph.

Venezuelo-Brasilian transect (Graph 12). Falcón and Tapirapés converge at the larger sizes. Duida tends to be higher than Falcón, showing influence of Villavicencio. Manaus and Itapiranga agree closely with Falcón. The other Brasilian localities all agree very well with Tapirapés.

Napo-Brasilian transect (Graph 13). Amapá and Limón Cocha do not differ significantly, and of the intervening samples Iquitos, Javarí and Paraná do Jacaré fit well with both, but Manaus and Itapiranga disagree, and are Guyano-Venezuelan in character.

Ucayalo-Brasilian transect (Graph 14). There is a very clear break between Mutum-Paranã, on the Pampa Hermosa side, and Cachimbo, which agrees with Tapirapés.

Summary (Map 14). We may define:

1. An area of long tails, around Villavicencio, its influence extending to the Venezuelan and Ecuadorian borders to the north and south, and east to Duida.

2. The next area in tail length extending from Falcón to Guyana to Manaus, with a pocket of higher values in Trinidad.
3. An area of lower values for the young, but converging towards the values of area 2 in the adults, extending from Cachimbo to S. Paulo.
4. One area of low values extending from Surinam to Amapá.
5. An area of equivalent low values in Ecuador and western Amazonia.

Females

From a consideration of Tables 115 and 116 and of Map 15, a geographic pattern emerges. Beginning with the lowest ranks, we see that Nassau and Amapá (ranks 11 and 12) belong together, separated from the sample of rank 10 by almost 15 mm. Next we have ranks 7, 9 and 10 in the southern half of the Western transect, the total range being 8.0 mm. Pampa Hermosa agrees with the Guyanas. Rank 9 belongs to Falcón. Villavicencio has rank 2 and a homogeneous group (ranks 3 to 6, range 3.1 mm) occupies NE Venezuela and Guyana. The difference between Falcón and Western Guyana is 2.9 mm. Tapirapés has the longest tail, 145.9 mm at 65 mm body lenght. Thus again it is reasonable to analyze the transects.

North Venezuelan transect (Graph 15). The three local samples that are combined to form NE Venezuela agree perfectly among themselves, so we think it valid, as well as very convenient, to keep them combined to study variation within this transect. NE Venezuela agrees perfectly with Trinidad (and is thus omitted from the graph), and both differ from Falcón. Plotting the remaining specimens it is easy to see that only one sample can be unambiguously ascribed, that from the Distrito Federal. In spite of its short range, it is possible to calculate for it a good regression line ($r^2 = .85$), which is seen to be significantly above Trinidad. Tail lengths thus have a maximum at the Distrito Federal and diminish to the east and west.

Guianan transects (Graphs 16 and 17). Essequibo, Western Guyana and Dunoon overlap so closely that it is sufficient to plot one of the lines (Western Guyana). It is easy to see that this line is never far from and converges towards NE Venezuela, so that in practice there is no difference. Nassau, however, is significantly lower; Matarony coincides with Nassau.

Along the first transect there is a break between Guyana and Nassau: it occurs between La Haye and Paramaribo.

Along the second transect the break is between Akyma and Tafel Berg. Roraima belongs clearly with Guyana.

Western transect (Graphs 18 and 19). We have here 3 units: (1) Villavicencio; (2) Pampa Hermosa plus Santa Cecilia (perfect overlap); (3) Limón Cocha. The differences are statistically significant.

The specimen from the Colombia-Venezuela border falls on the Villavicencio line. That from South Colombia, on the contrary, falls on the Limón Cocha line. Not all Ecuadorian specimens can be assigned to either Pampa Hermosa or Limón Cocha. However, Rio Llushin tends more toward Pampa Hermosa, while Riobamba falls adjacent to (but below) the upper end of the Limón Cocha line. This indicates some variability inside the area. The Marañon specimens agree very well with Pampa Hermosa.

The southern samples also agree with Pampa Hermosa (Graph 20), with the exception of Alto Purus, with rather short tails — too short even for Limón Cocha.

Colombo-Guianan transect (Graph 20). Puerto Lopez, Duida, the Brasil-Venezuela border, and one specimen from Southern Guyana agree perfectly with Villavicencio. The other Southern Guyanan specimens belong with Nassau.

Guiano-Brasilian transects (Graph 21). This graph shows quite clearly that Southern Guyana is really a transitional region. Itapiranga agrees closely with Ṭapirapés. Manaus begins by agreeing with Nassau and ends up on the prolongation of Tapirapés. Paloemeu and Tiriós agree with Nassau. Maués is intermediate and Cachimbo belongs with Tapirapés.

Venezuelo-Brasilian transect (Graph 22). The high count influence reaches Maués, which is intermediate; the northern samples fit Falcón perfectly, Manaus excepted. The samples from Cachimbo and south agree perfectly with Tapirapés.

Napo-Brasilian transect (Graph 23). The only important thing demonstrated is that the Amazonian specimens fit the Napo regressions well.

Ucayalo-Brasilian transect (Graph 24). This shows only that Rio Juruá fits Pampa Hermosa, and Loreto is compatible with Tapirapés.

Summary (Map 16). In general we have:

1. One area of long tails from Cachimbo to S. Paulo.
2. Another, small, area of long tails from Villavicencio, to the longitude of the Catrimani.
3. One area of intermediate values in Venezuela, Trinidad and Guyana, with highest measurements in the Federal District of Venezuela.
4. One area of short tails and high intersample variability in Ecuador and Peru.
5. The shortest tails are in Surinam, French Guyana and Amapá.
6. Central Amazonia is an area of complex intergradation.

Sex differences

In all cases the males have longer tails than the females (Table 117). In one case the difference is not significant: Pampa Hermosa, which shows the smallest difference but has also the smallest samples (6 and 7 specimens).

If we take (last column of Table 117), as a rough measure of dimorphism, the female tail length as percentage of the male and plot the data in a map (Map 17), a striking pattern emerges: the samples with .89 or less are on the northern half of the range, from Villavicencio to Amapá, those with .91 or more on the southern part, from Tapirapés to Santa Cecilia.

Combined pattern

The general patterns of males and females are extremely alike; both include the same 5 basic areas, with minor differences only in the extent to which their influences are felt in central Amazonia. If we compute (Table 118) Spearman's coefficient of rank correlation between ranks of males and females, we obtain a value of .88. Inspection of Table 118 shows that the largest shift in position is that of Tapirapés, whose females are 4 places above the males; this is the most striking difference between male and female patterns.

LENGTH OF TIBIA

Males

Table 119 presents the data on the regression of length of tibia on body length in the major samples. A very high proportion of the lines (10 out of 13) have regression coefficients between .29 and .35. Dunoon, Villavicencio and Tapirapés are the exceptions.

Dunoon is a small sample, with a short range of body lengths; it will be commented on again later.

Villavicencio, which has the lowest correlation coefficient, is a good-sized sample, but its range is also narrow, and there is no way of improving it by addition of neighboring localities. However, a plot of it (Graph 25) in comparison with a sample of good spread (Falcón), shows that the upper end of the distribution of the tibial length is severely censored. In fact, a parabola would give a better fit, but there is no reason to further quantify this discrepancy.

Tapirapés (Graph 26), although showing very good correlation (body length explains 89 percent of the variance of the tibia) is more variable than the remaining samples, but otherwise quite normal: there is a good spread and an excellent fit. Its difference from the others is really intrinsic.

After commenting on these 3 unusual samples, we must turn to the ranking of the samples (Table 120 and Map 18). The geographical pattern is clear: (1) in the northeastern part of the range are the samples with ranks 1 to 5 and 6; (2) Limón Cocha and Santa Cecilia have ranks 4 and 6, and agree closely with high ranking samples of the preceding group; (3) the Venezuelan samples and Trinidad are a little below; (4) Tapirapés and Pampa Hermosa have adjacent ranks (9 and 10) and definitely lower values; (5) finally, Villavicencio remains isolated with its lowest rank of 12. We move on to the transects.

North Venezuelan transect. Completely homogeneous.

Guianan transects (Graphs 27 and 28). There are small differences within the area, Amapá in particular differing from W Guyana and Nassau. However, the other samples bridge the gap, and there is no geographical pattern to the differences. The only sample that does not fit tightly is Dunoon. When compared with W Guyana (Graph 27) it is clear that this is a pocket of slightly higher values.

The smaller samples in Guyana fit perfectly with the larger samples from the area (Graph 28). So do the others of the transects, with the exception of Georgetown, which is ambiguous, and of Roraima, whose only specimen has a very short tibia.

Thus we have a clean break between the Venezuelan and the Guyanan areas, with essential homogeneity from Western Guyana to Belém.

Western transect (Graphs 29 to 31). The gap between Falcón and Villavicencio is bridged by the localities on the Colombia-Venezuela border. Bogotá agrees perfectly with Villavicencio. Towards the south (Graph 30), South Colombia is intermediate between Villavicencio and Limón Cocha (or Santa Cecilia, which is extremely close). The Ecuadorian samples all fit very well with local major samples. Continuing towards the south (Graph 31) the sample from Marañon (8 specimens, with excellent spread, permitting the computation of a good regression) is intermediate between Santa Cecilia and Pampa Hermosa. The remaining localities are all ambiguous or intermediate.

Colombo-Guianan transect (Graph 32). Puerto Lopez fits perfectly Villavicencio. Duida is intermediate. Southern Guyana, Catrimani, and Lucie are decidedly on the Guianan side.

Guiano-Brasilian transects (Graph 33). It is easy to see that the influence of Tapirapés goes north only to Cachimbo. All the other samples have much longer tibias.

Venezuelo-Brasilian transect (Graph 34). The Duida specimens seem to be intermediate between Falcón and Tapirapés. But Manaus and other localities in northern Amazonia being on the Guianan side, it is clear that the low Duida values are due to the influence of Villavicencio (see above), not of Tapirapés.

The southern localities either agree with Tapirapés or are below it. Cana Brava may have significantly shorter tibiae; in spite of the 4 specimens falling within the range of Tapirapés, all 4 are below the line.

Napo-Brasilian transect (Graph 35). This transect is important because it is decisive in judging whether the Napo samples may be considered geographically continuous with those of the Guianas. We have in the graph two extreme Guianan samples (Dunoon excepted), Nassau and Amapá. It is obvious that the two areas are in continuity.

Ucayalo-Brasilian transect (Graph 36). Except for Cachimbo, all samples show long tibiae agreeing with Ecuador and the Guianas.

Summary (Map 19). In general we can define 5 areas:

1. Very short tibiae around Villavicencio.
2. Another area of short tibiae in Brasil, from Cachimbo south.
3. Another area of low values around Pampa Hermosa.
4. An area of intermediate values in northern Venezuela and Trinidad.
5. The remainder of the range is characterized by long tibiae.

Females

Table 121 brings together the data on the regression and Table 122 the sample ranks at 65 mm body length. They show that there is a large group of samples (W Guyana to Amapá, and Santa Cecilia plus Limón Cocha) with extremely close values of the regression coefficient (.30 to .33) and showing about the same values at 65 mm body length (20.3 to 21.1 mm). Next come the Venezuelan samples, with $b = .28$ or .29, and 19.4 to 19.8 mm of tibia; with this group belongs Pampa Hermosa, with a higher b (.31) but presenting a 19.4 mm tibia at body length 65 mm. Finally we have Tapirapés and, last, Villavicencio, with much shorter tibiae.

The ranks, plotted in Map 20, make excellent geographical sense. Areas of homogeneity occur in northern Venezuela, in the Guianas and in Ecuador. Isolated samples with low values are in Villavicencio, Tapirapés and Pampa Hermosa.

North Venezuelan transect. This transect is perfectly homogeneous.

Guianan transect (Graph 37). In this area there are minor, but at times significant differences between samples, but none geographically arranged and all bridged by other samples within the area. For instance, W Guyana is a little higher than Nassau, but Amapá fills the gap perfectly. From Haul Over east all samples agree with the Guianan ensemble. However, Roraima constitutes a decided pocket of low values, below even NE Venezuela.

Western transect (Graph 38 to 40). Graph 38 takes us from Falcón to Santa Cecilia. The Colombia-Venezuela border is on the Falcón side; Southern Colombia agrees with Santa Cecilia. Thus the low area of Villavicencio is very restricted both to the south and north.

In Graph 39 we go from Limón Cocha (which is perfectly superimposable on Santa Cecilia) to Pampa Hermosa, which differs significantly from both. The Ecuadorian samples are distributed symmetrically about Limón Cocha. Marañon, however, is decidedly higher, with values exactly comparable with Western Guyana. This area is an exact replica of the Guianan one, with small differences between closely packed samples; the same regressions are found in both areas.

Graph 40 completes the Western transect; all southern samples agree reasonably well with Pampa Hermosa.

Colombo-Guianan transect (Graph 41). Puerto Lopez closely agrees with Villavicencio. Duida has Venezuelan values, and the remaining samples fall on the Guyanan side.

Guiano-Brasilian transect (Graph 42). We find strangely high values in Maués; these are the longest tibiae seen in this study. Manaus, starting at somewhat low values, converges rapidly toward Guianan tibiae.

Venezuelo-Brasilian transect (Graph 43). We find agreement with Tapirapés only in the south; even Cachimbo cannot be called intermediate. The W Guyana line has been added in this graph to verify the position of the Amazonian samples. Venezuelan influence can be said to occur as far south as Tapurucuara — from then on values get too high.

Napo-Brasilian transect (Graph 44). This transect is essentially homogeneous, with a high pocket, already mentioned, at Maués.

Ucayalo-Brasilian transect (Graph 45). The high values of Rio Juruá indicate that Pampa Hermosa is not transitional between the Ecuadorian long tibiae and the central Brasilian short ones; rather Tapirapés and Pampa Hermosa are two isolated areas of lower values.

Summary (Map 21). The broad picture is:

1. One area of very low values around Villavicencio.
2. Another area of low values from Tapirapés south.
3. One area of intermediate values in northern Venezuela.
4. Another area, of comparable values, around Pampa Hermosa.
5. The remainder of the range is occupied by populations with long tibiae.

Sex differences

Only three samples present significant sex differences, all in the northeaestern area: Dunoon, Amapá and Nassau.

Dunoon males have a regression coefficient significantly larger than that of the females — and of other males. They are the discrepant sex.

In Amapá and Nassau the lines are parallel, but the males have significantly longer tibiae.

Combined pattern

Maps 19 and 21 show perfect parallelism of male and female broad patterns. The only aberrant sample which has both sexes represented (Roraima) is seen to be really different.

A comparative study of the male and female ranks (length of tibia at 65 mm body length, Table 123), shows that Spearman's coefficient of rank correlation is high (.92). Furthermore, it is quite obvious that the shifts in rank, which are numerous, happen always inside one geographical unit: no Guiano-Ecuadorian sample changes place with a Venezuelan one, and the three short-tibiaed samples keep the same rank in both sexes.

It is also possible to assign two of the shifts (Nassau and Amapá) to sex differences, the female having shorter tibiae and the male rank being higher.

HEAD LENGTH

Males

Table 124 brings together the data on the regression of head length on trunk length in the major samples. It is immediately apparent that two samples have relatively low correlations: Essequibo and Villavicencio. These samples have also low values of the regression coefficient.

In Table 125 we give the ranks of the samples at trunk length 48 mm. Plotting the lines together we can discern 7 groups of samples: (1) samples of rank 1 to 4 (Santa Cecilia, Limón Cocha, W Guyana and Dunoon) are practically superimposable; (2) the samples of rank 5 and 7 (Tapirapés, Falcón and Nassau) are also homogeneous; (3) Trinidad (rank 9) and NE Venezuela (rank 10) are again superimposable; (4) Pampa Hermosa is intermediate between groups (2) and (3); (5) Essequibo starts with high values and converges towards group (3); (6) Amapá starts also with long heads and converges towards group (2); finally (7) Villavicencio, with the flattest distribution of all, diverges from all other samples.

Plotting these groups on Map 22 we find much less regularity than in the characters previously analyzed. Thus the study of the transects will focus not only on transitions, but also on irregularities.

North Venezuelan transect (Graph 46). We do not consider the NE Venezuelan sample in this case. Computing regression lines for the Carabobo, Distrito Federal and Caripito samples we see that Carabobo overlaps exactly Falcón; Distrito Federal converges towards Falcón, and Caripito towards Trinidad. Pie del Cerro and Anzoátegui cannot be assigned; Bejuma goes with Falcón, as does Yacua; Sucre agrees with Trinidad. Thus we see that this is an area of great local variability.

Guianan transects (Graphs 47 and 48). The first transect shows clearly that Amapá is intermediate between Dunoon and Nassau, which has no geographical logic. As to the small samples, none tends towards NE Venezuelan values. They are all Guianan in character, but very irregularly so. Some blanket two extreme distributions (Moengo Tapoe, Georgetown). Others are non-assignable (Tibiti, Paramaribo, Mana). St. Élie and Cayenne can be assigned to Dunoon, and Belém to Amapá. Matarony has very short headed young.

In the second transect we notice a very high value in Auyán-Tepui. Akyma clearly belongs with W Guyana; Roraima and Poeloegoedoe blanket the extreme distributions; Kroetoe can be assigned to Nassau.

Again a very spotty area.

Western transect (Graphs 49 to 51). In spite of the marked difference in regression between Falcón and Villavicencio, it is difficult to assign individual specimens, as the range of Villavicencio is very short. The specimens from the Colombia-Venezuela border vary from Villavicencio to Santa Cecilia values. Bogotá is compatible both with Falcón and Villavicencio. The South Colombian specimens agree with Santa Cecilia.

In the transect from Limón Cocha to Pampa Hermosa (Graph 50), we see that Marañon is intermediate, and so are the other small samples, with the exception of Miazal, with an exceptionally long head

The southern samples (Graph 51) agree closely with Pampa Hermosa.

The southern part of this transect is much more regular than the northern one.

Colombo-Guianan transect (Graph 52). Puerto Lopez agrees with Villavicencio. Duida and Southern Guyana have rather high values, in agreement with the first ranking samples. The Catrimani specimen has a short head. Lucie falls exactly on the Nassau line.

Guiano-Brasilian transects (Graphs 53 and 54). Southern Guyana has already been commented upon. Manaus is also clearly on the side of the long head samples. Cachimbo and Itapiranga agree with Tapirapés.

The second transect (Graph 54), between two superimposable samples, shows only that the Paloemeu specimen is much above Nassau.

Venezuelo-Brasilian transect (Graph 55). It is impossible to draw separately the Falcón and Tapirapés lines. The only new information contained in this graph is that the southern samples agree quite well with Tapirapés. The samples between Falcón and Tapirapés are on the long head side, with the exception of Itapiranga, which falls exactly on Tapirapés.

Napo-Brasilian transect (Graph 56). The specimens tend to agree with Santa Cecilia and Limón Cocha, except Itapiranga and Belém, which agree with the second ranking group of samples.

Ucayalo-Brasilian transect (Graph 57). No sample is unambiguously assignable, but they seem to agree better with Pampa Hermosa.

Summary (Map 23). We may discern a broad pattern only in part of the range. Starting from Falcón:

1. In northern Venezuela, from the Distrito Federal west, an area of moderate heads.
2. This area intergrades to the southwest with an area of short heads around Villavicencio.
3. This area intergrades to the south with an area of maximum head length in Ecuador, extending into Amazonia.
4. This area intergrades to the south with an area of moderate heads in Pampa Hermosa, extending east into Brasil.
5. From Cachimbo south there is another area of moderate heads.

The rest of the range is rather complex:

6. In NE Venezuela and Trinidad, very short heads, with pockets of higher values.
7. In the Guianas and Amapá there is a very spotty distribution of very long and short heads, without geographical regularity.
8. Central Amazonia is occupied by mixed populations.

Females

Table 126 shows the data on the regressions, which are quite regular and uniform. Table 127 presents the samples arranged according to head length at 48 mm trunk length. Comparing the individual regressions it appears that the 13 samples can be divided into 3 groups (all being practically superimposable, within the group): (1) Dunoon, Nassau, Santa Cecilia, Amapá, Falcón, Limón Cocha, and W Guyana; (2) Tapirapés, Essequibo and Pampa Hermosa; (3) Villavicencio, NE Venezuela and Trinidad.

Plotting these groups in Map 24, a more regular geographical distribution is indicated than was the case with the males, the only large anomalies being the low values of Essequibo and the high values of Falcón.

North Venezuelan transect (Graph 58). Distrito Federal and Yacua (in contradiction to geography) agree perfectly with Falcón; the remainder (Carabobo, Bejuma, Rancho Grande) are not assignable.

