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THE SPECIES OF HISPANIOLAN GREEN ANOLES (SAURIA, IGUANIDAE)

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INTRODUCTION

Certain Hispaniolan anoles of moderate to small size are dwellers in the crowns of trees, green in color, almost without other color or pattern, with short legs and long heads, and with relatively uniform squamation. These seem to be a natural species-group and not an assemblage of forms convergently adapted to the tree-crown niche.

In many external details the Hispaniolan green anoles are strikingly similar; in most squamation characters the several species have overlapping variabilities, and there are only relatively few characters that assist in discriminating fully valid species.

DEFINITION OF THE HISPANIOLAN GREEN ANOLE SPECIES-GROUP

The nearly uniform green color and the tree-crown habitat provide the most immediate diagnostic features of this group. Coinciding with these are a number of morphological characters:

1. Head long ($> 20\%$ snout-vent length).
2. Legs short (80 - 120% head length).
3. Middorsal and flank scales smaller than ventrals, granular, subequal in size or very slightly and *gradually* enlarged in the middorsal line.
4. Ventral scales hexagonal to square, subimbricate or juxtaposed, smooth or weakly keeled but never mucronate.
5. Mental wider than long, 4 scales + 2 sublabials in contact with infralabials. Smallest anterior gular scales not smaller than $1/6$ first sublabial and usually larger.
6. Dewlap small or vestigial.
7. Lamellae under fourth toe always more than 20.
8. Tail round or trigonal, never distinctly compressed; 4-5 dorsal scales per verticil.

SPECIES DIFFERENCES

The green anoles of Hispaniola divide into two subgroups, each a superspecies with two species. The species of the first subgroup (*Anolis chlorocyanus* Duméril and Bibron 1837, and *A. coelestinus* Cope 1862) are widespread and very common in the lowlands and up to at least 1500 meters; those of the second subgroup (*Anolis aliniger* Mertens 1939, and *A. singularis* n. sp.) occur only at elevations well above sea level and appear always to be scarce. The species of subgroup 1 occur sympatrically with those of subgroup 2, but the species within each subgroup are primarily allopatric. The two wide-ranging species of the first subgroup show enough geographic variation to permit description of subspecies; the subspecies will not, however, be discussed in this paper, which is concerned solely with species differences.

In a majority of the characters in which anoles are distinguished by taxonomists, there is conspicuous overlap between these two subgroups and even more overlap between the species of a single subgroup. It is significant that, lacking the distributional evidence that is now available, Mertens (1939) described *aliniger* (of the second subgroup of my terminology) as a subspecies of *chlorocyanus* (of the first subgroup) and was not very sure (p. 62) that *coelestinus* was a species distinct from *chlorocyanus*.

Table 1 shows the extent of this overlap very strikingly. Though in the better represented species of the first subgroup there are evident differences in the means of the several numerical characters, it is quite as evident that there are individuals it would not be possible to place on these characters alone.

Tables 2 and 3 show the very few qualitative characters that seem useful in discriminating the species of Hispaniolan green anoles. Size also differs. *A. chlorocyanus* and *A. coelestinus* may exceed 70 mm in snout-vent length, *A. aliniger* and *A. singularis* do not reach much over 50 mm.

SUBGROUP 1: *A. CHLOROCYANUS* – *A. COELESTINUS*

These two species overlap very little geographically. One has a distribution north, the other south of the Cul de Sac trench (still partly below sea level) which formerly divided Hispaniola into northern and southern islands. At the southern edge of this trench, now dry and very arid land, there is contact and sporadic real sympatry, always it appears, with one species or the other predominating. The actual zone of contact has never been mapped and is known at the moment only from occasional transects. *A. coelestinus* occurs in Port-au-Prince and extends to Damien, but *A. chlorocyanus* occurs in the area too.

Even in this area of contact there is no indication of reinforcement of species differences in body squamation. There are only average differences in the size of the head scales which are reflected in counts of loreal rows, scales across snout, scales between interparietal and supraorbital semicircles, etc. However, the best differences between the two species are in body color (the presence in *coelestinus* of the labial white streak which is continued above the shoulder, and its absence in *chlorocyanus*), and in dewlap color and squamation (very large dewlap scales and black dewlap skin in *chlorocyanus*, small dewlap scales and relatively unpigmented skin in *coelestinus*) (Fig. 1). Thus, in color characters there is some evidence of reinforcement of species difference because of secondary contact.