Guianan transects (Graphs 59 and 60). Essequibo is a low-value enclave in an area of large heads. Along the first transect, two localities (Paramaribo, and Moengo Tapoe) cannot be assigned. Matarony and Mana have very short heads and Georgetown agrees with Essequibo. Haul Over, Pickersgill, La Haye and Cayenne fit well with Dunoon and Nassau.

About the second transect (Graph 60) nothing can be said except that Tafel Berg has quite long heads.

Western transect (Graphs 61 to 63). In the first part of the transect (Graph 61), Villavicencio stands alone — the nearest locality to the north agrees with Falcón, and the nearest one to the south with Santa Cecilia.

From Limón Cocha to Pampa Hermosa (Graph 62) there is not much regularity: the northern samples (Sumaco, Misahualli, Rio Llushin, and Riobamba) tend towards Pampa Hermosa, while Marañon is intermediate.

The southernmost samples (Graph 63) agree well with Pampa Hermosa.

Colombo-Guianan transect (Graph 64). The influence of Villavicencio reaches the Brasil-Venezuela border and Catrimani.

Guiano-Brasilian transects (Graphs 65 and 66). Southern Guyana agrees clearly with Dunoon. Itapiranga, Manaus and Cachimbo agree with the short-headed samples. Maués cannot be assigned.

Along the second transect (Graph 66) one sees that Paloemeu and Tiriós go with Nassau.

Venezuelo-Brasilian transect (Graph 67). Puerto Ayacucho has a short head, showing influence of Villavicencio. Otherwise the only thing that can be said is that the southern localities agree well with Tapirapés.

Napo-Brasilian transect (Graph 68). It is quite clear that the large-head area extends to Maués, but not to Manaus and Itapiranga.

Ucayalo-Brasilian transect (Graph 69). Rio Juruá seems to belong with Limón Cocha and not with Pampa Hermosa (or Tapirapés).

Summary (Map 25). The general picture is:

1. One area of large heads, from Falcón to Amapá, with enclaves of shorter heads in Guyana and Surinam.
2. A large enclave of shorter heads in NE Venezuela and Trinidad.
3. Another area of large heads from Ecuador to the middle Amazonas.
4. An area of shorter heads in the southern part of the range, in Brasil and Peru (Pampa Hermosa to Tapirapés to S. Paulo).
5. One area of short heads in Villavicencio.
6. In northern Amazonia there are intermediate values.

Sex differences

In all samples the females have relatively longer heads than the males. In 5 samples the difference is not significant: Trinidad, NE Venezuela, Dunoon, W Guyana, and Santa Cecilia. In 3 cases the difference is due to the regression coefficient: Amapá, Nassau and Villavicencio. In these cases the females start with smaller heads, but their line crosses the male line, being steeper. In 5 cases the difference is due to the regression constant: Falcón, Essequibo, Tapirapés, Pampa Hermosa and Limón Cocha. In these cases the lines are parallel, but the females are above the males.

If we take into account only the presence or absence of significant differences (Map 26), a geographical pattern can be perceived: an area of homogeneity in western Venezuela and Guyana, and an area of longer-headed females in the remainder of the range, with Limón Cocha as an enclave.

It we take into account the mode of difference (Map 26), we have a complex pattern, differing from that for either sex.

In view of the great differences in grouping of the samples for each sex it is not practicable to compare ranks or even positions within groups.

Combined pattern

There are many differences between the male and female patterns (Table 128). Spearman's coefficient of rank correlation is .75 against .88 in the case of tail length and .92 in the case of the tibia. The only major resemblances are the short head areas in Villavicencio and Tapirapés.

It may also be noted that Essequibo in every case differs from the neighboring samples.

BODY LENGTH

Table 129 shows the largest body length for males and females in each sample. Plotting these values for the males (Map 27), a very clear geographic pattern becomes evident: long bodies (70 to 78 mm) in the region from Santa Cecilia to Pampa Hermosa, and smaller bodies (less than 70 mm) in the remainder of the range.

If we divide the territory in areas enclosing sections of the transects, and plot the maximum body length within each (Map 28), the pattern of the major samples is thoroughly confirmed, and added to: the area of long bodies extends to Itapiranga along the Amazonas.

Repeating the same operations for the females (Maps 29 and 30) an exactly similar pattern results.

We may then draw Map 31, embodying all these data, and showing: (1) an area of high body lengths from Santa Cecilia in the north to Pampa Hermosa in the south and Manaus (along the river) in the east; (2) shorter bodies elsewhere.

Sex differences

In 5 cases the female maximum body length is 3 to 10 mm more than male; in one case it is 2 mm less; in the remaining 7 cases the sexes differ by zero or 1 mm. There seems to be a tendency towards larger females, but it neither is statistically significant nor shows any geographic regularity.

RELATIVE SIZE OF ARM SCALES

In what follows we call "large" those upper arm scales which are much larger than the middorsals, and "small" those which have approximately the same size as the dorsals. We have found no sexual dimorphism or ontogenetic variation in this character.

Among the major samples, Nassau and Amapá have 100% small scales; all others have 100% large scales. Interest thus centers on the 2 Guianan transects, on the second Guiano-Brasilian transect, and on the situation in Southern Guyana.

Along the first Guianan transect there is a sharp break between La Haye and Tibiti. Small scales are found in all localities east of Tibiti, all the way to Belém.

Along the second Guianan transect the break is also sharp and occurs between Akyma and Kroetoe.

Along the second Guiano-Brasilian transect, Tiriós is the southern limit of the small scales.

In Southern Guyana, we have 12 specimens. Of these 10 have small scales and 2 have large scales.

Thus the general picture (Map 32) is:

1. One area of small scales from Surinam to Belém.
2. One area of large scales elsewhere.

CHARACTER CORRELATIONS

We have checked for correlation between pairs of characters within the major samples. This has been necessary both for reasons of method and also as an element of the general picture of geographic differentiation. From the methodological point of view it is indispensable to make sure that characters closely correlated in all samples are not treated separately, but instead as a single character. On the other hand, the presence of imperfect correlations — those found in a sizable proportion of the samples but breaking down in certain localities, for one or both sexes — need to be studied from the geographical viewpoint.

We had 11 samples, 2 sexes and 9 characters, totalling 198 cases to test. Of these, 72 were found to exceed the 5% level of significance; they are listed in Table 130.

The largest number of cases in which a pair of characters was found significantly correlated was 16, out of a possible 22. Thus it has been considered unnecessary to treat any pair of characters as a single character.

If we assemble the data of Table 130 by characters, localities and sexes (Tables 131 and 132), it is immediately seen that the sex ratio does not differ significantly from 1/2, for the ensemble, or for any locality or character. Table 132 also shows that there is no geographical regularity to the distribution of the number of significant correlations.

The pair of characters most frequently correlated is length of tibia x head length, 16 out of 22 times. Next comes scales between semicircles x scales across snout, significantly correlated 7 times. Three pairs of characters are correlated in 4 samples, 3 in 3 samples, 5 in 2 samples and 18 only once.

It is very difficult, perhaps impossible, to judge what constitutes a significant number of instances in which a given pair of characters is significantly correlated. We have, however, tried the following rough approximation.

The pairs of characters were divided in two groups: those obviously "meaningfully" correlated, and apparently "nonsense" ones, the latter being those with no evident physical reason for correlation. It is possible, of course, and indeed probable, that some pairs, at least, are linked through genetic or physiological mechanisms not at present known.

The "meaningful" pairs are:

1. Related to extremities: between tail, head, and tibia (3: tail x head, tail x tibia, head x tibia).
2. Related to climbing: between tail, tibia, and fourth toe lamellae (3).
3. Related to general scale size: between loreals, scales across snout, scales between the semicircles and the interparietal, and ventrals (6).
4. Related to the scalation of the head: between loreals, scales across snout, scales between semicircles, and scales between semicircles and interparietal (6).

These represent (since some pairs occur in more than one group) 14 out of 36 possible pairs. The other 22 pairs would then be nonsense pairs. The 14 meaningful correlations correspond to 308 pairs x samples x sexes; of these 47 are significant. The nonsense pairs correspond to 484 cases, of which 25 are significant. Chi square (Table 132) is highly significant, i.e., there is a strong material basis (certainly underestimated by the rough method used) for association between certain pairs of characters.

Geographic differentiation

We now abandon in our analysis those character pairs correlated only once or twice, as they obviously could not reveal any pattern. Those correlated 3 and 4 times (Table 130) show no geographical regularities.

Scales across snout x scales between semicircles, significant in 7 cases, shows the following distribution: Trinidad (males), Essequibo (males and females), Dunoon (males and females), Amapá (females) and Limón Cocha (males). The only discernible regularity is the agreement between Dunoon and Essequibo for both sexes.

The head x tibia correlation is present at least in one sex in each sample; thus it is more interesting to consider the distribution of absence of this correlation. In the males, Falcón, Trinidad and Santa Cecilia fail to show correlation; the first two are in the same general area, while Santa Cecilia disagrees with neighboring Limón Cocha. In the females, the 3 samples that do not show correlation are widely scattered: Amapá, Pampa Hermosa and Villavicencio.

The general conclusion that can be reached is that the correlation between head and tibia is important in the *chrysolepis* group, but locally unstable.

ANALYSIS

INTERIM SUMMARY: CORE AREAS

Maps 1 to 32 summarize our data in terms of major patterns. They have been made by projecting on to standard outline maps the verbal summaries of highs and lows, presences and absences, breaks and points of transition that have been made above. Like the verbal statements, they are necessary extrapolations from the data of our samples as interpreted in terms of the various statistical tests we have employed. Boundaries have been drawn according to the available samples. It is thus possible, in fact probable, that additional materials will alter the exact contours and the minuter details of the patterns we here portray. We do not expect, however, that any future evidence will substantially challenge or subvert the picture that we here present.

The maps, we must emphasize, show major trends only and neglect very local or minor ones. However, the character analyses and tables provide all that we know about matters of detail, and these, when relevant, have been considered in the following discussions. What the maps as an ensemble demonstrate is the reality of large patterns present in character after character, consistent in their general localization but not in the exact borders of their ranges.

Inspection of the maps in fact reveals four areas of consistent difference. Though the borders of these differ with every individual character there are yet residual core areas or nuclei which are, each in its own way, definable in terms of the characters studied.

We may therefore usefully speak of four core areas (Map H) :

I. The eastern Guianas, from Surinam to Amapá.

II. Venezuela, Trinidad, and the northern half of Guyana.

III. Amazonian Colombia, Ecuador and Peru.

IV. Central and south-central Brasil.

In what follows we first analyze these core areas as such, and then the regions of intergradation between them.

In the analyses of the core areas we take into account, for each character and for each sex separately, whether the area is:

A. Internally homogeneous and well set-off from the adjacent areas.

B. Internally homogeneous but continuous with one or more adjacent areas, or with part of one or more.

C. As a special case of B, internally homogeneous and continuous with others, but with only one of the other core areas presenting unique values for the character.

D. Internally heterogeneous.

Core area I. This area (Surinam to Amapá) is:

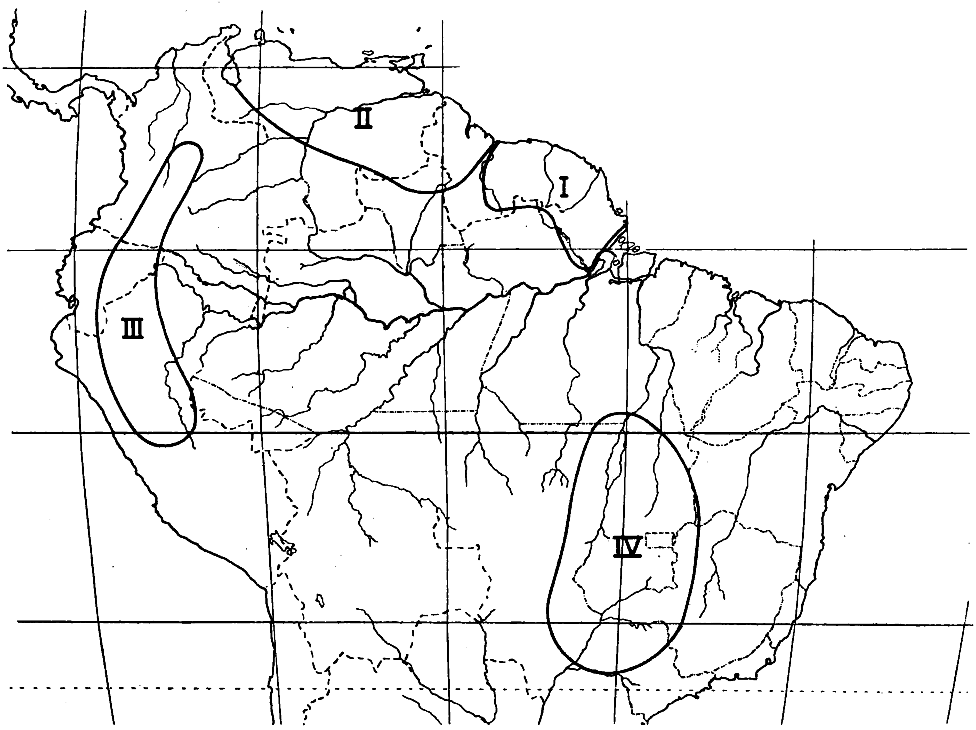
A. Internally homogeneous and well set-off in 13 cases out of 22 (the 11 quantitative characters, each sex always counted separately) ; fourth toe lamellae (males and females) ; scales across snout (males and females) ; scales between supraorbital semicircles (females) ; scales between interparietal and supraorbital semicircles (males and females) ; ventrals (males and females) ; tail length (males and females); arm scales (males and females). The latter character (upper arm scales smaller than dorsals) is unique to this area.

B. Internally homogeneous, but not differentiated from other areas, in 3 cases: continuous with area II and with the northern part of area III in scales between semicircles (males) and length of tibia (females); continuous with the eastern part of area II in head length (females).

C. Internally homogeneous and in continuity with all other areas except one, which is distinguished by one unique character, in 4 cases: loreals and body length (males and females), in which the part of area III south of Villavicencio stands alone.

D. Internally heterogeneous in 2 cases: head length and length of tibia (males).

It is easily seen that this is a very homogeneous and well differentiated area.



Map H. *Anolis chrysolepis;* core areas.

Core area IV. Core area IV, which extends from the north end of the Ilha do Bananal, in Central Brasil, to the northern half of the State of S. Paulo, is also a very clear core area. Listing patterns of differentiation as above, we have:

A. It is homogeneous and well set-off in 11 cases out of 22: fourth toe lamellae (males and females); scales across snout (females); ventrals (males and females); tail length (males and females); length of tibia (males and females); head length (males and females).

B. It is continuous with other areas in 3 cases: with area II in scales across snout (males); with area II and the northern part of area III in scales between interparietal and semicircles (males and females).

C. In agreement with other core areas (6 cases) it lacks the unique character of area I in arm scales (males and females), as well as that of area III in body length and in loreals (males and females).

D. It is internally heterogeneous in scales between semicircles (males and females).

The Brasilian locality of Loreto (Maranhão), from which a single female is available, agrees in every case with Tapirapés.

Core area II. This area, extending from Falcón, in northwestern Venezuela, to Guyana, is a little less homogeneous internally than the 2 previously discussed areas and a little less well set-off.

A. In 6 cases it is both homogeneous and distinct: fourth toe lamellae (males and females); scales across snout (females), tail length (males and females); length of tibia (females).

B. It is homogeneous but continuous with adjacent areas in 6 cases; with area I and the northern part of area III in scales between semicircles (males); with the northern part of area III in scales between semicircles (females) and in ventrals (males); with area IV in scales across snout (males); and with area IV plus the northern part of area II in scales between the interparietal and semicircles (males and females).

C. It does not participate (6 cases) in the uniqueness of area III as regards loreal and body length (males and females) nor in the uniqueness of area I in regard to arm scales (males and females).

D. It is heterogeneous in head length (males and females) and in ventrals (females); in length of tibia (males) the area could be called homogeneous except for a pocket of low values in Dunoon.

Core area III. This is an area different in kind from the preceding ones. It is quite evidently the product of the fusion of several (probably 3) centers of differentiation and also of some introgression from adjacent areas. Yet it seems to us that the process of fusion has reached a stage which makes it justifiable to treat the area as a single unit, although of a different order than the others.

A. In no character is the whole of area III both internally homogeneous and distinct from the adjacent ones. Loreal scales (males and females) have higher values in this area than elsewhere, but in both cases these values are distributed along a cline, increasing from the north towards the south, to Pampa Hermosa in the case of males, and to the Marañon in females. In fourth toe lamellae exactly the same clines are found. The clines to Pampa Hermosa are practically symmetrical about the Equator, and we have not been able to correlate them with any environmental gradients.

We think it more likely that they are introgression clines. Given 3 isolated populations arranged in a geographically linear sequence, each one having evolved its own peculiar values of a given character, secondary contact between them may result in a cline between each pair of localities. If, by chance, to the linear arrangement of the localities there corresponds a linear arrangement of the values of the character (e.g., in the present case, Pampa Hermosa with larger values than the Napo samples and these with larger values than Villavicencio) then the juxtaposition of the two clines will result in a single cline, including all 3 localities.

This would be in keeping with the general pattern of variation within the area (see below) and also with two peculiarities of the clinal variation observed: (1) the presence of shorter clines, in the females, for the same characters in which the males show complete clines (for them the chance linear arrangement of character values would not have happened) and (2) the frequent irregularities within the long clines observed (interactions between the areas in secondary contact showing local variations).

B. In no case is area III internally homogeneous but continuous with adjacent areas.

C. Area III agrees with areas II and IV in not having upper arm scales smaller than dorsals (males and females), a character unique to area I.

D. In all the remaining cases area III shows some degree of heterogeneity — but is is possible to discover some regularity in this. In 11 cases one of the geographically extreme samples (Villavicencio, to the north, or Pampa Hermosa, to the south), disagrees with the rest of area III. In 7 cases the aberrant sample is Villavicencio. In 2 cases, tail length (males and females) the area stands alone; in 5 others it is continuous with adjacent areas: with Falcón (part of area II) in ventrals (females); with the whole of area II in scales between interparietal and supraorbital semicircles (females); with areas I and II in scales between supraorbital semicircles (males); with areas I, II and IV in body length (males and females), a character in which the remainder of area III stands alone.

In 4 cases the sample which disagrees with the remainder of area III is Pampa Hermosa; scales between semicircles, scales across snout, fourth toe lamellae, and loreals (females). In the last 2 cases there is a cline from Villavicencio to the Marañon, but Pampa Hermosa, which fits a complete cline in the males, falls completely off for females.

In 6 cases both extreme samples disagree with the remainder of area III. In length of head and of tibia (males and females) both Villavicencio and Pampa Hermosa stand out, and are not continuous with adjacent areas. In ventrals and in scales between interparietal and supraorbital semicircles (males), Villavicencio is continuous with area II and Pampa Hermosa intermediate with area IV.

In only one character (scales across snout, males) do we find a break in the middle of area III: between the neighboring localities of Santa Cecilia and Limón Cocha.

Thus it is to be seen that, while it is practically impossible to diagnose area III on the basis of any single character, and while the signs of a recent fusion of nuclei of differentiation and of the influence of adjoining areas are plainly visible, it has a general personality and can be treated as a single unit, though, as already said, of a different order than the other core areas.

INTERIM SUMMARY: INTERGRADATION

It can be readily seen from Map H, as well as from the character analyses, that the relationships between pairs of core areas vary greatly. This is in some measure due to accidents of sampling (e.g. the low density of samples and specimens in southwestern Amazonia), but principally to the actual distances between the boundaries of the core areas. Thus we cannot follow a uniform pattern of discussion, but must adapt our argument to each individual case.

In addition, the nature of our data, as well as certain of the results of our previous analysis, require the preliminary statement of the following provisos: (1) since not all samples contain both males and females, the study of intergradation must, in some cases, be made separately for each sex; (2) since in some small samples there is not one specimen in which a particular character can be measured or counted, some localities are at times omitted for some characters; (3) there is no point in tracing the transition between areas when one of them is noticeably irregular for the character in question; (4) characters in which adjacent areas agree are, of course, omitted.

Finally, it must not be forgotten that, as stated in the section on methods above, some breaks as here outlined are based on a few or even single specimens. We have been cautious in stressing only very obvious differences, but it may be expected that better sampling will introduce minor changes in the picture.