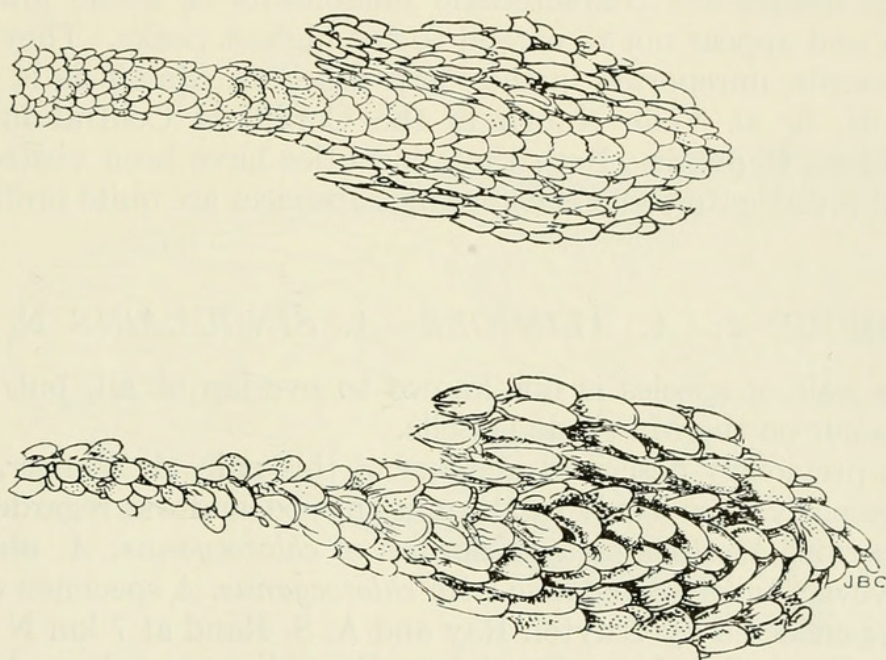


FIG. 1. Scales along edge of dewlap. Above: *Anolis coelestinus*, MCZ 64883, Ça-ira near Leogane, Haiti; below: *Anolis chlorocyanus*, MCZ 80719, Nan Palmiste, Gonave Island, Haiti. Drawn to the same scale; the specimens have the same snout-vent length.

Both body color and dewlap color differences, while they hold over most of the species ranges, are lost or weakened in populations of these species remote from the zone of contact. Thus the Isle Vache population of *coelestinus* lacks the white labial to shoulder streak of other *coelestinus* populations. At least preserved specimens of *coelestinus* remote from the Cul de Sac tend to show darker dewlap, occasionally almost to a degree that

would be confusing were not the dewlap scales consistently small.

In *chlorocyanus* also, geographic variation slightly weakens the diagnostic differences. The population described by Mertens from the vicinity of Santo Domingo City as *A. chlorocyanus cyanostictus* has reduced the black of the dewlap and exhibits a cadmium yellow basal spot.

However, both the Isle Vache population of *coelestinus* and the Santo Domingo City population of *chlorocyanus* are very small segments of the total range of these species. The non-distinctive segment of *coelestinus* is isolated on an island far to the west; the exact range of *chlorocyanus cyanostictus* is very limited and on present evidence very uncertain: typical *chlorocyanus* have been collected in Santo Domingo itself.

Both species are characteristic inhabitants of mesic lowland forests and appear not to extend to the highest peaks. They are, for example, unreported in the Forêt des Pins, Massif de la Selle in Haiti, or at Valle Nuevo in the Cordillera Central in the Dominican Republic. Both these localities have been visited by several investigators and the apparent absences are quite probably real.

SUBGROUP 2: *A. ALINIGER* – *A. SINGULARIS* N. SP.

This pair of species is not known to overlap at all, but they both occur on the Massif de la Selle.