Intergradation between core areas I and II. We omit from consideration head length and length of tibia (males) because of irregularities, and scales between supraorbital semicircles (males), head length and length of tibia (females) and loreals (males and females) because of continuity between areas I and II.

The transition can be studied along 3 transects: along the coast (first Guianan transect), a little farther inland (second Guianan transect) and across the southern part of Venezuela and Guyana (part of the Colombo-Guianan transect). Given the narrowness of the transition zone in the north, and the absence of one of the sexes in some samples, the analysis is presented separately for males and females.

Here more than anywhere else the caveat applies about small number of specimens in the transition area.

Males. Along the coast there is a clean break between Dunoon and Tibiti (thus practically at the Guyana-Surinam border) in fourth toe lamellae, scales across snout and scales between interparietal and semicircles. In ventrals the counts increase gradually from northeast Venezuela eastward, but the characteristic high values of area I first appear east of Tibiti at Paramaribo. Along the second Guianan transect the three discernible breaks occur between Akyma in Guyana and Kroetoe in Surinam. In the case of scales between interparietal and semicircles there is not a clean break. Southern Guyana agrees with area I in scales across snout and scales between interparietal and semicircles; it is clearly intermediate in fourth toe lamellae, ventrals, tail length and arm scales.

Females. Scales between semicircles, scales between interparietal and semicircles, and arm scales, break between Dunoon and La Haye, and fourth toe lamellae between Dunoon and Tibiti, all practically on the Guyana-Surinam border. All other characters break further east: scales across snout between La Haye and Tibiti, tail length between La Haye and Paramaribo and ventrals between Paramaribo and Moengo Tapoe. Inland the major break is between Akyma and Tafelberg: fourth toe lamellae, scales across snout, scales between semicircles, scales between interparietal and semicircles, tail length and arm scales. Ventrals again break more to the east, between Tafelberg and Nassau. Southern Guyana agrees with area I in scales between interparietal and semicircles, with area II in scales across snout, and is intermediate in fourth toe lamellae, ventrals, tail length and arm scales.

Summary. The transition belt is narrow in the north, especially in males, but covers a wider area to the south.

Intergradation between core areas II and III: the special case of Villavicencio. The relationships between core areas II and III can be studied in northern and central Colombia and in southern Venezuela (Western and Colombo-Guianan transects). The region of Villavicencio has rather complex relationships with the remainder of area III and with adjacent area II, and deserves special consideration.

In 4 cases it has a unique position, differing significantly from the localities immediately to the north and to the south. The extent of its influence towards the east, however, varies: only to nearby Puerto Lopez in length of tibia (males and females), thus forming a small pocket of very low values; to the Duida region in tail length (males); and to the Brasilian territory of Roraima in head length (females).

In 2 cases the localities in the Colombia-Venezuela border agree with Villavicencio: in head length (males) the area extends to Puerto Lopez, but in tail length (females) to the Duida region.

In all these instances the Villavicencio values are quite distinctive, and the area behaves as if it were a core area.

In 6 cases Villavicencio clearly belongs to area III. In loreals and fourth toe lamellae (males) we find one cline along the whole pre-Andean belt; in the latter case Puerto Lopez is also involved. In 4 cases Villavicencio agrees with large segments of area III: from the Venezuelan border to Santa Cecilia in scales across snout (males); from Villavicencio to the Marañon, east to Duida, in scales across snout (females); clinally from Falcón to the Marañon, restricted to the pre-Andean belt in loreals (females), or extending to Duida, in fourth toe lamellae (females).

In 7 cases parts of area III including Villavicencio are continuous with area II (in some of them also with areas I and IV). In scales between semicircles (males), scales between interparietal and semicircles (males and females) and ventrals (males) the break within area III occurs on the Colombia-Equador border; in scales between semicircles (males) the break occurs south of the Marañon. In the case of body length (males and females) Villavicencio disagrees with the remainder of area III and agrees with areas I, II and IV. Finally, in the case of ventrals (females), Villavicencio and the adjacent part of area II, Falcón, form a well-differentiated pocket.

It is thus seen that the Villavicencio region has probably been a core area that has been swamped from the south (principally) and from the north, but that still preserves some of its former distinctness.

In spite of swamping and intergradation, the general break between Villavicencio and area II is quite evident, and we can consider area III well set-off to the north, with a broad intergradation belt extending from Villavicencio to Falcón.

Intergradation between core areas III and IV: the special case of Pampa Hermosa. The transition between these two core areas is to be studied along the Ucayalo-Brasilian transect, but special attention must be paid to the Western transect, since Pampa Hermosa, its southernmost major sample, also shows evidence of independent variation, similar to if less pronounced than that of Villavicencio.

In one case (scales across the snout, females) the difference between Pampa Hermosa and the samples to the north is sharp, and no other locality agrees with it. In two cases, fourth toe lamellae and scales between semicircles (females), the small southern samples agree with Pampa Hermosa.

In four cases, length of tibia and head length (males and females) the variation from Limón Cocha south is gradual, but, as we are dealing with body proportions, it is not possible to find out whether the small samples are clinally arranged.

Thus, as in the case of Villavicencio, the presence of sharp breaks and of intergradation belts are definite indications that Pampa Hermosa may represent a swamped core area.

In two cases Pampa Hermosa is itself transitional between areas III an IV: scales between interparietal and semicircles, and ventrals (males).

In studying the transitional localities between Pampa Hermosa and Tapirapés, along the Ucayalo-Brasilian transect, we omit 3 characters, fourth toe lamellae (females), loreals (females), and length of tibia (males) since the differences between the two extremes are absent or too small. We also omit head length (males), because the data are inconclusive.

The 16 cases in which the transition can be studied can be divided into 4 categories. (1) A break west of Cachimbo, in 6 cases: loreals (males and females), scales across snout (females), ventrals (females) and tail length (males and females). (2) A break at the approximate longitude of the Juruá, 3 cases: scales between interparietal and semicircles (females) and body length (males and females). (3) A gradual transition in 4 cases: scales across snout (males), scales between semicircles (males), scales between interparietal and semicircles (females) and ventrals (males). (4) In 3 cases the geographically intervening samples are not morphologically intermediate between Pampa Hermosa and Villavicencio: head length (females), length of tibia (females) and fourth toe lamellae (males).

This pattern indicates, on one side, that the interactions between the areas differ from character to character, and also that there is a marked influence of the areas to the north on the differentiation along this southernmost line.

The data on transitions between areas III and IV indicate that the belt of intergradation is an extremely broad one, extending along some 15 degrees of longitude.

Amazonia. From this vast region we have relatively few samples, and none of them large enough to constitute a major sample. The materials available thus do not permit a detailed analysis of variation in the area. They are, however, sufficient to indicate that we must not expect additional materials to demonstrate the presence of further core areas, since in no case we find extreme values of any single character or an unusual combination of characters; on the contrary, the picture is always one of intergradation, although frequently quite complex.

In view of this complexity it is impossible to present a unified picture, and we shall discuss the following areas separately:

1. The single locality, Tiriós.
2. The Mount Duida region, with mention, when relevant, of the samples between the Brasil-Venezuela border and the upper Rio Negro (females only).
3. The localities on or near the main course of the Amazon, considered in 2 groups: western (Iquitos to Benjamin Constant) and eastern (Paraná do Jacaré to Manjuru).
4. Southern Amazonia, with a western group of localities (from the Brasil-Peru border to Mutum-Paranã) and one eastern locality (Cachimbo).

Tiriós. This locality is in complete agreement with area I in 19 out of 22 possible cases. It may well be considered as part of that core area, with the exception of 2 characters in which area I is both homogeneous and well set-off: in scales across snout (males) Tiriós belongs with areas II and IV, which are continuous with one another; in ventrals (females) it clearly intergrades with area IV. With regard to head length (males) nothing can be said, as area I is irregular in this respect.

Duida. We shall not mention the cases in which the northern Amazonian samples (females only) agree with Duida, noting only the single case of disagreement.

Duida belongs clearly with core area III or one of its parts in tail and head length (males and females). It falls in with the northern part of area III in the following cases in which that part is continuous with other areas: scales between supraorbital semicircles (males), scales between interparietal and semicircles (males and females), and scales across snout (females). It belongs to area II (alone or in continuity with areas I and IV) in scales across snout (males), loreals (males) and length of tibia (females). It has an intermediate position between area III and the areas to the north and east in fourth toe lamellae (males and females), loreals (females), length of tibia (males) and ventrals (males and females). In the case of loreals (females) the northern Amazonian samples differ from Duida by agreeing with core area II.

Main course of the Amazon. The western part of this area belongs with core area III in 11 cases: fourth toe lamellae (females), loreals (males), scales across snout (females), scales between semicircles (males and females), ventrals (males), tail length (males), head length (males and females), body length (males and females). In the case of head length the eastern samples still agree with area II, but in all other cases there is intergradation in the Manaus-Manjuru region. This intergradation is with area I, separating areas II and IV, which have very similar values, in the case of fourth toe lamellae (females), and in all other cases is of a complex nature. In body size naturally intergradation cannot be detected.

In 6 cases intergrading values are found from Iquitos to Manjuru: loreals (females), scales across snout (males), scales between interparietal and semicircles (males and females), ventrals (females), and tail length (females).

In the case of fourth toe lamellae (males) the western area belongs to core area II and the eastern one is intermediate between core areas II and IV. Finally, in length of tibia the whole region belongs to a continuous arc composed of core area I and parts of core areas II and III.

Southern Amazonia. The relationships of the southwestern area have been discussed with regard to the intergradation between core areas III and IV, and it has been noted that in the case of fourth toe lamellae (males), head length (females) and length of tibia (females) the strong influence of the northern areas (I and II) reaches the Ucayalo-Brasilian transect, and the localities between Pampa Hermosa and Tapirapés are not morphologically intermediate between the geographically extreme samples.

Cachimbo is rather close geographically to Tapirapés (core area IV) and agrees with it in 8 instances: fourth toe lamellae (females), scales across snout (females), ventrals (females), tail length (males and females), length of tibia (males) and head length (males and females). It also agrees with area IV in 4 cases in which the latter is continuous with other areas: loreals (females), scales across snout (males) and scales between interparietal and semicircles (males and females).

Cachimbo has intermediate values between area IV and the areas to the north in 3 cases: fourth toe lamellae (males), and scales between semicircles (males and females). A less clear pattern of intergradation is seen in the case of ventrals (females). Finally, in length of tibia (females), Cachimbo disagrees with Tapirapés and belongs to a continuous area to the north.

Summary. It is obvious that Amazonia is a highly heterogeneous region. The influence of single core areas or of core area combinations is felt, in many cases, far from and even at points diametrically opposite the core area. Even in western Amazonia, where the influence of core area III is strongly felt, there are instances of the prevalence of values of some characters evidently associated with areas II and even I, several hundred kilometers away. This area of heterogeneity is the geographical center of and represents more than 70% of the total territory of *chrysolepis,* which gives a measure of its importance to any analysis of the history of the group.

DEWLAP COLOR

General statement

One character of prime importance we have thus far not discussed: dewlap color. In other anoles we know that the dewlap is a major element in display within and between species, and color differences between the dewlaps of sympatric species are certainly conspicuous in all multispecies anole comunities.

In all members of the *chrysolepis* species group the dewlap is small. It is always somewhat more developed in males than in females and it is boldly colored, at least in males, blue, black, or red, or blue and red. With two important exceptions, discussed at length below, variation in dewlap color is geographic and coincides well with the nuclear areas defined on other grounds above.

Because we have had limited living material or even notes on specimens in life, we describe below first the condition of preserved specimens. A note on the interpretation of preserved material is therefore necessary: because such colors as reds and yellows are almost always leached out of preserved specimens, the contrasts that remain are between light and dark areas. Further, since preservation usually expands melanophores, preserved specimens will frequently show greyish skin or greyish scales in those areas which should be lightest. Confidence may nevertheless be had in the reality of the contrast between areas with densely concentrated melanophores and areas mostly devoid of them. Below, the terms "black", "blue", and "dark" apply to melanophore concentrations, the terms "light", "lighter" or "white" to areas with few melanophores. Rarely if ever there are areas with no melanophores.

We describe first the quite characteristic dewlaps found in the four core areas. Notes on color in life are added wherever possible.

Core area I. (Surinam to Amapá). Males, skin intense blue or black, scales light or sometimes, at dewlap edge, dark or black. Females, skin light, scales dark, especially at edge, or light like the skin. Philip Silverstone *(in litt.)* has made available descriptions of the dewlap of specimens in life from French Guiana. Summarized these are: males "blue with buff scales" and females "yellow with yellow and brown scales".

Core area II (Venezuela, Trinidad and northern Guyana). Males and females, skin and scales light or scales darker. Many descriptions are available of dewlap color in life in this area: uniformly red.

Core area III, central and southern part (Amazonian Ecuador and Peru). Males and females, edge skin light, scales light or dark, lateral skin blue or black, scales lighter. Descriptions of color in life make it clear that this is a tricolor dewlap: edge skin red, lateral skin blue, lateral scales white.

Core area IV (Central Brasil to S. Paulo). Males, skin dark, scales usually lighter; females, edge lighter, because of massing of lighter scales, lateral skin and scales dark. The frontispiece plate provides the color in life for a male.

In all of these areas the concordance between dewlap color and other characters is, within our expectations, quite good. In two areas where other characters are transitional we find dewlaps also to be so. In Southern Guyana we find within the same sample dewlaps typical of core areas I and II. And in the Brasilian state of Acre and adjacent Peru we find side by side dewlaps characteristic of core areas III and IV. In Amazonia we find, besides the special cases mentioned above and below, predominantly red dewlaps (more frequently with an infusion of black) to the north of the river, and black dewlaps to the south. There is much variation in the area.

There are, however, two areas in which dewlap color is anomalous in quite another way: in each of these two areas two dewlap color types coexist, without any indication that the case is one of transition between core areas.

We need to examine these with particular care because such coexistence of dewlaps would ordinarily in *Anolis* imply the existence of distinct species. As will appear below we found one of the cases to imply species status; in the other this is not true.

The Villavicencio light dewlaps: a case of polymorphism

In the general vicinity of Villavicencio in Colombia dewlaps are either boldly tricolor — blue black with white scales and a red edge — as in nuclear area III or they are reddish, orangeish, even whitish with or without a tinge of blue at the base. We have treated the animals showing these light-colored dewlaps as a distinct sample to be compared with sympatric and adjacent samples of animals with tricolor dewlaps as in the remainder of nuclear area III. The relevant localities are:

1) Villavicencio. 2) Apiay. 3) Finca Guadualito (Rio Güejar, area of Serrania La Macarena). 4) Finca "El Diamante" (between Caño Sumia and Rio Negro, region of Rosaleño). From these localities we have 7 males and 13 females.

Map B shows the localities in the general Villavivencio area in which the two types of dewlap mentioned above have been found. In parallel to the manner in which the analysis of individual characters in previous samples of *chrysolepis* was conducted, and in view of the fact that the localities (Rio Tuña and Florencia) assembled in the character analyses as "South Colombia" do not always agree with Villavicencio, we have arranged our comparisons as follows:

1. Villavicencio "light" versus Villavicencio "tricolor" (major sample of previous discussion); in the former we have included the specimen from Rosaleño, a locality 29 km from Villavicencio, since the major sample contains specimens from San Martin, Restrepo, and Acacias, as well as material from some older collections for which the exact meaning of the name "Villavicencio" on the label cannot be ascertained but is quite likely to imply localities some distance away.

2. Rio Güejar (light) versus South Colombia (Rio Tuña and Florencia), and San José de Guaviare (tricolor). The Rio Güejar locality is sufficiently far from Villavicencio to be separately compared, and the obvious standard of comparison is to be found in the adjacent localities to the south.

3. Apiay (light) versus Puerto Lopez (tricolor). These two localities are very close.

No significant differences were found in the comparisons made (Tables 134 to 139, Graphs 70 to 75). This would indicate that the light dewlap is probably a morph of *chrysolepis*, restricted to the general Villavicencio area. This idea is strengthened by the consideration of those characters which, as we have noted above, show exceptional values in the Villavicencio region, especially the body proportions.

Tail length in the Villavicencio basic sample ranks first in males and second in females (Tables 114 and 116), the geographically closest samples having much shorter tails. Graphs 70 and 71 show the perfect agreement of the light dewlapped specimens with the regression line of the Villavicencio major sample.

Length of tibia in the major Villavicencio sample ranks last for males and females (Tables 120 and 122); again the light dewlapped specimens agree closely with the regression line. In this character the South Colombia specimens disagree with Villavicencio and tend to the larger tibial lengths found to the south, while the Rio Güejar females agree with Villavicencio.

In the case of relative head length (Tables 125 and 127, Graphs 72 and 73), the light dewlapped specimens also agree with the major Villavicencio sample.

Thus we feel justified in interpreting the presence of light dewlaps in the Villavicencio area as implying dimorphism within the species *chrysolepis;* the two contrasting dewlap types appear not to be associated either with sex or with any of the meristic and metric characters studied, and there is thus no ground for inferring the existence of a second species sympatric with *chrysolepis.*

The Upper Amazonian black dewlaps: a distinct species, *A. bombiceps* Cope.

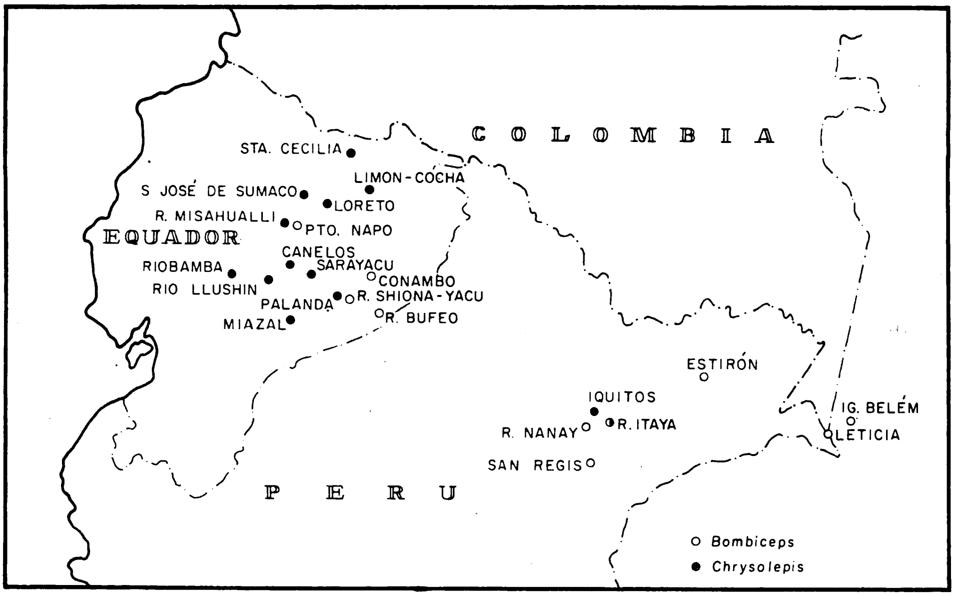
The second area in which two types of dewlaps occur is a narrow zone from Ecuador to westernmost Brasil (Map I) in which all-black dewlaps are sympatric with tricolor ones. Here again we have treated the all-black-dewlap animals as a new sample and have tested them against adjacent and sympatric tricolor-dewlap populations.

The upper Amazonian localities from which we have specimens with entirely black dewlaps (which we shall call *Anolis bombiceps* Cope; see further below) are shown in Map I, as well as those with normal (for the area) *chrysolepis* red edged dewlaps.

We have no single locality with reasonable numbers of *bombiceps,* so we have assembled all available specimens in one sample. This has been compared, in tables and graphs, with (1) the geographically nearest large samples of *chrysolepis* (Santa Cecilia and Limón Cocha), (2) the small samples of *chrysolepis* in the area of occurrence of *bombiceps* and (3) a "combined *chrysolepis*" sample, constituted by assembling the small *chrysolepis* samples. This latter was built up in order to have a sample with approximately the same degree of heterogeneity as the *bombiceps* sample, and has been used for the necessary statistical comparisons.

Tables 140 to 146 present the comparisons of scales counts. In the males, significant differences were found in 4 characters out of 6: loreals, scales across snout, scales between semicircles and interparietal, and ventrals. In the females only 3 characters were found to differ significantly: scales between interparietal and semicircles, fourth toe lamellae, and ventrals. Thus, the aggregate difference involves 5 characters: 2 common to males and females, 2 peculiar to males and 1 peculiar to females. Once more one sees a degree of independent variation between the sexes.

Relative tail length (Graphs 76 and 77) and head length (Graphs 80 and 81) are significantly less for male and female *bombiceps* than for sympatric *chrysolepis*. There are no differences at all in relative length of tibia (Graphs 78 and 79).



Map I. Localities of *Anolis chrysolepis* and of sympatric *Anolis bombiceps*.

Thus we find 6 characters separating males and 5 separating females of the two species in the area of overlap. One of the characters that separate males has only statistical value, as there is no difference in range. All other characters show lack of overlap of extreme values, and can be used for diagnosis; although it is possible that increasing sample size might also increase the degree of overlap, consideration of the large *chrysolepis* samples indicates that this effect should not be too important. Of course each character permits only imperfect diagnosis, and it is important to check the degree of precision attainable by the simultaneous use of all characters. This we have checked by the individual consideration of each character, which is the least efficient method (for instance, discriminant analysis or other methods of multiple comparisons would afford better precision) and so keeps us on the side of safety and closer to the physical meaning of the characters.

Only 3 specimens out of 20 (15%) cannot be unambiguously identified by this rough method. Of these 3 specimens, 2 are very young ones, and consequently their body proportions are not useful; furthermore, ventral scales could not be counted in any of the 3 specimens. Thus we find that the separation between *bombiceps* and *chrysolepis,* on the basis of meristic and metric characters is quite real, although not very pronounced.

One qualitative character permits consistent unambiguous separation of the two species, the relationship between upper arm and dorsal scales. In *bombiceps* the arm scales are smaller than the dorsals, in *chrysolepis* of this area distinctly larger.

The character that first called attention to the presence of *bombiceps* is its uniformly black dewlap, contrasting with the red-edged dewlap of *chrysolepis* in the region. However, we find in some specimens a thin lighter line along the edge of the dewlap which, while not reaching the *chrysolepis* condition, may in life approach it..

These facts seem to us to justify the following conclusion: in western Amazonia (from the Napo and the Marañon to westernmost Brasil) occurs one species of the *chrysolepis* group, sympatric with and very close to *chrysolepis* itself but readily distinguishable from it on the basis of a radical difference in dewlap color and in one qualitative scale character (relative size of arm scales), as well as by statistical differences in several scale counts and body proportions. The presence in some specimens of dewlaps tending in the direction of the tricolor dewlaps that locally characterize *chrysolepis* leads us to consider the hypothesis that there may be introgression between the two species, a point to which we will return below.

SYSTEMATICS

LEVELS OF DIFFERENTIATION

The analysis above has revealed, quite in accordance with expectation, several levels of differentiation. We have discerned three principal types: (1) mosaic differentiation in which characters vary rather randomly with reference to each other over larger or smaller areas, (2) a differentiation that shows close character concordances over rather extensive core areas, and (3) differentiation of populations that are able to maintain their character complexes intact in spite of sympatry.

We believe all three types of differentiation to represent adaptations to local selection pressures, but, while the mosaic type of differentiation may often occur when populations are in essentially continuous contact, the macro-differentiation of the second and third sorts implies for us prolonged breaks in genetic contact. The core areas within species that we have discovered we believe to have been refugia during periods of species contraction. It is during such periods of contraction that we conceive the concordance of characters characteristic of these core areas to have been built up. The bio-historical phenomena envisioned here we call attention to by naming the populations of the core areas as *subspecies* if genetic contact has been reestablished during species reexpansion but we, of course, recognize them as *species* if they maintain their genetic integrity i.e. are reproductively isolated after secondary contact.

It is true that taxonomically it is somewhat inconvenient that the areas of mixed populations should be large (the Amazon Valley, for example), but the two aspects of rather chaotic variation and of basically rather regular character concordances, occurring within one species, are equally important. We do not wish to emphasize the first at the expense of the second. It is one of the significant results of the analysis here carried out that the hypothesis of merely mosaic differentiation must be decisively rejected.

The reality of the core areas has in fact long been recognized by the species names that have been applied to the populations of all but one of these areas. Our more elaborate study requires us to modify only a little the rather impressionistic and certainly imperfectly documented taxonomy of previous workers. To translate the great body of our results into correct nomenclature we need only (1) formalize our discovery that the populations of the core areas are connected by intermediate populations by reducing species names to subspecies and (2) describe one new subspecies from Central Brasil.

For the rest, the discovery in sympatry with animals of core area III of black-dewlap animals (*A. bombiceps*) that are distinct in several other characters carries us clearly to the species level. The sample is poor, the characters of the animals in life, whether of color, behavior or ecology, not known, some of the differentiating characters (especially in females) not so sharp as might be wished, yet the reality of species separation is unmistakable. This is a local, apparently not very successful, perhaps even dwindling, early derivative of the *chrysolepis* complex.

NOMENCLATURE

Thirteen names have been proposed for anoles recognizable as members of the *chrysolepis* species group. We list these below in chronological order, with their type localities.

Draconura nitens Wagler, 1830. "America".

Anolis refulgens Duméril & Bibron, 1837. "Surinam".

Anolis chrysolepis Duméril & Bibron, 1837. "Guyane et Surinam".

Anolis planiceps Troschel, 1848. Caracas, Venezuela.

Anolis scypheus Cope, 1864. Type locality not given.

Anolis nummifer O'Shaughnessy, 1875. Demerara Falls, British Guiana.

Anolis turmalis O'Shaughnessy, 1875. "Island of Grenada".

Anolis lentiginosus O'Shaughnessy, 1875. "Surinam".

Anolis bombiceps Cope, 1876. Nauta, Peru.

Anolis longicrus Roux, 1907. "Surinam".

Anolis nitens bondi Fowler, 1913. "Cariquito", Venezuela.

Anolis incompertus incompertus Barbour, 1932. San Martin near Villavicencio, Meta, Colombia.

Anolis eewi Roze, 1958. Cumbre de Torono Tepui, Chimantá Tepui, Bolivar, Venezuela.

In assigning names to a wide ranging, geographically differentiated, relatively well known species complex, certain principles may usefully be applied: (1) Names of uncertain application should be disregarded. (2) Names of uncertain geographical provenance should not be employed, unless they are very accurately determinable. (3) Names never used since their proposal should not be used, unless no other name is available for the taxon in question.

In accordance with these principles we reject two of the earliest names attributed to the *chrysolepis* complex.

Nitens Wagler, 1830, is probably, but hardly with certainty, applicable to some member of the *chrysolepis* group. On the basis of the description it could be assigned, if at all, only on the basis of color characters: "*Virescens supra, nitore cupreo-aureo, subtus albo-virens, argenteo-splendens; cauda tota aureo-viridi, macula supra ossacrum duabus arcuatis obscuris; femoribus digitisque obsolete fasciatis.*"

However, nothing supplements this inadequate description. The type is lost, the type locality ("America") insufficiently defined, and the usage of the name extremely confused, having been used primarily for one of the color morphs possible to *chrysolepis* group animals in Surinam (Boulenger, 1885) or British Guiana (Beebe, 1944) or Venezuela (Shreve, 1947). Such a name could be employed only arbitrarily, and we therefore set it aside.

Refulgens "Schlegel" in Duméril and Bibron, 1837, type from Surinam, falls on other grounds. It has at best only page priority over the familiar name *chrysolepis,* but it has never been used except in synonymy or in type lists since its proposal. It is at once a *nomen oblitum* and a name that can be discarded on the first reviser principle.

In the same publication Duméril and Bibron describe *Anolis chrysolepis* on material from French Guiana and Surinam. One of the

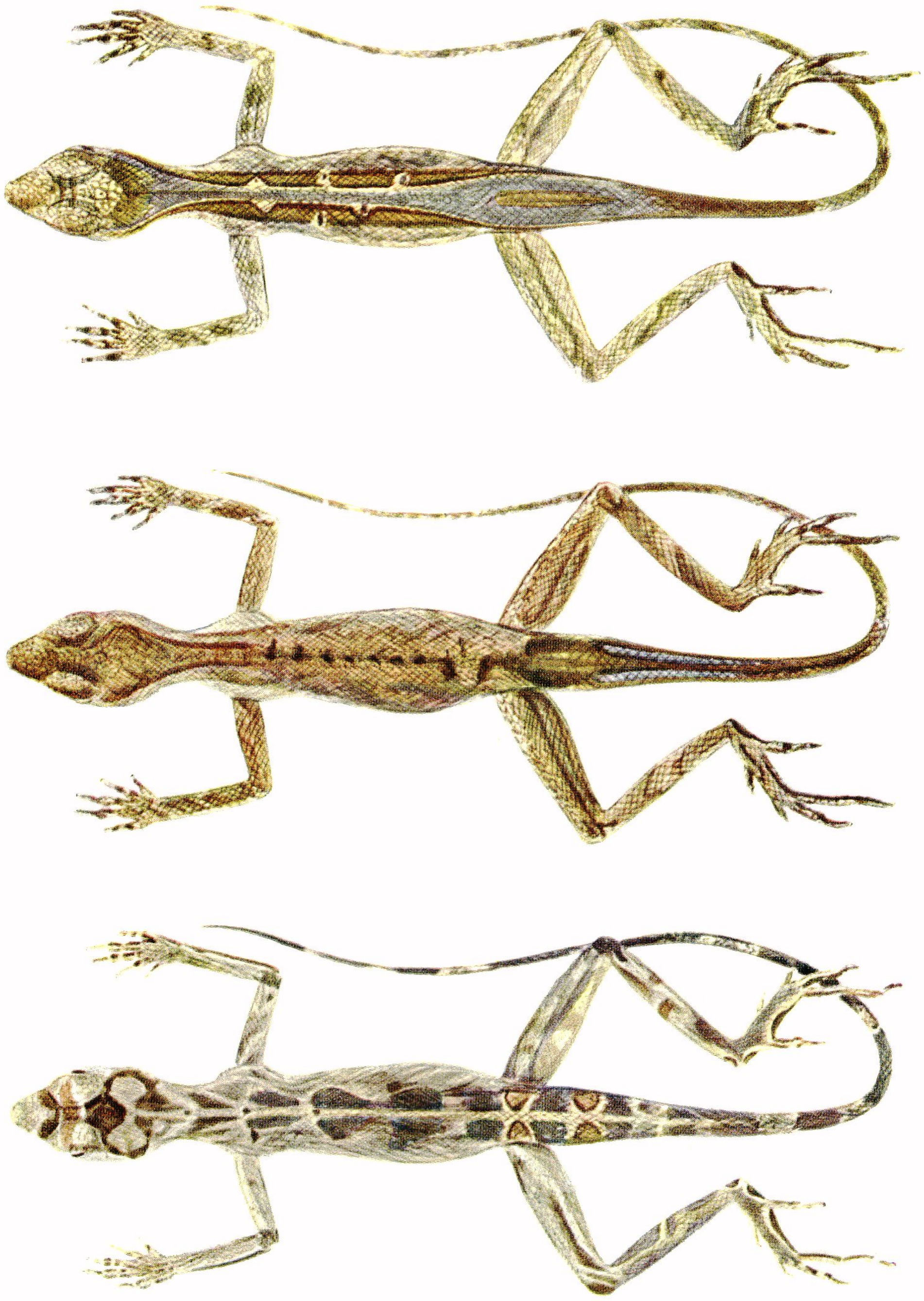


Plate 1. Upper and middle, *Anolis c. chrysolepis,* ♀♀, Lower Matarony, LACM 42105, 42112. Lower, *A. c. planiceps,* ♂, Manaus, MZUSP 10906.

Plate 2. *Anolis chrysolepis planiceps*, Kamakusa, Upper, ♀, AMNH 25125. Middle, ♂, AMNH 25131. Lower, ♀, AMNH 25123.

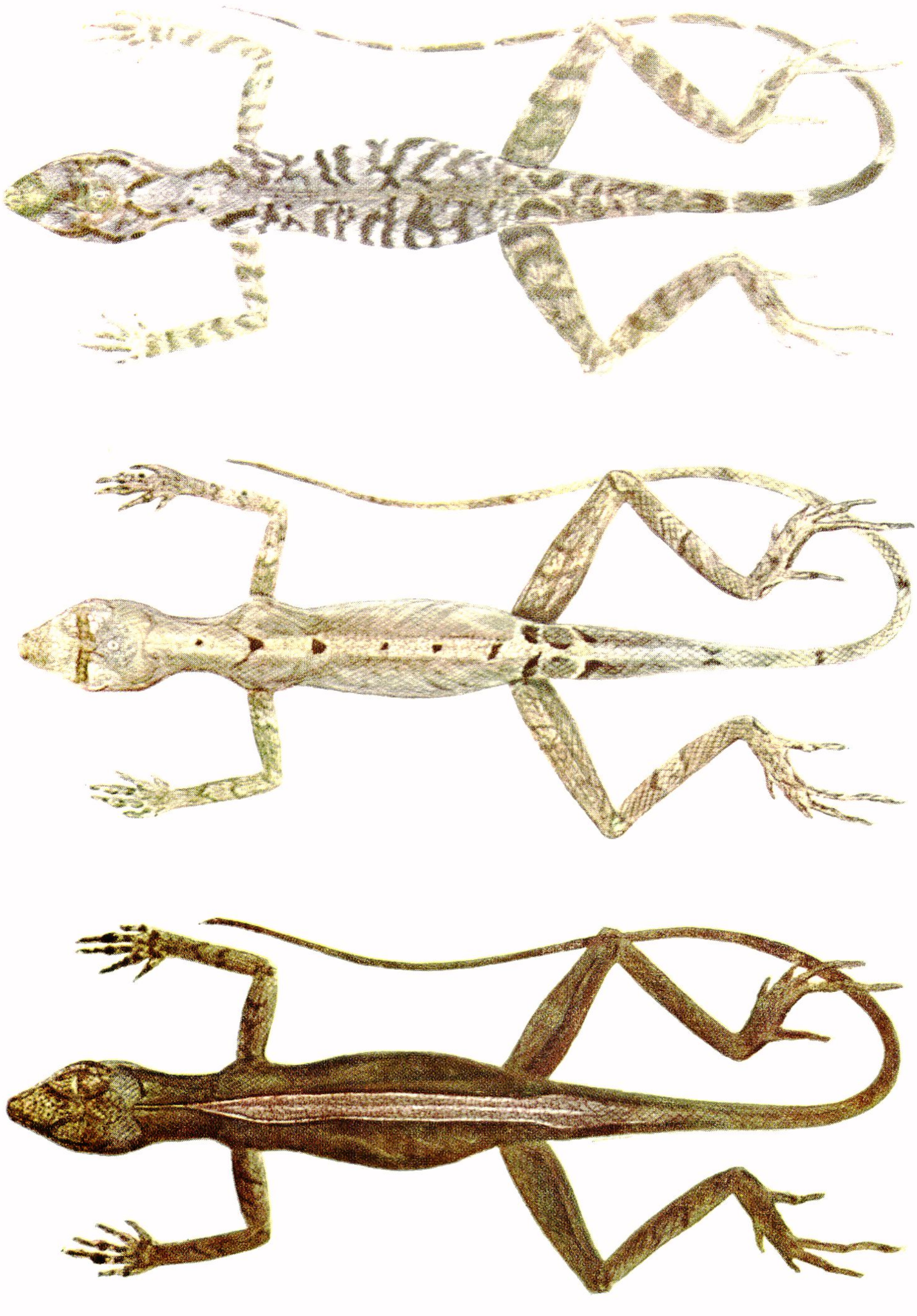


Plate 3. Upper, *Anolis chrysolepis planiceps,* ♀ , Arabupu, AMNH 38684. Middle, *A. c. brasiliensis* x *planiceps,* ♂ , Cachimbo, MZUSP 3990. Lower, *A. c. scypheus,* ♀ , Rio Bobonaza, MZUSP 11367.

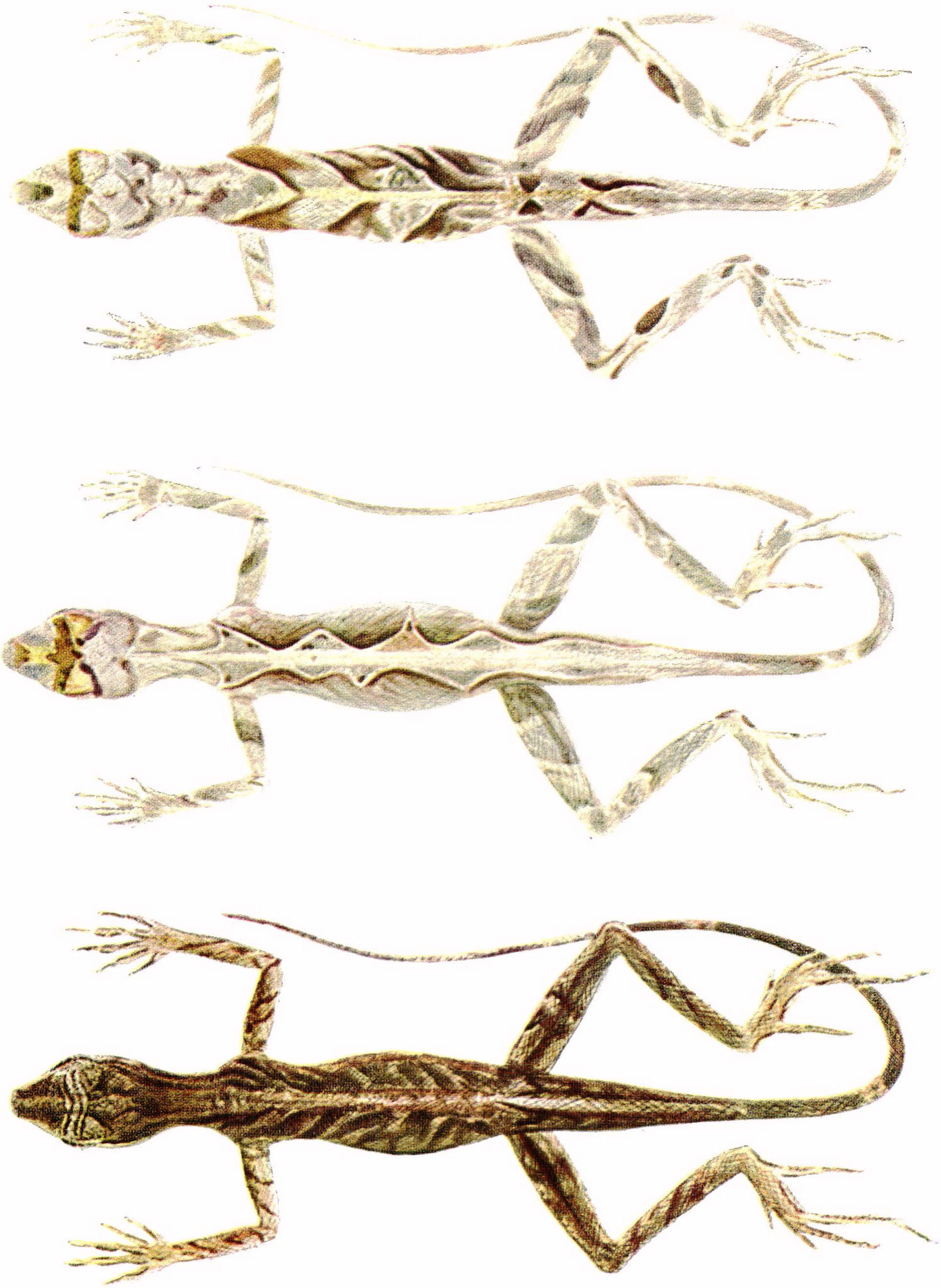


Plate 4. Upper and middle, *Anolis chrysolepis scypheus,* Pampa Hermosa, ♂, AMNH 56847, ♀, AMNH 56815. Lower, *Anolis bombiceps,* ♂, Conambo, MZUSP 13140.

syntypes has precise locality: Mana, French Guiana. We have examined this well-preserved specimen (Paris Museum 2436), and we choose it as lectotype.