The previously described member of this pair, *A. aliniger*, was until recently known only by the unique type, and was regarded by its describer Mertens as a subspecies of *chlorocyanus*. *A. aliniger* is, however, widely sympatric with *chlorocyanus*. A specimen of *A. aliniger* collected by Clayton Ray and A. S. Rand at 7 km N Carpintero Prov., San Juan, Dominican Republic, was collected on a tree ca. 45 meters from a specimen of *A. chlorocyanus* collected on a pole fence. The head scales of these two specimens are shown in Figure 2. In the Constanza area, La Vega Province, Dominican Republic, natives collecting for Juan Rivero brought in *A. aliniger* and *A. chlorocyanus* at the same time.

A. aliniger is one of the most peculiar of anoles, not indeed in general habitus which is that of a small and somewhat stockier version of *chlorocyanus* or *coelestinus*, but in the singular feature which gives it its name. This is the strange coloration of the axilla, bright orange or yellow followed by a larger or smaller spot of intense black. This is present in both sexes and very conspicuous in freshly preserved specimens, but the yellow or orange is, of course, quickly bleached out by alcohol. There is, however, an

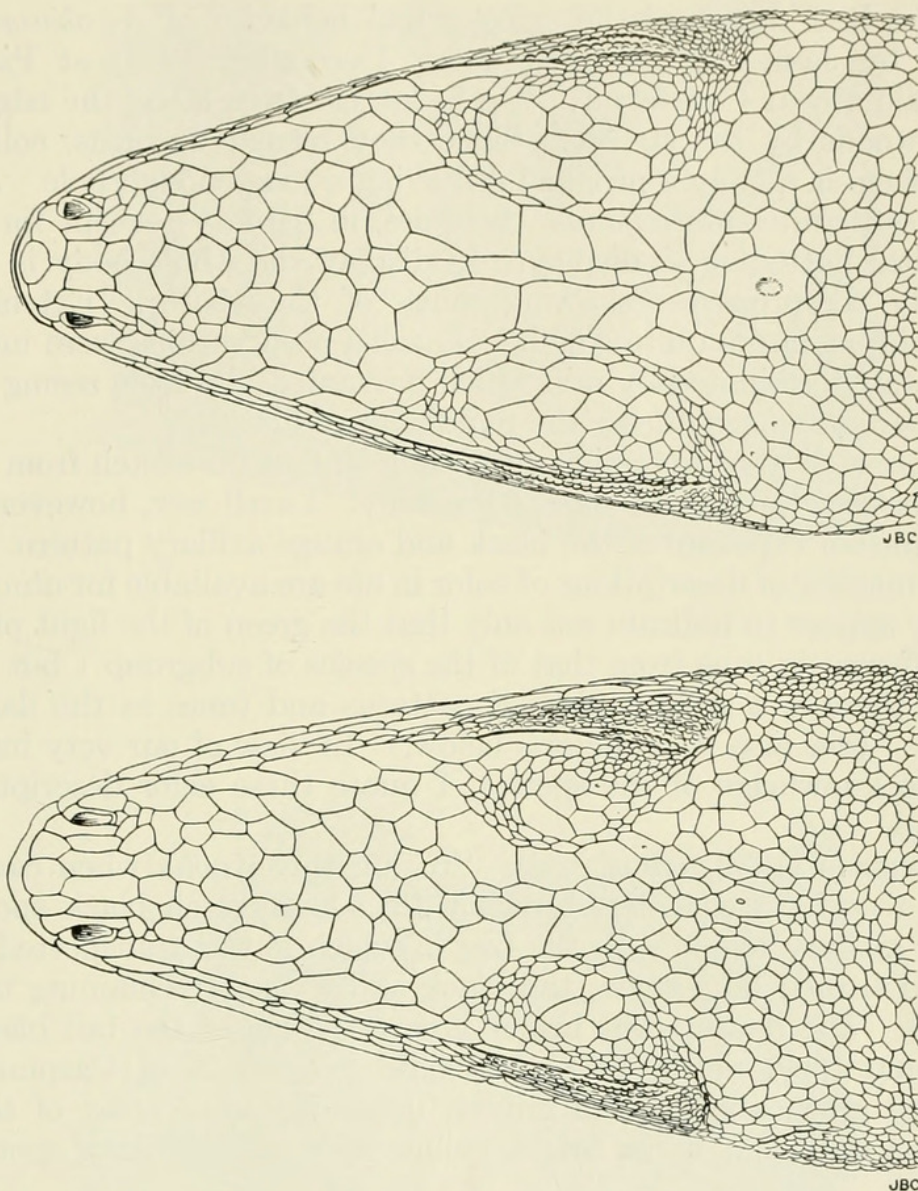


FIG. 2. Head squamation. Above: *A. aliniger*, MCZ 57463; below: *A. chlorocyanus*, MCZ 57473. Both specimens from 7 km N Carpintero, Prov. San Juan, Dominican Republic.

area of scaleless skin which represents the area formerly occupied by the orange spot (Fig. 3). Since the dewlap is hardly developed, almost non-functional, it is very possible that the orange, made more conspicuous by the black behind it, is a flash pattern used in some fashion in high intensity agonistic behavior. This is at present a mere suspicion; the only specimens of *aliniger* seen have been merely captured and preserved, or only very briefly observed.