Chrysolepis Duméril and Bibron, 1837, is then the earliest satisfactory name for any member of the group. As the most familiar name in the complex, it is fortunate that this should be so. However, current usage of the name, dating from Boulenger (1885) and applying the name to the populations of Trinidad and Venezuela, is not strictly correct and must be modified. While the Trinidad-Venezuela populations remain in the species *chrysolepis,* application of the name in its strict sense must be restricted to the populations of core area I (Surinam, French Guiana and Amapá in Brasil). These have usually gone under the name *lentiginosus* O'Shaughnessy, 1875, regarded as a full species. *Longicrus* Roux, 1907 (Surinam) falls along with *lentiginosus* into the synonymy of *chrysolepis s. str.*

With the realization that the Venezuelan-Trinidadian animals cannot be referred to *chrysolepis chrysolepis* comes the necessity to find another name for these animals of core area II. The earliest available name appears to be *planiceps* Troschel, 1848 (type seen), with the type locality "Caracas". *Nummifer* O'Shaughnessy, 1875, from British Guiana and *turmalis,* with the same author and date but the erroneous locality "Island of Grenada" (perhaps originally "New Grenada") prove on examination of the types to be only color varieties of *planiceps. Nitens bondi* Fowler, 1913, from "Cariquito", Venezuela (= Cariaquito in the Paria Peninsula, see Gazetteer) was described from a very poorly preserved type that displays no discernably distinctive characters. We have specimens from Yacua, very near Cariaquito, that are unequivocal *planiceps* and we unhesitatingly refer *bondi* to the synonymy of the latter. *Eewi* Roze, 1958, from Chimantá Tepui, Venezuela (type examined), was erroneously compared in the description with *A. fuscoauratus,* and falls within the variation of *planiceps.*

The *chrysolepis* group anoles of the Peruvian-Ecuadorian region (core area III) have since Boulenger (1885) always been placed under the name *scypheus* Cope, 1864. Examination of the type demonstrates, despite a type locality lacking or in error, the correctness of this allocation. The specimens from Villavicencio, Colombia, that have received the name *incompertus* Barbour, 1932 (type seen) are not in our judgment sufficiently distinct to merit separate taxonomic treatment, and we accordingly relegate *incompertus* to the synonymy of *scypheus.* (But see the discussions of the Villavicencio animals above).

The anoles of core area IV (Central Brasil to S. Paulo) appear never to have received nomenclatural recognition and may therefore be provided with a new name. We formally describe them below:

Anolis chrysolepis brasiliensis, ssp. n.

Type: MZUSP 10319, a male from Barra do Tapirapés, Mato Grosso, collected by Borys Malkin, 17-28.vii.1963.

Paratypes: males: AMNH 93459-464; MCZ 98285-88; MG 1705, 1707; MZUSP 10075, 10079, 10081-082, 10084, 12327-328, 12975-976, 12979, 12981, 12983, 12985. Females: AMNH 93455-458, 93465-466; MCZ 87913, 98284, 98289; MG 1706, 1708; MZUSP 9744, 10076-078, 10080, 10083, 10085-086, 12974, 12977-978, 12980, 12984.

Diagnosis: A Central Brasilian subspecies of *A. chysolepis* characterized by having: scales across snout 8-11; fourth toe lamellae 19-19 (males) and 15-18 (females); ventral scales 43-53 (males) and 40-50 (females); scales between supaorbital semicircles 0-2 (mode 1). Tibia very short.

Distribution: from northeastern Mato Grosso to northern S. Paulo.

TABLE C

Characterization of the subspecies of *Anolis chrysolepis*

		Scales across snout	Fourth toe lamellae	Ventrals	Dewlap	
					Scales	Skin
chrysolepis	♂	10 - 13	13 - 15	50 - 65	black	intense black
	♀	10 - 15	12 - 15	50 - 62	light	light
planiceps	♂	7 - 13	14 - 19	39 - 54	light	red
	♀	7 - 12	14 - 18	38 - 52	light	reddish
scypheus	♂	9 - 12	15 - 21	49 - 62	white	red at edge black at sides
	♀	9 - 18	14 - 19	47 - 60	as in ♂	as in ♂
brasiliensis	♂	8 - 11	16 - 19	43 - 53	dark at edge, lighter at base	blackish
	♀	8 - 11	15 - 18	40 - 50	lighter than ♂	lighter than ♂

Anolis bombiceps Cope, 1876

One name already published remains to be allocated: *bombiceps* Cope, 1876, with the type locality Nauta, Peru. The types appear to be lost but this is described as a species with a black dewlap and in three of four specimens with a white mark on each side of the throat. We have specimens from several localities near Nauta, which satisfactorily fit this description. *A. bombiceps* Cope appears to be the name of the black-dewlap animals sympatric with *Anolis chrysolepis scypheus* of core area III.

THE ECOLOGY OF *ANOLIS CHRYSOLEPIS*

In the definition of the *chrysolepis* group above we described these anoles as forest animals. For *A. chrysolepis* itself we have clear and positive observations reporting this species as an animal of well-shaded forest, occurring on the lower trunks of trees and on the ground (in French Guiana primarily on the ground, P. Silverstone, *in litt.*) There are repeated observations of its cryptic coloration and of its habit of hopping over the forest floor for a few yards and then freezing into invisibility. The available reports, published and from field collectors and our own observations provide a satisfactory coverage of the ecology of the species over most parts of its range (P. Silverstone, *in litt.*, French Guiana; Beebe, 1944, Test, Sexton & Heatwole, 1966, Rancho Grande area; E. E. Williams and Carlos Rivero-Blanco, personal observations, vicinity of Caracas; F. Medem, *in litt.*, Villavicencio; J. D. Lynch, *in litt.*, Apiay, Colombia and Napo region, Ecuador; Fitch, 1966 and George Key III, *in litt.*, Napo region, Ecuador; P. E. Vanzolini, personal observation, Manaus and Itapiranga, Amazonas; B. Malkin, *in litt.*, Barra do Tapirapés, Brasil).

For *A. bombiceps* we have a single comment: MCZ 112267, collected for J. R. Tamsitt by W. B. Head in Leticia (on the Rio Amazonas at the Brasil-Colombia border), is reported as found "on the ground at the edge of forest". This observation may hint at a less shade-living habitat for *bombiceps* than for most populations of *chrysolepis*. Even in *chrysolepis* there are for the Villavicencio region (including Apiay) reports of specimens taken in situations which, while somewhat open, are still shaded, e.g. palm and banana groves. Such reports, however, including that for *bombiceps*, involve so few individuals that no valid statements about populations are possible. The *chrysolepis* group remains essentially a forest group even though individuals, or even populations, may extend to edge situations.

The importance of a forest ecology for the group is obvious. Its distribution — present and past is then limited by the distribution of forests past and present, and hence by the factor of moisture. This factor then will be important in the history of the group.

Temperature, on the other hand, seems less limiting. As a species, *A. chrysolepis* has apparently broad tolerance to temperature. In fact, its range appoximates that of *Amphisbaena alba* (Vanzolini, 1968b) and includes a wide range of temperatures and of combinations of maxima and minima. Pertinent temperature data (in degrees Centigrade) selected from the *Amphisbaena alba* paper are

	Manaus	Northern S. Paulo
Absolute maximum	39	40
Absolute minimum	17	-5
Annual average	26	21
Maximum range	22	45

It seems quite evident that temperature variations have not played a major role in the history of the *chrysolepis* complex.

THE ANOLE COMPANIONS AND COMPETITORS OF *ANOLIS CHRYSOLEPIS*

The limits to the distribution of any species and a very considerable portion of its history may be dependent upon the presence and the role of its congeners and competitors. *Anolis* as a genus is somewhat unusual in the numbers of its species that may occur sympatrically. It is, of course, probable that part of this unusual feature is attributable to a wider generic concept in *Anolis* than in many lizard genera. Nevertheless, the generic concept does imply some community of ecological adaptation, and it is probable that the major potential competitors of *A. chrysolepis* are other anoles.

However, except at one point the distribution of *A. chrysolepis* relative to other anole species is such that it is quite improbable that competition with any other anole is responsible for holding *chrysolepis* within the known limits. Climate and concomitant vegetational barriers are more probable limiting factors. The possible exception is in the west where in Colombia *A. chrysolepis* has spilled over the easternmost Andes into the valley of Bogotá but has not spread further and in western Venezuela. In both cases it may be limited by, as it is certainly replaced by, the probably ecologically similar *A. tropidogaster* (see further below).

Most of the wide range of *A. chrysolepis* is in a broad sense Amazonian — the Guianas, Amazonian Venezuela, Colombia, Ecuador, Peru and Brasil. Over all of this area three species co-exist with *A. chrysolepis*: *A. punctatus*, *A. fuscoauratus*, and A. *ortoni*. Two of these are animals of shaded forest and often syntopic with *A. chrysolepis*. Of these two, *A. punctatus* is a green anole, similar in size to or larger than *A. chrysolepis*, but characteristically occurring higher in the trees; its home ranges will overlap with those of *A. chrysolepis* only marginally and occasionally. *A. fuscoauratus* is a smaller species than *A. chrysolepis* and more of a trunk animal than the latter; it is never reported as occurring on the ground as *A. chrysolepis* often is. The third widespread Amazonian anole sympatric with *A. chrysolepis*, *A. ortoni*, is a close relative of *A. fuscoauratus* and very similar in size. Like the latter it is a trunk anole but occurs only in more open situations and is unlikely ever to be syntopic with *A. chrysolepis*.

A fourth species, *A. auratus*, occurs in grasslands in northern and northwestern Amazonia, but because of its habitat in open sunny treeless areas it is even less likely to overlap *A. chrysolepis* than is *A. ortoni*.

In part of western Amazonia *A. trachyderma* (= *A. leptoscelis*) occurs with *A. chrysolepis*, *A. punctatus*, *A. ortoni* and *A. fuscoauratus*. Its ecology is unreported, perhaps because in the field it has been confused with *A. fuscoauratus* and *A. ortoni*, which it much resembles. Like these it is much smaller than *A. chrysolepis*.

In central Amazonia *A. phyllorhinus*, a leaf-nosed species, is sympatric with *A. chrysolepis*. Its ecology is quite unknown, but it is again much smaller than *A. chrysolepis*.

A. transversalis is sympatric with *A. chrysolepis* in western Amazonia. It is as large as *A. chrysolepis*, but it is a relative of *A. punctatus*, and its morphology, especially the number of fourth toe lamellae, suggests that like the latter it is a high tree species.

It is noteworthy that in western Amazonia, in approximately the same region, each of the three Amazonian species groups — the *punctatus* group, the *fuscoauratus* group and the *chrysolepis* group — have an additional species — respectively, *transversalis, trachyderma* and *bombifrons*. The ecological relationships must therefore be significantly more complicated in this region than in the rest of Amazonia. It is probable, however, that in western Amazonia as in its eastern part all the anole species are co-adapted so that they avoid competition by such differences as those in size or in part of tree inhabited or by sun-shade preferences.

In Venezuela *A. chrysolepis* extends beyond the range of the general Amazonian fauna quite to the coast. In the coastal range is is sympatric with *A. squamulatus* and *A. tigrinus* but apparently not syntopic, since the latter two species are characteristic of the cloud forest, in which *A. chrysolepis* does not occur (Test, Sexton & Heatwole, 1966).

To the west in Venezuela and Colombia *A. chrysolepis* approaches and in the Bogotá region is known to overlap *A. tropidogaster*. The latter is a smaller and apparently forest-edge species, but little is known of its ecology. There is, however, considerable structural similarity between it and *A. chrysolepis,* and some degree of ecological as well as geographic overlap would not be surprising. This is the one case in which competition and competitive exclusion seem at all possible but insufficient information exists.

In western Venezuela *A. chrysolepis* may possibly come in contact with *A. biporcatus,* but this is a larger green species, and, like A. *punctatus,* is known to be highly arboreal. Competition with *A. chrysolepis* is unlikely.

In core area IV *Anolis chrysolepis* is not known to share its forests with any other anole, although the surrounding grasslands have *A. meridionalis,* and in the Atlantic forest, not far to the east, *A. punctatus* occurs quite as far south as does *A. chrysolepis* inland, and a form of *fuscoauratus* occurs in southern Bahia and Espirito Santo (Williams, unpublished). *A. punctatus* again without *A. chrysolepis,* occurs even further south to the west in Amazonian Bolivia. Thus the isolation from other forest species of *A. chrysolepis* in the central Brasilian forests of core area IV is not a matter of latitude but of some special historical factor which has prevented other anole species from reaching this area at the appropriate time.

Special historical factors must in similar fashion be invoked to explain the absence of *A. chrysolepis* from the Atlantic forest of east Brasil. None of the anole species known from the Atlantic forest could have excluded *chrysolepis*. *A. punctatus, A. fuscoauratus* and *A. ortoni* co-exist with *A. chrysolepis* over the wide expanse of Amazonia. The only other anoles are *A. nasofrontalis* and *A. pseudotigrinus* of Espirito Santo well south in the Atlantic forest, unknown ecologically but small species, which on size alone must be eliminated as significant competitors for *A. chrysolepis.*

REVIEW OF GEOGRAPHIC DIFFERENTIATION

The scheme of geographic differentiation at which we have arrived permits us by itself, even were there no paleoecological data, to delineate the main features of the history of the *chrysolepis* complex. The important points are:

1. There are two sympatric species of the *chrysolepis* group in South America: one, *bombiceps*, with a small range in westernmost Amazonia, and the other, *chrysolepis*, occupying the whole territory of the species group.
2. In *chrysolepis* we define four core areas, one of which is probably the result of the fusion of 3 smaller units. These cores are all peripherally situated and their combined area is about one quarter of the total territory.
3. The core areas are defined as areas of maximum overlap of distinctive distributions of a number of characters. All 12 characters studied play a part in the definition of the cores, but 4 of them are relevant in all cases: dewlap color, fourth toe lamellae, scales across snout and tail length.
4. In the cases where the boundaries of the core areas are not very far apart, one finds either sharp breaks in character values or smooth intergradations. In the Amazonian region, central for all four core areas, however, the patterns of transition are complex.

It is obvious that the present pattern of differentiation of the *chrysolepis* group must have arisen because of the past presence of "barriers" cutting off segments of the complex in specific ways at specific times. The internal evidence of the structure of the *chrysolepis* complex can therefore specify the relative width and the relative timing of the barriers, not, however, their *absolute* width or *absolute* duration, nor in fact their *exact* place.

We read the implications of the present distribution pattern of the complex as follows:

The species level difference between *bombiceps* and *chrysolepis* requires that the initial barrier between these two species be at least older and probably also wider or stronger than any that subsequently separated populations of *chrysolepis*. A first stage on the putative history must therefore find a plausible original home in western Amazonia for *bombiceps* and some quite separate presumably distant home for *chrysolepis*.

The core areas within *chrysolepis* again imply barriers but whether these should be considered to all intents and purposes contemporaneous or ordered in some sequence is not easily decided. It is simplest to treat them as essentially contemporaneous. The evidence does, however permit some discussion of their width or strength, i.e. their effectiveness.

Core area I is strongly marked in several characters. It must therefore have been especially sharply set off by barriers to the west and south. Some barrier must also have always existed to the southeast since *chrysolepis* appears never to have invaded the Atlantic forest which is close to core area I in this direction.

At present core area I and eastern Amazonia are both separated from the Atlantic Forest by the Brasilian open formations of cerrado and caatinga. That these areas have not always been covered with open formations and that eastern Amazonia and the Atlantic Forest were at some not distant time connected is clear from the presence in the Atlantic Forest without any evidence of significant differentiation of such characteristically Amazonian species as *Anolis punctatus* (Williams and Vanzolini, 1963), *A. fuscoauratus* and *A. ortoni.* But the path that was open between Amazonia and the Atlantic forest for *A. punctatus* etc. must somehow have been closed for *A. chrysolepis.* On grounds as cogent as those on which we infer barriers elsewhere, we must infer that some effective barrier between core area I and the Atlantic Forest has existed during the whole history of *chrysolepis.* Competitive exclusion appears not to apply, since no suitable competitors are known. Extinction could be postulated, but this would have no known reason for parallel.

The refugium for core area I presumably lay somewhere within its present east Guianan-Amapá range. For the differentiation of this core area we thus visualize a unit population essentially in its present area but marked off on all landward sides by stringent barriers. Only the one barrier to the southeast between it and the Atlantic Forest still exists today.

Core area II is less strongly marked than core area I. Some of the barriers surrounding it we therefore infer to have been weaker or less long lasting than those that set off core area I. Present distribution of concordant characters seems to imply a coastal distribution for this isolated population. Presumably to the east a strong but not wide barrier separated it from core area I. Toward the west distance even more than strength of barrier may have been effective in separating it from the subunits of core area III.

The three subunits of core area III are in an approximate north-south line along the eastern slopes of the Andes. They are widely separated from the other core areas but rather less from each other. Moderate severity in barriers would be quite sufficient to give them the distinctness they manifest, but some of the peculiarities of one or more of the subunits may be due to interaction with sympatric adjacent *bombiceps.*

Core area IV is as a core area quite remote from the others. Distance alone would account for much of its individuality. It is peculiar, however, in two unique ways: its considerable latitudinal extent carries it into climates not experienced in the other core areas, and, phytogeographically, it occupies two similar but separate formations. To the north it occurs in the remnant forests within the relatively dry cerrado of the Brasilian highlands; to the south it is in the inland buffer forest that is the southwestward expansion of the Atlantic forest (Hueck, 1966). The failure of the core area to involve the Atlantic forest proper requires explanation, and some inland refugium in the Brasilian highlands needs to be provided.

HISTORY: DESCRIPTIVE

The origin of the *chrysolepis* species group.

The *chrysolepis* species group belongs to the *beta* section of the genus *Anolis* (Etheridge, 1960). This section has its area of abundance and presumably its place of origin in the Mexican-Central American region. In Mexico there are only *beta* anoles. As far north as Costa Rica there are only three species of the alternative *alpha* group in a very large anole fauna. In South America the *betas* coexist with the *alphas* over the whole area of the continent that is tenanted by any anoles. However, in South America the *betas* have the aspect of recent invaders. Many of them are mere outliers of Central American or even Mexican species. Others are obvious derivatives of such outliers. The South American *alphas* on the other hand have the aspect of old native groups with many highly differentiated and often local forms, e.g. the proboscis anoles (Williams, 1965). It is believed that all the *betas* are post-Pliocene invaders.

Even rather recent invasions may give evidence of having occurred in several waves. So it is with the *beta* anoles. *Anolis meridionalis,* which occurs as far south as any South American anole, bears also internal evidence of relative primitiveness. As Etheridge (1960) has shown, a large number of inscriptional ribs ("parasternalia") appears to be a primitive anoline feature. Uniquely among South American *betas* *A. meridionalis* has a high number, and this, along with its southern distribution, suggests its interpretation as the surviving representative of the first wave of *beta* anole invasion of South America.

The remaining South American *beta* anoles cannot be sorted out easily or unequivocally into earlier and later arrivals. One grouping — but one not wholly satisfactory — is into trans-Andean and cis-Andean species, the trans-Andean species, in and west of the Andes, closer to their Central American source, the cis-Andean species with for the most part a much greater penetration of the continent. (A few species are both cis- and trans-Andean).

However, closeness to ultimate source seems an uncertain clue to time of arrival. Just as deepness of penetration might imply an old incursion, on the hypothesis that time is needed to spread over great distances, so species identity of South American and Central American populations should imply recency of invasion — on the hypothesis that accumulation of difference has at least a rough positive association with age. There is, however, much ambiguity: *Anolis fuscoauratus* has a cis-Andean distribution from Bolivia to Pernambuco in Brasil. Yet this species is indistinguishable on scale characters and not consistently distinguishable in color from the form currently known as *A. limifrons* in Mexico and Central America. Two other species, *A. ortoni* and

A. trachyderma (= *A. leptoscelis*), are clearly close relatives of *A. fuscoauratus* and perhaps endemic South American derivatives. Thus the evidence points in two opposed directions: the wide distribution of *A. fuscoauratus* and the existence of apparent local derivatives seem to imply at least modest antiquity, while the absence of difference between *A. fuscoauratus* and "*A. limifrons*" appears to imply a very limited time span.

In this particular case the solution may be to postulate two independent invasions of a *fuscoauratus* stock: an earlier one which left behind the two South American endemics and a later one which has involved the wide and speedy spread of an undifferentiated population.

In any event the *A. fuscoauratus* stock is surely a younger invader than *A. meridionalis;* it has not penetrated as deeply; it lacks the primitive features of the latter. As *A. fuscoauratus* it is probably younger than such a form as *A. chrysolepis,* which shows no very close Central American affinities, but the invasion that produced *A. ortoni* and *A. trachyderma* may have been in some very rough way contemporaneous with some phase of the differentiation of *A. chrysolepis*, and *A. fuscoauratus,* even in its later invasion may well be older than, fom example, *A. lemurinus,* which has only a trans-Andean range in South America and has achieved there only subspecific differentiation, and is without any known South American derivatives.