The best report of the ecology and behavior of *A. aliniger* is that by James Lazell (field notes, December, 1963) at Paraje la Palma near Constanza: "Up in largish trees along the edge of the woods by the stream. Since they retreat upwards, collecting them is merely a problem of having a long enough pole. Just like *coelestinus-chlorocyanus*, therefore, in habits — except for the vertical flattening in display. In display the whole body is vertically compressed — showing much of the venter. Extended, the throat fan is quite small." Lazell's observations were unfortunately terminated by rain which prevented him from seeing any further specimens during the remainder of his stay.

The vertical compression, according to Lazell's sketch from life, emphasizes the yellow color of the belly. Lazell saw, however, no instance of exposure of the black and orange axillary pattern.

A number of descriptions of color in life are available for *aliniger*. They appear to indicate not only that the green of the light phase is different in tone from that of the species of subgroup 1 but also that there is a greater play of patterns and tones in the darker state. (See also *A. singularis* below.) In view of our very inadequate knowledge of the species, I quote these color descriptions in full.

Mertens (1939, translated): "In life this *Anolis* when caught was a uniform chocolate-brown with a large pitch black spot in each axillary region. In the bag in which it was transported the lizard turned blue-green, the black axillary spot remaining unaltered. The dewlap was bright green, the tip of the tail black."

Rand (field notes, 1958). Female — 7 km N of Carpintero: "Gray green above, head grayer, upper lip white, rear of thigh with a dark line, axilla bright yellow with smaller black spot behind it."

Lazell (field notes, 1963): "Duller and bluer green than *coelestinus-chlorocyanus*. Venter, throat fan and frosted spots on sides (especially shoulder region) bright saffron yellow. Orbital skin butter yellow. Axillary spot plain black.

"Changes, when unhappy, to lichenate frosted grey-brown with white. A pattern of large dark bilaterally arranged spots emerges with transverse bands — especially posteriorly. Loreals and irregular stripe through eye emerge slate blackish."

Schwartz (field notes, 1964). ASFS V 1625 — 12 km S of Cabrera de Loma: "Dorsal ground color blackish brown to olive with green sacral 'butterfly' marking and tail banded olive and cream. A white subocular mark. Ventral ground color dull greenish."