The *chrysolepis* species group thus looks to be a member of a middle group of *beta* invaders of South America. Its position within such a group cannot now be determined. It may, however, stand in some special relationship to its western neighbor, *A. tropidogaster.* External morphology says that the relationship might be ancestor-descendant, but the more advanced karyotype of *tropidogaster* (Gorman, 1968) suggests that the relationship is less direct.

It is worthwhile here to observe that the several *beta* invasions have not been ecological equivalents. *A. meridionalis,* south of the Amazonas and the oldest *beta* invader, is a grassland animal restricted to open formations. *A. auratus,* primarily north of the Amazonas, but now known to have reached its southern banks, perhaps very recently, is the ecological equivalent of *A. meridionalis.* In contrast, *A. chrysolepis* and *A. fuscoauratus,* though invaders of the same cis-Andean region, are strongly tied to forest, and their histories must have been totally different from those of *A. meridionalis* and *A. auratus.* We deal here with very distinct events and, again quite clearly, with the alternation of dry and wet periods in tropical South America.

Cycles of differentiation within the *chrysolepis* group.

Given then the arrival in cis-Andean South America of a proto-*chrysolepis* stock at a time neither very recent nor very ancient, we have the need to explain in historical terms the patterns of distribution and differentiation we have before us.

In the attempt to do this the concept of core-areas will be very important. We have inferred their existence and their importance from the basic data above. We may now interpret them as areas which were at one time or another refugia during periods in which the *chrysolepis* group was undergoing periods of contraction and fragmentation.

But if the core areas are to be interpreted in this way, we confront also periods of expansion and recontact of populations. With these two phenomena only we should be able to explain all the varying degrees of distinctness of populations which we have seen in front of us.

Clearly in the case of the *chrysolepis* group fragmentation has not involved major physiographic barriers (there are none to be seen within its range) and there is no reason to invoke orogenic movements or events of any great antiquity. We must then look to climatic and vegetational phenomena. We may infer that the whole history, the fragmentations and coalescences of the *chrysolepis* group involve, since these are forest animals, the history and the fragmentations and coalescences of the forests in which they live.

We shall show below the wealth of independent evidence that such fragmentations and coalescences of the Amazonian forest have in fact taken place. But we emphasize here that we would be driven to postulate these radical changes in forest cover singly and solely on the basis of the intrinsic patterns of differentiation within the *chrysolepis* species group.

Thus, on the basis of the intrinsic patterns of differentiation in the *chrysolepis* group we require more than one cycle of forest contraction and expansion but not any sequence of special complexity. We may specify the following hypothetical history.

Prologue: a dry period such that cis-Andean proto-*chrysolepis* is separated from its parent stock to the west.

Act. I. Expansion: a wet period in which proto-*chrysolepis* expands in good forest in an arc from circa Surinam to circa West Amazonia. Some barrier now and in the future separates the species from the Atlantic forest.

Act II. Contraction: a dry period fragments proto-*chrysolepis* into *chrysolepis* circa Surinam and *bombiceps* in West Amazonia.

Act III. Expansion: *chrysolepis* and *bombiceps* expand. Dewlap and arm scale differences develop by character displacement in the area of overlap.

Act IV. Contraction: both *bombiceps* and *chrysolepis* contract, but *chrysolepis* finds several refugia, including one in the Central Brasilian highlands and *bombiceps* continues in only one.

Act V. Expansion: *chrysolepis* re-expands, certain of the refugia fail to maintain their difference. *Bombiceps* is overrun. *Chrysolepis* populations coalesce confusedly in Amazonia.

HISTORY: THE MODEL AND THE EVIDENCE

In 1966 Williams and Vanzolini said of the Amazonian species *Anolis punctatus* and *A. transversalis* (p. 203) : "These are animals of forests and it is best to explain their history in terms of the history of forests". This was phrased at that time as a testable hypothesis of general application to South American forest animals; we have now applied it to a second case. Let us develop the hypothesis more fully.

The model

We postulate for the Amazonian area a rapid sequence of cycles in the late Pleistocene and Holocene, each involving a drier and a wetter phase.

We suppose that to the dry phases correspond enormous retreats of the rain forest of such an extent that the forest survives only in refugia separated by wide tracts of open formations.

Alternately, in the wet phases forest spreads outward from the refugia, coalescing to cover again vast areas.

In the wet phases the species isolates that had differentiated in the refugia of the dry phases spread out along with the forest, meeting each other and interacting in various ways. In these extreme cases in which genetical isolation was achieved during the preceding dry phase interaction results in character displacement and thus further differentiation. In other cases, wherever a degree of genetic compatibility still exists, the result of interaction is extensive recombination with a great increase in variability, which can be the raw material for a next phase of segregation.

The difference between this hypothesis and those which until very recently were classic lies in the recognition of the recency, vastness and radical nature of the changes that occurred in the equatorial regions during the late Pleistocene and the Holocene. We may contrast our statement above with that of Darlington (1957) (our italics):

> "Within the tropics, even at low elevations, temperatures probably decreased somewhat during glacial ages, but rainfall probably increased. Lakes increased in size at least in some places, and tropical forests probably tended to expand and steppes and deserts to contract. Opposite changes probably occurred during the warmer, drier interglacials. The effect on tropical faunas may have been considerable in marginal areas but was apparently not great in general. *Existing lowland tropical faunas are huge and complex, with many species of animals closely adapted to the plants around them. Such faunas are obviously old and have suffered no great disaster during the Pleistocene*".

Many years after Darlington, and in spite of the rapidly growing body of evidence on climatic changes, Schwabe (1969) still says (our italics):

> "The *Hylaea,* filling the whole of the Amazon basin, is by far the largest closed area of rain forest in the tropics (in conjunction with the Orinoco basin it covers 4.5 million square km, while the entire Amazon catchment covers about 7 million sq. km); besides it is one of the

landscape types of highest biotic maturity known. *The extraordinarily high number of species of both animals and plants present within small areas can only be understood as the outcome of a long ecological evolution which must have taken place in the absence of any destructive natural catastrophes.* If one ignores this maturation proceeding without any major disturbance, the extraordinary biotic diversity of the area, viewed in the light of its typically uniform and smoothed physiography, must be considered an almost insoluble paradox."

It is a trivial comment on the quotation from Darlington that we are still uncertain whether glacials and interglacials severally coincided with wet or dry periods in the tropics. It *is* important that on modern evidence (not, of course, the evidence of *chrysolepis* alone, but many kinds of evidence) the effect of Pleistocene and Holocene climatic changes was not marginal or minor but central and major. The tropical faunas did not indeed suffer a disaster but they were certainly profoundly changed. Much of what we see now as tropical diversity and distribution must be Pleistocene or even Holocene in origin.

The essential premise in the italicized sentences above is that diversity, complexity and close adaptation are obviously old. This is a premise we now have reason to discard.

Recent years have seen the crystallization of evidence for a contrary point of view. Moreau (1966) has carefully and eloquently stated the African evidence for the lability of tropical forests. One statement is particularly vivid (Moreau, 1966: 51): "It would seem on present evidence that, as Chapin (1932) has remarked, 'the equatorial forest of Africa has been in the past one of the stable environments'. However, soil surveys have now shown, nearly the whole of this forest is rooted in Kalahari sand, redistributed by the wind at a time placed by the geologists towards the end of the Middle Pleistocene (cf. Brain, 1962) and the dating of 75.000 to 52.000 years ago suggested by de Heinzelin (1963) for aridity in the equatorial latitudes of Africa".

The evidence for paleoclimates

In what follows we'll briefly review the available evidence on vegetational cycles in the northern half of South America, from two viewpoints of major importance to our model, the vicissitudes of the Amazonian forest, and the time scale of the events.

This evidence is of several kinds. First, floral and faunal distributional patterns are readily interpreted in terms of cycles of subdivision and coalescence of the forest, and, complementarily, of the open numerous geomorphological features that demonstrate former dry epiformations. Then, in the present territory of the hylaea are found sodes; this sort of evidence is also present in areas peripheral to Amazonia but relevant to our case. Finally, pollen profiles from Colombia and Guyana also indicate very clear climatic cycles.

Floral evidence. The floral composition of the hylaea reflects a former subdivision of its area, with the evolution of isolates. Ducke & Black (1953) say: "It is a strange fact that within the hylaea the longitude plays a far more important role than the latitudes, in the composition of the flora. The difference in the floras of Belém and Santarém is much more striking than that of Belém and Cayenne, though the distance of the latter is greater. The collections show a greater number of species for the Middle and Northwestern Amazonia than for the Eastern and Western part of the region; ...".

On the other hand, the vast expanses of open formations that exist on both sides of the hylaea are floristically related among themselves and to the numerous enclaves (Map J) within Amazonia (Ducke & Black, 1953; Egler, 1960; Tamayo, 1961; Goodland, 1966); a former continuity is thus clearly suggested

Zoological evidence. The faunal evidence makes it apparent that in times relevant to present distribution patterns both forest and open formations have alternately occupied much broader areas than they do now.

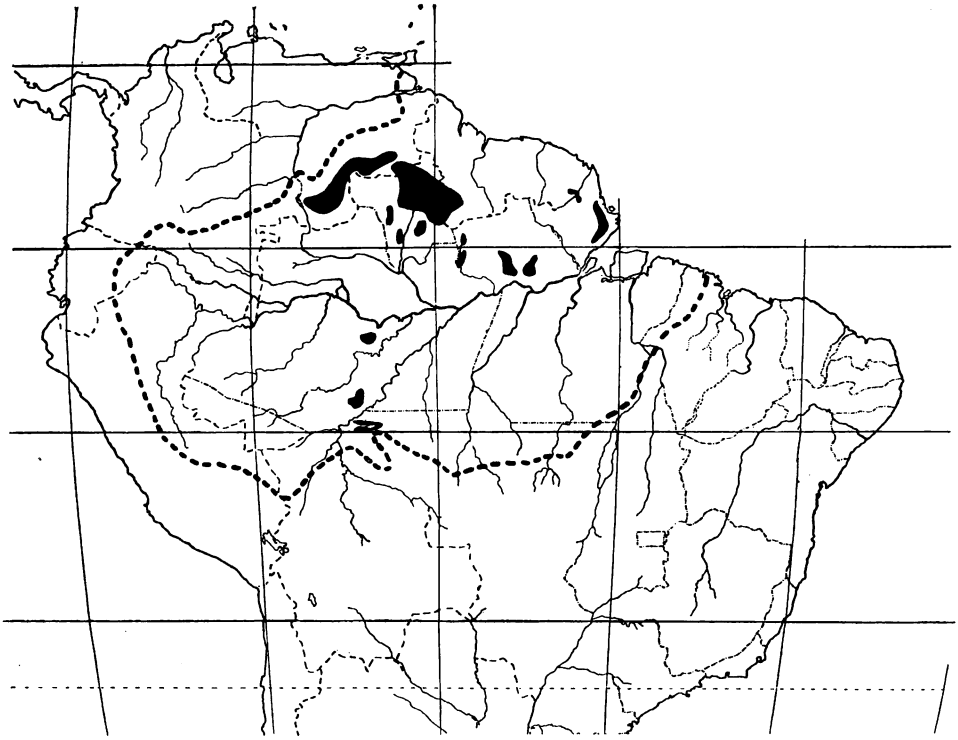
The basis of such evidence is, in all cases, that, as shown by repeated field observation, animals attached to one type of formation (forest on one side, open formations on the other) will not migrate through the contrasting type of environment. The South American rattlesnake is not found inside the forest; the forest geckos of the genus *Coleodactylus* are not found in the open.

The faunal evidence is threefold: (1) cases that indicate former connections between the Amazonian and Atlantic forests, over areas that are covered today by open formations, cerrados (savanna-like) and caatingas (fully xerophytic); (2) cases that indicate that open formations once occupied at least large parts of what is today Amazonian hylaea; (3) cases that indicate complex cycles in Amazonia.

The first type of evidence was briefly reviewed by Vanzolini (1963), for reptiles. It consists in the existence of disjunct distributions of deep forest animals in the hylaea and in the Atlantic forest, and, in some cases, in forest islands in the caatingas of northeastern Brasil. Examples are (*loc. cit.*): *Diploglossus fasciatus* (in the Atlantic forest and in the Brasil-Peru-Bolivia border); *Anolis punctatus, Lachesis muta, Bothrops bilineata,* and *Corallus enydris* (all in Amazonia and in the Atlantic forest).

That open formations at least once occupied a large part of Amazonia is indicated by the fauna of "campos" enclaves in the hylaea. Snethlage (1910, 1913) showed that the bird fauna of the Amazonian campos is part of the general open formation fauna of Brasil. Similar examples are known in the reptiles. For instance, the South American rattlesnake (*Crotalus durissus* ssp.) is present in practically all enclaves that have been explored (Hoge, 1965). One of us (PEV) has found the iguanid lizard *Tropidurus torquatus* in an enclave in the upper Rio Trombetas ("campos do Ariramba"); this characteristic and widely distributed open-formation species is conspicuously absent from the surrounding forest, and, more significantly still, from contemporary urban clearings in the area.

A third, and more complex, type of distribution pattern that supports the idea of rapid and drastic vegetational cycles in Amazonia is exemplified by *Coleodactylus* (Vanzolini, 1957; Rivero-Blanco, 1968), a genus of small geckos that live in forest leaf-litter. One species, *C. meridionalis,* has an enormously disjunct distribution: on one hand it is in northeastern Brasil, on the other in the general region of the borders of Brasil with Venezuela and Guyana. This disjunction is not accompanied by any major morphological differentiation, so we may presume former continuity in relatively recent times. In Amazonia, intervening between the disjunct populations of *meridionalis,* we find another, more advanced species of *Coleodactylus, C. amazonicus.* This species must have evolved in some refuge at a time of maximum open-formation spread and, subsequently, with the new advance of forest, filled the Amazonian gap in the distribution of the genus, excluding *meridionalis* from it and maintaining the disjunction initiated by the presence of open formations.



Map J. Approximate location of open formation enclaves in the Amazonian forest (courtesy of Aziz N. Ab'Saber).

The case of the *Anolis chrysolepis* group obviously belongs in this last category.

Geomorphological evidence. Ab'Saber (1967) has recently reviewed the geomorphology of Brasilian Amazonia, and pointed out features indicating several dry phases. These features are of four principal types:

1. Laterites (duricrusts, Thornbury, 1954: 77, 83), which can only be formed when xeric conditions follow a humid episode.
2. Gravel beds, deposited by torrential, even braided drainages.
3. Pediments, slope profiles formed when dry climates follow a humid episode (Bigarella, Mousinho & Silva, 1965; Thornbury, 1954: 283 seq.).
4. Stone-lines, the buried paleo-pavements of xeric formations (Ab'Saber, 1962); their cross-sections appear in road cuts as lines of anfractuous, unsorted, little worked coarse gravels, such as are characteristic today of the ground of the caatingas.

All these features are present inside Amazonia, in such a manner that it becomes clear that the effective formative conditions prevailed during several separate periods. A very definite level, the Belém-Marajó level (Moura, 1943), underlain by laterites and gravels, is recognizable in many parts of Brasilian Amazonia, being quite evident in Belém, in the island of Marajó, and in Amapá. In the Santarém region, in the heart of the hylaea, one finds additionally an upper river terrace, protected by coarse gravels, and clear signs of pedimentation on the neighboring hills. Laterites and gravel beds were found by Pimienta (1965) in the lower Tocantins, and by Barbosa and Ramos (1959) and Takeuchi (1960) in the Brasilian Território de Roraima (formerly Rio Branco). In Amapá Ab'Saber has seen stone-lines whose gravels are made of re-worked fragments of laterite, indicating in all certainty at least two wet and two dry episodes. East of Belém he has seen forest growing on alluvial deposits overlying a discontinuous stone-line, as well as pure-sand terraces.

Evidence of dry phases comes also from four areas in the immediate periphery of the hylaea, three of them inside the present distribution of the *chrysolepis* group.

Ab'Saber (pers. comm.) reports the following facts in Central Brasil: (1) several pediments, one of which very well marked, in the Cuiabá region of Mato Grosso; (2) gravel beds protecting the low terraces of many rivers in Minas Gerais, Goiás and Mato Grosso; (3) stone-lines in the neighborhood of Brasília.

Garner (1958, 1966, 1967), interpreting the "disorderly and unstable" multi-channel drainage pattern of the Caroni River, which flows from the east end of the Brasil-Venezuela border (Serra de Pacaraima) to the Orinoco near its delta, says that "the key cause is a change of climate from arid conditions to humid ones".

Again Garner (1959), investigating the conditions of deposition of coarse clastic materials in the valleys of the Cordillera Oriental of Peru, arrived at the conclusion that "The physiography of the range as a whole is largely a response to alternating arid-humid conditions" (p. 1347). He predicates for the region a series of 8 episodes, of which three of "severe aridity" and one, the most recent, post-glacial, "sub-arid".

Goosen (1964) found a "llanura eolica", that he dates from the Pleistocene-Holocene transition, in the Llanos Orientales of Colombia. Wind-deposited sediments are a classic feature of arid climates.

Palynological data. Pollen profiles, due to van der Hammen and co-workers, are available from the Colombian Andes, from the Llanos Orientales and from northern Guyana.

All of them tell the same story: "Pollendiagrams and C14 datings from northern British Guyana (near sealevel) showed a savannah-period during the Würm-glacial, with a grass-savannah, poor in species. ... A pollen-diagram from the region of extensive Savannahs east of the Andes (Llanos Orientales), showed that the enormous extensions of these Savannahs should be quite recent, and therefore probably anthropogene. But smaller Savannah-areas must have existed throughout the Holocene, showing minor fluctuations" (van der Hammen, 1963).

"In the Sabana de Bogotá we can clearly distinguish an alternation of climatic phases in the Holocene. These phases are the following: VIII, wet; VII, dry; VI, wet; V, dry and warmer; and IV, dry and colder" (van der Hammen, 1961).

These data from the eastern Cordillera of Colombia have been abundantly confirmed by many other profiles from the same general area, all remarkably coherent (van der Hammen, 1962; van der Hammen & Gonzalez, 1960, 1964, 1965, 1965a). They have also afforded C14 dates of great interest to us, as discussed below.

Absolute dates

The Amazonian geomorphic features that indicate climatic cycles have neither been extensively surveyed nor rigorously correlated, and have not yet afforded absolute dates. All they tell us so far is that phases of open formation spread have existed and have left their mark. In order to obtain an estimate of the time scale of the events we are forced to have recourse to data from adjacent areas, and to restrict ourselves to the latest dry episode.

We have C14 data from two areas, the eastern Andes of Colombia and southeastern Brasil.

The Colombian pollen profiles are in remarkable agreement in showing contemporary levels of strong predominance of grasses. Van der Hammen (1962) ascribes these levels to a dry period and says: "... la edad del cambio de vegetación... debe estar aproximadamente entre 3095 y 1990 años, es decir, alrededor de 600 a.d.Cr. ... Es muy interesante notar que este mismo cambio se encontró en varios diagramas de polen del Páramo de Palacio, en Cundinamarca, y que en este sitio también se pudo determinar la misma edad aproximada por medio de Carbono 14 (van der Hammen & Gonzalez, 1961b)".

In coastal southeastern Brasil there are two dates for the beginning of the latest dry period, 3513 ± 56 and 3284 ± 48 years; and one date for its end, 2680 ± 150 years B.P. (Bigarella, 1965, using

C14 dates from Hurt, 1964). Wood from the lowest of the low terraces in Santa Catarina, also dating from the end of the dry period, show C14 ages of 2700 ± 100 and 2390 ± 90 years (Bigarella, pers. comm.).

The Colombian and southeastern Brasilian dates are in very good agreement. The same can be said of the assignment to the Dunkirkian of the latest drier phase in northeastern Brasil by Tricart (1958), on the bases of geomorphological correlations (not of C14 dating).

It seems thus safe to say that much of South America went through a short and very pronounced dry period centering about 2500 years ago. To this phase are assigned the southeastern stone lines (Bigarella & Ab'Saber, 1964, "Schuttpflaster"), which are directly overlain by deposits ascribable to the present humid phase. The presence of stone lines in Amazonia in the same geomorphic context leads us to think that the last phase of refuge isolation of the *chrysolepis* species group has this very low age. We could perfectly make ours the terms in which Moreau (1966) has described the situation in Africa: "In sum, it is hardly possible to exagerate the sweeping nature and, on the geological time-scale, the rapid succession and recent date of the ecological changes on the surface of Africa. Those we have been discussing form only the latest section of a succession that has filled the Pleistocene; but a species need be only some 20,000 years old to have witnessed the full range of the continent's ecological vicissitudes".

Forest refugia

In a consideration of forest refugia we have, besides the indirect evidence provided by the core areas of differentiation of forest animals, direct evidence of two sorts.

First there is the absence of signs of past dry climates in limited areas within regions where such signs are abundant and regular. For example, two pediments, well evident over hundreds of kilometers, testify to two dry phases, during which the coastal Serra do Mar of south-eastern Brasil was at least partly bare of forest (Ab'Saber, *in* Azevedo, 1965). In some limited tracts of the Serra the pediments are absent, indicating that at the time of pedimentation these sections were forested. Similar evidence is found in the Serra dos Aimorés, state of Espírito Santo — a region which has very probably functioned as a core area for several groups of vertebrates. The absence of stone lines is another good symptom of locally milder conditions during dry times.

Garner (1959: 1364) says: "It seems doubtful that the Cordillera de la Costa of Venezuela has recently experienced an arid interval comparable in severity with that of eastern Peru and western Ecuador as shown by the absence of residual coarse clastic material".

Another evidence for forest refugia is the occurrence today, in several areas of Brasil, of the conditions that patterns of animal differentiation and geomorphological features lead one to associate with refugia.

A large area of northeastern Brasil is occupied by caatinga, a xeric, summer-deciduous, semi-arid plant formation, showing the type of gravel pavements that, after inhumation, result in stone-lines (Ab'Saber, 1959). In the midle of the caatingas; under the same climate and on the same lithology, on hills or mountains well oriented with relation to the prevailing winds or with a better supply of underground water, there are forest islands, locally called "brejos" (Dresch, 1957; Lima, 1960, 1966; Andrade, 1964; Andrade & Lins, 1964). Some of these refugia are quite sizable, as the Serra de Baturité (Pinto & Camargo, 1961) and the Serra de Ibiapaba (Snethlage, 1926), both in Ceará. The fauna of the brejos is typically a forest fauna, completely different from that of the surrounding caatingas, and containing disjunct Amazonian forms and a certain proportion of endemics (Snethlage, 1926; Vanzolini, 1963; Pinto, 1954; Pinto & Camargo, 1961).

In the region of the Brasilian cerrados, in the southeast of the state of Goiás, there is also a large forested area, the so called "Mato Grosso de Goiás" (Waibel, 1948), not as well set off at present as the northeastern brejos, but with a definite individuality, and certain to become an isolated forest upon any deterioration of the present mesic climate (Kuhlmann, *in* Galvão, 1960).

Inside the four core areas that we have defined above occur highlands that very probably have housed the refugia that are the veritable cores of the core areas.

Thus in core area I we find the Tumuc Humac mountains, a crystalline massif apparently with no signs of pedimentation (Ab'Saber, pers. comm.). In core area II are the northern mountains of Venezuela, already commented upon. Core area III includes the eastern slopes of the Andes; even in the absence of direct evidence, one could not imagine a more favourable area for the establishment of refugia, given the complex topography and the exposure to easterly winds. It is not hard to accept the hypothesis of several Andean refugia linearly arranged, to explain the composite nature of core area III. Finally, we have the Central Brasilian highlands, with indented cliffs on the north side, and especially, we have the Mato Grosso de Goiás, as candidates for the position of refugia within core area IV.

Post-script: a convergent case, speciation in Amazonian birds

Haffer (1969), using different materials and methods, has arrived at conclusions identical to ours with respect to the role of recent climatic cycles in speciation in Amazonia, and strikingly similar as to the location of forest refuges in the area.

Starting from the concept of sharp Quaternary climatic cycles, he has identified areas of relatively lower rainfall, which would probably become denuded during the dry phases of climatic cycles, and of higher precipitation, capable of supporting refuges during the same phases. Within the latter areas he looked for topographic features which would favor the survival of forest in dry times. He then looked for evidence of the differentiation of bird forms within the proposed refuge areas. This evidence he has found to be of two types, the presence of differentiated forms (mainly members of superspecies) and the nature of the contact between adjacent vicariant forms.

Haffer found evidence of 6 major cis-Andean forest refuge areas (besides other, trans-Andean refuges, outside our present scope). 1) Napo refuge, mainly the lowlands of Eastern Ecuador from the Andes to the Marañon river; 2) East Peruvian refuges, several variously isolated lowland forests along the Peruvian Andes and farther east on the low mountains between the Rio Ucayali and the Juruá-Purus drainage; 3) Madeira-Tapajós refuge, the lowlands between the middle Rio Madeira and the upper Rio Tapajós; 4) Imerí refuge, a small area around the Sierra Imerí and Cerro Neblina between the headwaters of the Rio Orinoco and the upper Rio Negro; 5) Guiana refuge, on the northern slope and foreland of the mountains of the Guianas; 6) Belém refuge, in the region south of the mouth of the Amazon river west to the lower Rio Tocantins.

A comparison between this pattern and ours shows:

1. The two agree with respect to the Guianan (core area I), Napo (middle part of core area III) and East Peruvian (southern part of core area III) refuges.

2. Haffer has found no evidence of refuges corresponding to our core areas II and IV and to the northern part of core area III.

3. We have found no core areas where Haffer has his Imerí, Madeira-Tapajós and Belém refuges.

Given the different materials, the very preliminary character of both analyses, the newness of the argument, and the fact that the patterns of individual taxa are certain to differ in detail, with its consequent lack of awareness of many colateral problems and facts, we find the agreement very encouraging, in fact almost amounting to proof. But the differences also suggest some comments.

We have not seen enough materials from the area east of the Tocantins (only 2 specimens) to form an idea of the influence of a Belém refuge on the differentiation of *chrysolepis*. It may be even the case that the species is a recent immigrant into the area, which would be in accordance with its absence in the Atlantic forest. But Aziz Ab'Saber (pers. comm.) has flown over northern Maranhão and seen, in the region of Perizes, unmistakable signs of persistent presence of tropical forest there. The Belém refuge is very probably real.

Our materials do not indicate a Madeira-Tapajós refuge. On the contrary, between the Araguaia and the Tocantins *Anolis chrysolepis* has been able to go as far south in S. Paulo as did the Atlantic forest anoles along the coast. We may presume that the refuge where *chrysolepis brasiliensis* differentiated is not juxta-Amazonian, but located much to the south, and that its connection with the Amazonian forest has been through broad and extensive gallery forest — or perhaps even unbroken forest — in Central Brasil. Such an area, within the range of *brasiliensis*, comes immediately to mind: the "Mato Grosso de Goiás" (see above). This is definitely not an orographic forest (Waibel, 1948), but there is some geomorphological evidence, especially the pattern of rock decomposition (Ab'Saber, pers. comm.) of a long persistence of forest cover.

THREE *OBITER DICTA* ON TROPICAL EVOLUTION

CHARACTER DISPLACEMENT, ECOLOGICAL CHANGE, AND "SWAMPING"

The most characteristic feature of the species *bombiceps,* the small arm scales, is not distinctive as against all populations of its sister species *chrysolepis,* but only against adjacent populations. This is classic character displacement (Brown & Wilson, 1956).

As we have mentioned above, however, dewlap color in some specimens of *bombiceps* is similar to that of the sympatric core area III *chrysolepis.* This similarity might be attributed to introgression and might imply that *bombiceps,* with a relatively restricted range and apparently smaller populations, is in the process of being "swamped" by its widely dispersed abundant relative. There would seem therefore to be a contradiction: *bombiceps* is said on the one hand to have acquired greater species difference by character displacement and on the other is said to be losing its species identity by "swamping". We know too little of *bombiceps* to discuss this in more than tentative terms, but we have been led by consideration of this problem to examine some of the possible circumstances which might be significant either for character displacement or "swamping".

As is now generally accepted, we assume that each local population responds to local selection. If in isolation a concordant character complex is built up at the species or a lower level, it is built up in response to the local selection of that particular historical period.

Character displacement likewise will, unless species are in continuous contact over a long period, occur in response to the conditions of the historical moment of contact.

Character displacement in the morphological features, including size, ascertainable in museum specimens, is certainly accompanied by physiological-ecological changes that are in fact likely to be more important. In *Anolis* we know from other studies (Schoener & Gorman, 1968; Williams & Rand, in prep.) that differences in the height and size of perch ("structural habitat") and in thermal preference ("climatic habitat") are the kinds of non-morphological co-adjustement usual in sympatric species.

We may reasonably assume that some such non-morphological changes took place during the *bombiceps-chrysolepis* interaction. In this case we know the ecology of *chrysolepis* over much of its range, but nothing of that of *bombiceps.* It is permissible, however, to proceed on theoretical grounds.

Since changes in structural habitat in *Anolis* usually involve some morphological change (Williams & Rand, in prep.), especially in number of lamellae under the toes (Collette, 1961; Williams, 1963; Williams & Rand, in prep.) and since *bombiceps* does not differ morphologically from *chrysolepis,* it seems unlikely that *bombiceps* and *chrysolepis* differ in structural habitat. It is, however, extremely likely that, in the absence of structural niche difference, *bombiceps* and *chrysolepis* differ in climatic habitat, i.e. in sun-shade preference. We have in fact based a history of *chrysolepis* on fluctuations in the distribution of forest.

We, however, cannot assume out of hand that it was *bombiceps* and not *chrysolepis* that altered its ecology when the two came into contact.

It may be that we have in the equivocal or anomalous reports of the ecology of the light-dewlap phase of *chrysolepis* in the Villavicencio region an indication that somewhere in this general region the contact of *bombiceps* and *chrysolepis* first occurred, and the *chrysolepis,* not *bombiceps,* was ecologically displaced toward edge or more open situations.

If *chrysolepis* were displaced toward edge or open situations, there would be elements of instability in the phenomenon. The *chrysolepis* populations of the Villavicencio area never lost genetic compatibility with the adjacent forest populations, and gene flow from these should tend to return all *chrysolepis* to shade-dwelling preference, except to the degree that local counter selection, including that derived from contact with *bombiceps,* promoted edge and open adaptation. The more complete the contact of the Villavicencio refuge with forests to the north and to the south, the greater the extent and density of total forest, the greater would be the tendency to the submergence of the special qualities, especially open adaptation, of the Villavicencio population. (We emphasize again that we may here totally misstate the actual case; we are exploring theoretical possibility).

The points that we would here emphasize go to the issue of the apparent paradox of character displacement followed by swamping:

(1) All ecological adaptations, including those arising by character displacement, are subject to the dynamics of the situation in which they occur. Thus ecological character displacement achieved at one stage of a climatic cycle may cease to be relevant or effective at another. In such a case as *bombiceps* and *chrysolepis,* the climatic differences evolved during a period of thin or limited forest contact might be attenuated or abolished during a subsequent period of maximal forest extent and density. There would then result either maximized competition with attendant attrition of one or the other species, or, very possibly, introgression.

(2) In the success of ecological adaptations to reduce competition the abundance of the two species may be very important. Any factors that reduced critically the numbers of one species relative to those of the other might again break down ecological displacement, and might again, either accentuate the attrition of the smaller species, or alternatively, permit introgression.

This is, of course, very speculative. We introduce it because it calls attention to some pertinent ecological questions and indicates the need for detailed field evidence of an ecological nature, in our specific case in the general western Amazonian area.

CORE AREAS, DISPERSAL, REFUGIA AND A MODEL OF TROPICAL DIFFERENTIATION

By analysis of characters we have inferred the existence of "core areas". Their reality, we think, cannot be validly disputed. Their evolutionary significance is also unmistakable.

The simple existence of core areas of concordant characters, coterminous or not, implies build up of independent character complexes, *ergo* genomes, in the separate areas. This in turn implies some impediment to disruption of these complexes by gene flow during the critical period of their origin. This phenomenon is, of course, the familiar central concept of "geographic speciation": geographical barriers to gene flow should exist if this process is to go to fruition.

For tropical environments such as the large continental tropical forests a problem in this regard has seemed to exist: where in uniform continuous tropical forests can the barriers needed for species origin exist? This is, of course, a wrong question; it assumes as a historical fact a past uniformity and continuity that is not demonstrated. For our part we infer from our discovery of core areas that the uniform continuous tropical forest is a phenomenon of the present and was not continuously true for Amazonia in the recent past. We have seen above that this inference is abundantly buttressed and sustained by independent evidence of very varied sorts.

It is implied by descriptive terms used that open formations are an impediment to the dispersal of shade-loving forest animals, and forests to that of sun-loving animals of open formations. It is true that for individual species (and individual animals) there may be greater tolerance of relatively unfavorable conditions than a simple-minded definition of the two contrasting ecological types appears to imply. There are unquestionably population pressures (and sometimes also characteristic dispersal phases in the life cycle) that induce individuals of a characteristic restricted ecology to cross unfavorable areas. There are, however, two points to be considered; (1) it is not required for the buildup of character complexes that gene flow be totally stopped, but only that it be diluted below a critical level; (2) for terrestrial animals unfavorable areas of any considerable extent are more severe blocks to dispersal than comparable sea barriers surrounding oceanic islands, since the latter may be bridged by passive dispersal, e.g. rafting, while on a continent an animal must disperse across the unfavorable area of its own motion and on its own energy, and on its own initiative.

In our own study the existence of core areas within a species implies for us cycles of species contraction and expansion. Since all the populations are conspecific, original genetic community is implied. The origin of the core areas marks a period of limitation of this genetic continuity by contraction into refugia. The present contact and interaction of core areas implies restoration of more complete genetic continuity.

A point to be emphasized is the speed with which the process that we envision has taken place. This is interesting not for itself alone but because the climatic cycles, on which we base everything else, are rapid in terms of the geological scale. In consequence, the relief of the continent will be changed very little during 2-3 successive cycles and refugia during dry phases would therefore occur in approximately or even exactly the same positions.

A population that has differentiated during one dry phase in a certain refugium will most probably be confined during the next dry phase to the same refugium. If the humid phase has not been too long, at the beginning of the second dry phase the refugium has already a differentiated population, not a random sample of the species. Very likely this population will continue differentiating at a fast rate.

A population in this situation is mathematically analogous to an insular population that receives mainland colonists from time to time.

In suggesting pulsations of species expansion and contraction this conception recalls Brown's (1957) central-peripheral speciation theory. From this our model differs in that the center is never a refuge, but there are only peripheral refugia. The central, and by far the largest, area, has here the specific and very important function of providing a site for extensive recombination, resulting in augmented variability. The vastness of the area favors mosaic differentiation, and so provides improved chances of differentiation in the next phase of isolation. This is in a way an application of the "founder principle" to large continuous continental areas. Doubtless there are cases in which the literal center of a species range is its optimum habitat, and certainly the literal edge of a species range is, from the very fact that it is the edge, relatively unstable and unfavorable. But too literal an interpretation of Brown's hypothesis in terms of "center" and "periphery" involves a false precision, as pointed out by Brown himself. Surely it is frequent for a species to have more than one optimum area and surely these occur wherever the accidents of geography and ecology require them to be. However, the role of areas of recombination should not be underestimated. In the specific case of the hylaea this may be a very important factor.

The refugia we postulate are in three of four cases orographic: in dry periods forests have persisted on certain mountain slopes. In the fourth case, the central-south Brasilian, especially favorable conditions for gallery forest may have been of importance. Thus the areas we identified by analysis of species characters turn out to be independently predictable on geomorphological and phytogeographic grounds.

The congruence of independent evidence is the strongest possible support for the reality of the model of tropical species differentiation that we propose. The very conditions that we require on the basis of knowledge of the internal structure of a species have in fact been asserted on totally different grounds by workers in quite disparate fields. The model we have chosen seems fully substantiated for the case for which we propose it.

THE ORIGIN OF TROPICAL DIVERSITY

The existence of high diversity in the tropics is undeniable, even though it varies immensely from group to group. How so many species may live together has lately been the subject of much, though not very fruitful, controversy. The problem of the origin of these numerous species has not had nearly the same attention. To say that tropical environments are favorable is merely to acknowledge that tropical forests have many more species of plants than temperate forests, but at the same time to ignore that the latter may be equivalent or richer in biomass.

Indeed, most authors have not even faced the problem of origin. It is difficult to see why this has been so. The origin of tropical species should, on its face, have much to do with their subsequent contact and interaction. An explanation of tropical diversity in terms of its origin ought therefore to be a prime current problem in evolution and ecology.

Perhaps the problem has been glossed over because of the emphasis of so many writers on the climatic uniformity and environmental constancy in the tropics. It is obviously not easy to propose a scheme by which static and unchanging conditions will produce complex tropical radiations. In fact if the dogma of tropical uniformity and stability were to be believed, it would seem almost necessary to invoke the justifiably unpopular conception of internal unselected propensity to change.

In actuality it is a major feature of the tropics, considered as a whole, that there may be very radical climatic changes within short distances. This is true not only with changes in altitude but, even in the lowlands, rain forest may rather abruptly adjoin desert or semidesert. The two largest of the world's rain forests, the Amazonian hylaea and the Congo forest, are each separated from adjacent forests by tongues of very arid country.

Such facts as these (and the islands of grassland with grassland animals *inside* the Amazonian forest) should demonstrate by themselves that the tropics are in no sense a unit region and that forest may be interrupted and invaded, that it is fragile. But the geomorphological evidence is more sweeping than this. When we read in Moreau (1966) that Kalahari sands underly a great part of the present African rain forest, we become aware that radical change and not stability is the reality. The less publicized South American data are not less positive in their documentation of periods of aridity that limited in extreme fashion the Amazonian hylaea.

The traditional conception of an *Urwald* — a very stable, very ancient forest evolving internally, affected little or not at all by the vicissitudes of the remainder of the world — has survived in spite of or in ignorance of the rising flood of evidence. It is, however, a myth, an idea that never had a substantive basis. It was at base a naive extrapolation from annual constancy in climate to eons-long stability.

With the disappearance of the myth of the Urwald the special conundrum that it seemed to pose disappears also. We do not require to invent new modes of speciation; we may instead work out the intricacies of tropical diversity in terms of mechanisms that we already know. The emphasis shifts from the origin to the maintenance of diversity, from history to ecology.

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GAZETTEER

In the following list of localities our basic reference is the Map of the Americas 1:1,000,000, of the American Geographical Society (from now on cited as the "AGS map") and its accompanying index. Recourse to this map and index permits an immediate identification of about 50% of the localities dealt with in a large scale project, which is amazingly good and a tremendous help.

For the localities mentioned in the index and shown in the map we give here the same citation as in the index: the number of the pertinent sheet, the nearest intersection of parallel and meridian, and a letter which places the locality with reference to the intersection: *a* to the NW, *b* to the NE, *c* to the SW and *d* to the SE.

Some localities are found in the map and not in the index, or vice-versa, or still are spelled differently in each; we note the cases that came to our attention.

Finally, for those localities not found in the AGS map the geographic position is given within brackets and we indicate the means by which they were identified: through the litterature, through colleagues (cited as *in litt.*), or through information contained in specimen labels. When the source of the information is not cited, it means that we are personally acquainted with it.

For all localities is given, within parentheses, the state, department, territory, or equivalent political division of the country.

The only exception is Ecuador: we use the old denomination "Napo-Pastaza", because we have not been able to obtain a map with the new political division.

We have kept as close as possible to the actual specimen labels, except in the case of very obvious and trivial misspellings. A small glossary of Portuguese and Spanish geographical terms precedes the gazetteer.

GLOSSARY

Alto (Sp., Port.). Upper. Usually refers to the upper course of a river, but frequently means the region through which it flows (e.g., Alto Purus, in Brasil).

Barra (Port.). Literally sand bar. By extension, the mouth of a river (e.g. Barra do Tapirapés, in Brasil).

Boca (Sp., Port.). Mouth of a river.

Caño (Sp.). Anything from a creek to a medium-sized river.

Cerro (Sp., Port.). An isolated mountain or well defined, short range of mountains with a prominent peak.

Chapada (Port.). A plateau, usually covered with cerrado.

Cocha (Sp.). Lake, pond. A Quechua work incorporated into the Spanish spoken in Peru, Ecuador and Colombia.

Finca (Sp.). Farm.
Hacienda (Sp.). Farm.
Igarapé (Port.). Creek. A Tupi word current in Amazonia.
Lagoa (Port.). Anything from a pond to a fair lake, communicating with a river (or the sea) or not. "Lago" (lake) is applied to very large bodies of water.
Loma (Sp.). Hills.
Paraná (Port.). An arm of a river embracing an island to one side of the main stream. A Tupi word current in Amazonia.
Pico (Sp., Port.). Peak.
Quebrada (Sp.). Gorge, usually containing a river.
Salto (Sp., Port.). Falls.
Serra (Port.), Sierra (Sp.). Mountains.
Yacu (Sp.). River. Quechua word current in Peruvian, Ecuadorian and Colombian Amazonia.

BOLIVIA

Buenavista (Santa Cruz). SE 20, 17-64d.
Reyes (Beni). SD 19, 14-67c.
San Javier (Beni). SD 20, 15-65b.
San Pedro (Beni). SD 20, 14-64d.
Sara, Prov. (Santa Cruz). SD 20, 16-64c.
Surutu, Rio (Beni). SE 20, 17-64d.

BRASIL

Alto Purus (Acre). [9-70c]. The region of the state of Acre, adjacent to Peru, through which flows the upper Purus.
Araçatuba (S. Paulo). SF 22, 21-50c.
Aruanã (Goiás). SD 22, 15-51c, under its old name of Leopoldina.
Barra do Tapirapés (Mato Grosso). SC 22, 11-51b, under the name Fecho do Tapirapés.
Belém (Pará). SA 22, 1-49d.
Belém, Igarapé (Amazonas). SA 19, 4-70b. In some Brasilian maps this creek appears as "Igarapé Preto".
Benjamin Constant (Amazonas). SB 19, 4-70c.
Bueno de Andrade (S. Paulo). [22-48a]. 15 km NNW of Araraquara.
Cachimbo (Pará). [9-55b]. Brasilian Air Force base in the Serra do Cachimbo, SW Pará. Shown in the "World Aeronautical Chart".
Cana Brava (Goiás). [14-47b]. A locality where the professional collector J. Blaser worked in the late twenties and early thirties. Near Nova Roma, on the Rio Paranã (Pinto, 1945).
Catrimani, Rio (Roraima). NA 20, 2-63b.
Chapada (Mato Grosso). SD 21, 15-56d. A locality on the Chapada dos Guimarães, North of Cuiabá (in the AGS map as Serra da Chapada).
Ducke, Reserva (Amazonas). [2-61c]. A forest reserve belonging to the Instituto Nacional de Pesquisas da Amazonia, on km 24 of the road from Manaus to Itacoatiara.

Equador. See Estirão do Equador.

Estirão do Equador (Amazonas). [4-70c]. Brasilian Army post on the lower Rio Javari (Faura Gaig, cap. 12).

Ibarra (S. Paulo). SF 22, 21-49c.

Itapiranga (Amazonas). [3-58a]. Town on the Paraná de Silves (SA 21, 3-58a).

Itapura (S. Paulo). SF 22, 21-51a.

Jacaré, Paraná do (Amazonas). [4-61b]. A long paraná on the right margin of the Amazonas, some 50 km below the mouth of the Purus.

Jaguara (Minas Gerais). SE 23, 19-44c.

Juruá, Rio (Amazonas). SB 19, 7-70b, as São Felippe. The specimens in the Museu de Zoologia da Universidade de S. Paulo labelled "Rio Juruá" were collected by E. Garbe in 1901-1902 around a locality then called São Felippe, later João Pessoa, and presently Eirunepé. (Pinto, 1945).

Loreto (Maranhão). SB 23, 7-45c.

Manaus (Amazonas or Pará). [4-58d]. Protestant mission on a tributary of the Maués-Açu, about 60 miles SE of Maués, on the Pará-Amazonas border (R. G. Zweifel, *in litt.*).

Maracá, Rio (Amapá). NA 22, 1-52d.

Maués (Amazonas). SA 21, 3-58d.

Mutum-paranã (Rondonia). A river. SC 20, 10-65b.

Navio, Serra do (Amapá). [1,52c]. This locality, an open-pit manganese mine, has been extensively collected in recent years.

Neblina, Serra or Pico da (Amazonas). [1-66c]. On the Brasil-Venezuela border, at the headwaters of the Rio Cauaburí.

Platon. See Porto Platon.

Porangatu (Goiás). [13-49c]. On the Belém-Brasilia highway, shown in the usual Brasilian maps under its old name of Descoberto.

Porto Platon (Amapá). [1-51c]. On the Rio Araguarí.

Porto Velho (Mato Grosso). [11-51b]. On the Rio Tapirapés, near Barra do Tapirapés (B. Malkin, *in litt.*).

Purus. See Alto Purus.

Ribeirão Azul (S. Paulo). [21-51a]. A Haseman locality not cited by Eigenman (1911), but unambiguously identified in Haseman's field notes for October 7, 1908, as "the present working terminus of the Noroeste do Brazil R. R. about 22 miles north east of Salto das Cruces of Rio Tietê" (transcribed by C. J. McCoy, Jr.). A locality on the railroad, 22 miles NE of "Salto das Cruzes" (Cachoeira das Cruzes) must be very close to the present Lussanvira. ("Lusanvira" in the AGS map).

São Paulo, Lagoa (S. Paulo). [22-52a]. A lake communicating with the Rio Paraná a little north of the city of Porto Epitacio.

S. Sebastião do Uatumã (Amazonas). [3-58b]. Town near the mouth of the Lago Uatumã, which is the lower course of the Rio Uatumã (SA 21, 2-59b).

Tapirapés. See Barra do Tapirapés.

Tapurucuara (Amazonas). SA 20, 0-65c, under its old name of Santa Isabel.

Tiriós (Pará). A Franciscan mission in the village of the Tirió Indians, about 2°N 56°W. In the AGS map (NA 21) Tiriós is misspelled "Trio".

Tucano, Rio (Amazonas). NA 19, 1-66c. A tributary of the Alto Cauaburí. (H. Reichardt, *in litt.*).

Uberlândia (Minas Gerais). SE 22, 19-48a.

Vista Alegre do Alto (S. Paulo). [21-49d]. 17 km NW of Monte Alto Paulista.

COLOMBIA

Acacias (Meta). NA 18, 4-74d.

Andagoya (Chocó). NB 18, 5-77b.

Apiay (Meta). [4-73b]. 78 km East of Villavicencio (F. Medem, *in litt.*).

Bogotá (Cundinamarca). NB 18, 5-74c.

Centro. See El Centro.

Cordillera de Bogotá (Cundinamarca). NB 18, 5-74c.

Cristo Rey, Loma de (Meta). [4-74b]. Suburb of Villavicencio (F. Mendem, *in litt.*).

El Centro (Santander). NB 18, 7-74d.

Florencia (Caquetá). NA 18, 2-76d.

Guadualito, Finca. [3-74a]. Rio Güejar, region of Serrania la Macarena (F. Medem, *in litt.*).

Güejar, Rio (Meta). NA 18, 3-74d.

Humbo (Boyacá). [6-74c]. Near Muzo (Nicéforo-Maria, *in litt.*).

La Mesa (Cundinamarca). NB 18, 5-74c.

Leticia (Amazonas). SB 19, 4-70d.

Mesa. See La Mesa.

Nariño. See Puerto Nariño.

Otanche (Boyacá). [6-74c]. In the Muzo district (Nicéforo-Maria, *in litt.*).

Puerto Lopez (Meta). NB 18, 4-73b.

Puerto Nariño (Amazonas). [4-70a]. On the Amazonas, some 80 km above Leticia (Nicéforo-Maria, *in litt.*).

Restrepo (Meta). NB 18, 4-74b.

Rosaleño (Meta). [4-73a]. "Between Vilavivencio and Caño Quenane, in the direction of Puerto Lopez, 28 km to the South of Villavicencio" (F. Medem, *in litt.*).

San José del Guaviare (Vaupés). NA 18, 3-73d.

San Lorenzo, Cerro (Magdalena). [11-74a]. Peak NW of Sierra Nevada de Santa Marta (Ruthven, 1922).

Santa Librada (Norte de Santander). [7-72a] On the extreme south of the state, southwest of Toledo (Nicéforo-Maria, *in litt.*).

Santa Teresita (Vichada). Not identified.

Sasaima (Cundinamarca). NB 18, 5-74c.

Tuña, Rio (Caquetá). [2-74c]. One of the headwaters of the Yari (F. Medem, *in litt.*).

Villavicencio (Meta). NB 18, 4-74b.

ECUADOR

Bobonaza, Rio (Napo-Pastaza). SA 18, 2-78b. Our Bobonaza specimens come from the Olalla farm between Sarayacu and Canelos.

Bufeo, Rio (Napo-Pastaza). [2-77b]. A tributary of the lower Bobonaza (G. Orcés V., *in litt.*). In the index to the AGS map there is mention of "Bujeo", with the same coordinates; the locality, however, is not shown on the map.

Canelos (Napo-Pastaza). SA 18, 2-78b.

Conambo (Napo-Pastaza). SA 18, 2-77a, b.

Churoayacu (Napo-Pastaza). [2-77b]. We have not found this locality, but the specimen label (from G. Orcés V.) reads "near Sarayacu, Rio Bobonaza".

Dureno. Not identified.

Limón Cocha (Napo-Pastaza). [0-77d]. On the Rio Napo, not far from the mouth of the Rio Jivino (G. Orcés V., *in litt.*).

Llushin, Rio (Santiago-Zamora). SA 17, 2-78a.

Loreto (Napo-Pastaza). SA 18, 1-77a.

Miazal (Napo-Pastaza). SA 18, 3-78b.

Misahualli, Rio (Napo-Pastaza). SA 18, 1-78b. Shown in the AGS map, but not listed in the index.

Napo. See Puerto Napo.

Palanda (Napo-Pastaza). [2-77a]. On the north bank of the Rio Bobonaza, not far from Teresa-Mamá (G. Orcés V., *in litt.*).

Puerto Napo (Napo-Pastaza). SA 18, 1-78d. In the AGS map as "Puerto Napo", in the index as "Napo" only.

Riobamba (Chimborazo). SA 17, 2-79b.

San José (Napo-Pastaza). SA 18, 1-78b, as Sumaco (= San José Viejo de Sumaco).

Santa Cecilia (Napo-Pastaza). [0-77a]. On the Rio Aguarico, a little above the mouth of the Rio Pushino (Fitch, 1968).

Sarayacu (Napo-Pastaza). SA 18, 2-78b.

Shiona-Yacu, Rio (Napo-Pastaza). SA 18, 2-77d. In the AGS map, but not in the index.

Tuvula. Not identified.

GUYANA

Akyma. NB 21, 6-58c.

Aremu River, or Arimu. Not mentioned as such in the index to the AGS map; however, in sheet NB 21 (6-59a) are found Little Arimu and Big Arimu.

Dunoon. NB 21, 6-58a.

Georgetown. NB 21, 7-58c.

Haul Over. [8-60b]. On the Aruau River (C. F. Walker, *in litt.*).

Kaburi River. NB 21, 6-59d.

Kamakusa. NB 21, 6-60d.

Kamarang River. NB 20, 6-61d.

Kamuni Creek. NB 21, 7-58c.

Kartabo. NB 21, 6-59b.
Kurupung River. NB 20, 6-60a.
Kuyuwini Landing. NA 21, 2-59c.
Machreba Falls (or Machripa). [6-60a]. We did not find this locality, but one specimen label says "on Kurupung River". Both spellings are found in the labels at hand.
Marudi River. NA 21, 2-59a.
Mazaruni River, Upper. NB 20, 6-60a.
New River. NA 21, 3-58d.
Onora. We haven't found this locality, but the collector's map, in the American Museum of Natural History, shows the collecting station of the dates of the pertinent specimens at 1° 35'N, 58° 30'W (R. G. Zweifel, *in litt.*).
Pickersgill. NB 21, 7-59b.
Shudikar-wau. NA 21, 1-59b.
Tukheit Hill. We haven't found a locality with exactly this name, but the specimen label further says "below Kaieteur Falls". In this position in the map (NB 21, 5-59a) we find "Tukeit Falls", which we take to be the locality.

FRENCH GUIANA

Cayenne. NB 22, 5-52c.
Mana. NB 22, 6-54d.
Matarony River. NB 22, 4-52a.
Sophie. [5-53c]. We haven't found this locality, but the specimen label says "South of St. Élie goldpit".

SURINAM

Brokopondo. [5-55a]. Near Boschland, ca 90 km South of Paramaribo, on the Surinam River (D. C. Geijskes, *in litt.*).
Gran Rio. NA 21, 4-56c.
Hanie. We haven't been able to find this locality. The specimen label reads "Gonini Exp.".
Kroetoe. NB 21, 4-56a.
La Haye, or Hague. NB 21, 6-56c.
Lucie encampment. On Lucie River. NA 21, 3-57a.
Moengo Tapoe. NB 21, 6-54c.
Nassau Mountains, or Gebergte. NB 21, 5-55d.
Paloemeu River, Upper. NA 21, 3-55a.
Paramaribo. NB 21, 6-55c.
Poeloegoedoe. NB 21, 4-54a.
Raleigh Falls. NB 21, 5-56c.
Tafel Berg. NA 21, 4-56c.
Tibiti. NB 21, 5-56b.

PARAGUAY

Centurión. SF 21, 22-53d.
San Luis (de la Sierra). SF 21, 22-57c.

PERU

Barranca (Loreto). SB 18, 5-77b.
Cenipa, Rio (Amazonas). SB 17, 5-78a.
Champuia, Igarapé (Loreto). [10-72d]. A tributary of the Upper Curanja, which is a tributary of the Upper Purus in Loreto, Peru, just across the Acre border. Shown in "World Aeronautical Chart".
Cushabatay, Rio (Loreto). SB 18, 7-75c.
Estirón (Loreto). [3-72d]. Near Pebas, some 30 km above the mouth of the Rio Ampiyacu (Faura Gaig, cap. 2).
Huallaga, Alto (Loreto). SB 18, 6-76b.
Iquitos (Loreto). SA 18, 4-73a.
Itaya, Rio (Loreto). SA 18, 4-73a.
Manayacu (Amazonas). [5-78a]. We haven't found this locality, but the specimen label reads "Rio Cenipa".
Nanay, Rio (Loreto). SA 18, 4-73a.
Nauta (Loreto). SB 18, 5-74b.
Pampa Hermosa (Loreto). SB 18, 7-75c.
Pebas (Loreto). SA 19, 3-72d, as Pevas.
Pedrera (Loreto). [7-75a]. The specimen label reads further "prov. Ucayali"; this indicates that the locality is in the district of Sarayaco (Stiglich, 1922).
Roaboya (Loreto). SB 18, 8-75b.
San Regis (Loreto). SB 18, 5-74b.
Santiago, Rio, mouth of (Amazonas). SA 17, 3-78a.
Tamaya, Rio (Loreto). SC 18, 9-74a.
Tapiche, Rio (Loreto). SB 18, 5-74d.
Yarinacocha (Loreto). [8-75d]. In the province of Ucayali, district of Masisea (Stiglich, 1922).

VENEZUELA

Agua Linda (Falcón). NC 19, 11-69d.
Arabopó, or Arabupu (Bolivar) NB 20, 5-61b.
Araurima (Falcón). NC 19, 11-69d.
Aroa (Yaracuy). NC 19, 10-69b.
Auyán-Tepui (Bolivar). NB 20, 6-63d.
Ayacucho (Táchira). NC 18, 8-72a.
Bejuma (Carabobo). NC 19, 10-68a.
Boquerón (Yaracuy). [10-69b]. 10 km northeast of Aroa (Williamson, 1923).
Canales. See Los Canales.
Caracas (Distrito Federal). NC 19, 11-67d.
Caripito (Monagas). NC 20, 10-63a.
Cariaquito (Sucre). NC 20, 11-62d. See Cariquito.
Cariquito. Type locality of *Anolis nitens bondi* Fowler. We find this spelling to be wrong; the locality is Cariaquito (q.v.) in the Peninsula of Paria (Stone, 1913).

Cocollar (Sucre). NC 20, 10-64b. Spelled "Cocoyar" in the AGS map and "Cocovar" in the index.
Cruz, Puerto de la. See Puerto de La Cruz.
Cuchivano (Sucre). [10-64b]. We haven't found this name, but the specimen label further reads "1 mi SW Cumanacoa".
Cuiguas. See Las Cuiguas.
Cumbre. See La Cumbre.
Duida, Cerro (Amazonas). NA 20, 3-66b.
El Limón (Distrito Federal). NC 19, 10-67a.
El Mene d'Acosta (Falcón). NC 19, 11-69b.
El Valle (Distrito Federal). [11-67d]. Near Caracas, to the south.
El Yaque (Sucre). NC 20, 10-64b.
Esmeralda (Amazonas). NA 20, 3-66b.
Fria. See La Fria.
Glycon Swamp (Bolivar). [5-61b]. The specimen label further reads "Mt. Roraima". Tate (1930) does not cite the name.
Guaira. See La Guaira.
Huá, Salto (Amazonas). NA 19, 1-66c.
La Cruz. See Puerto de La Cruz.
La Cumbre (Aragua). [10-68b]. We haven't found this locality. The specimen label reads "between Turiamo and junction with Maracay-Ocumare road, ca 390 m." This is in the Rancho Grande area.
La Fria (Táchira). NC 18, 8-82a.
La Guaira (Distrito Federal). NC 19, 11-67d.
Las Cuiguas or Las Quiguas or Las Quiggas (Carabobo). [10-68a]. Small locality in San Esteban (Williamson, 1923).
Latal (Sucre). [10-64b]. Locality between Cumanacoa and Cerro Turumiquire (M. G. Netting, *in litt.*).
La Victoria (Aragua). NC 19, 10-67a.
Limón. See El Limón.
Los Canales (Miranda). [11-67d]. We haven't found this locality, but the specimen label reads further: "Naiguatá".
Mene. See El Mene d'Acosta.
Naiguatá (Miranda). NC 19, 11-67d.
Naricual (Anzoátegui). NC 20, 10,65b.
Ocumare, Rio (Aragua). NC 19, 10-68b, as Ciénega de Ocumare.
Palma Sola (Falcón). NC 19, 11-69d.
Paují (Falcón). 11°01'N, 68°38'W (Rivero, 1961).
Pescada, Rio (Amazonas). [3-66b]. A tributary of the Orinoco in the Duida region (Tate & Hitchcock, 1930).
Pie del Cerro (Aragua). NC 18, 10-67a.
Puerto Ayacucho (Amazonas). NB 19, 6-68d.
Puerto Cabello (Carabobo). NC 19, 10-68a.
Puerto de la Cruz (Anzoátegui). NC 20, 10-65b.
Puerto de la Cruz (Distrito Federal). NC 19, 11-67c. Shown in the AGS map, but not listed in the index.
Quiguas. See Las Cuiguas.
Rancho Grande (Aragua). 80 km west of Caracas, 10°21'N, 67°41'W (Beebe & Crane, 1948. Text, Sexton & Heatwole, 1966).

Riecito (Falcón). [11-69d]. Locality close to Araurima (Basel Museum label).
San Esteban (Carabobo). NC 19, 10-68a. Near Puerto Cabello, to the south.
San Felix (Táchira). [8-72a]. Near Estación Táchira (C. F. Walker, *in litt.*).
San Rafael (Sucre). NC 20, 10-64b. Very close to Cumanacoa (Phelps & Phelps Jr. 1958).
Santa Lucia (Miranda). NC 19, 10-67b.
Santa Theresa, Hda. (Aragua). Not identified.
Sarare, Rio (Apure). NB 18, 7-72a. There are at least two localities with this name in Venezuela: one in Lara and this river in Apure. The collector of the present specimen was Geay, and thus the locality is the river Sarare (Pellegrin, 1899).
Siquire, Quebrada (Miranda). [10-67b]. We haven't found this locality, but the specimen label reads "11 km ENE" from Santa Lucia.
Summit Brook (Amazonas). [3-66b]. On Mount Duida (Tate & Hitchcock, 1930).
Tigre, Caño (Falcón). [11-69d]. We haven't found this locality, but the specimen label reads further "Agua Linda".
Torono-tepui (Bolivar). NB 20, 5-62b.
Tucacas (Falcón). NC 19, 11-68c.
Turiamo (Aragua). NC 19, 10-68b.
Turumiquire, Cerro (Sucre). NC 20, 10-64b.
Valle. See El Valle.
Vegas Falls (Amazonas). [3-66b]. On Cerro Duida (Tate & Hitchcock, 1930).
Victoria. See La Victoria.
Yacua (Sucre). NC 20, 11-62c.
Yaque. See El Yaque.