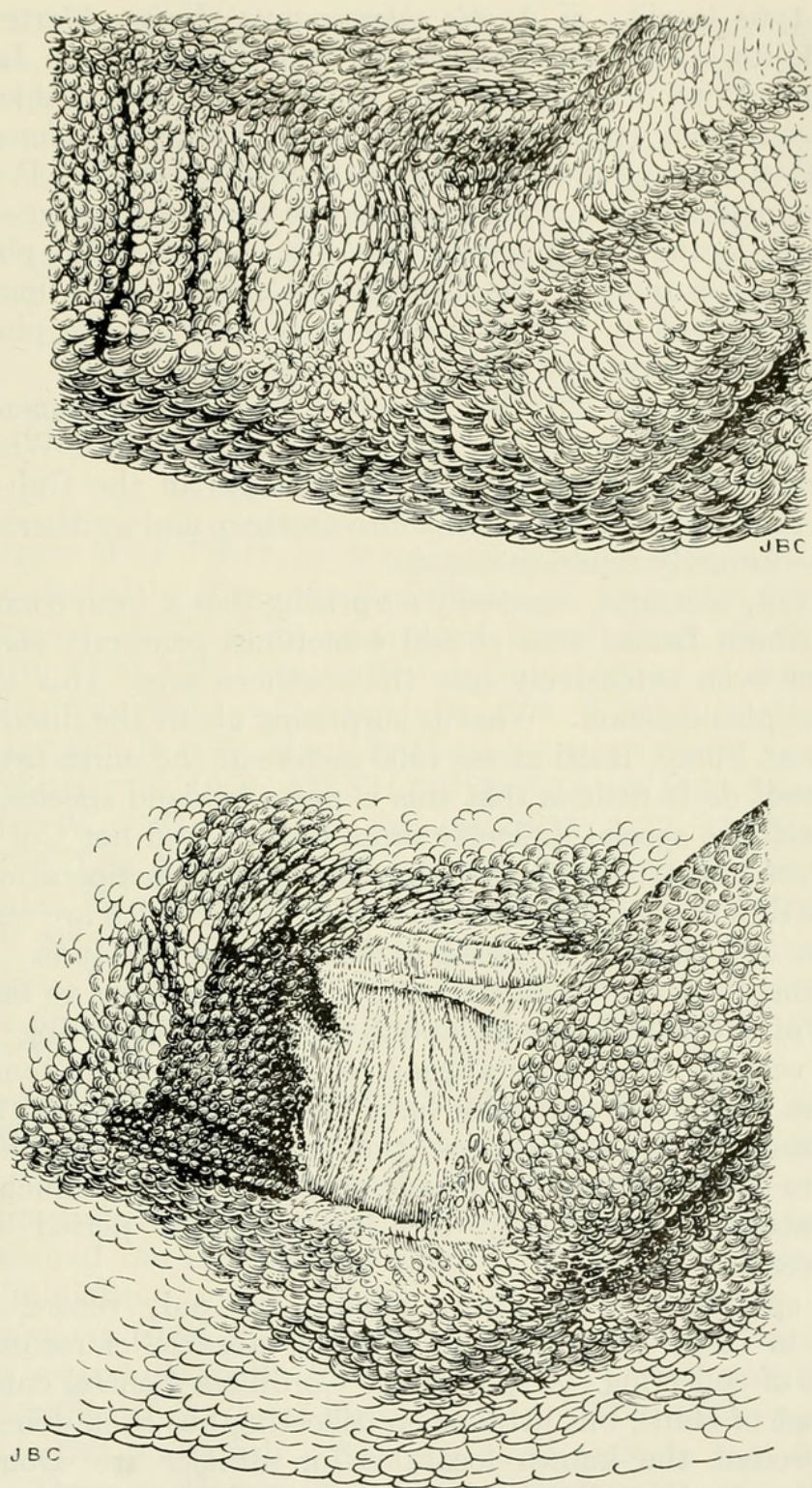


FIG. 3. Axillary squamation. Above: *A. chlorocyanus*, MCZ 57473, 7 km N Carpintero, Prov. San Juan, Dominican Republic; below: *A. aliniger*, MCZ 79341, Paraje La Palma, Municipio Constanza, Prov. La Vega, Dominican Republic.

The type locality of *Anolis chlorocyanus aliniger* Mertens was Paso Bajito on the northern rim of Valle Constanza in La Vega Province, Dominican Republic. Most of the recent specimens have been taken within that valley itself. However, a female has been taken in San Juan Province and a male in Dajabon Province. All specimens are from elevations near or above 600 meters.

These Dominican Republic localities appeared to place *A. aliniger* as an anole of the Cordillera Central or its immediate foothills, present at moderate elevations — within the pine zone — and widely sympatric with *A. chlorocyanus*.

It was with some surprise, therefore, that two specimens were found in a collection of *A. coelestinus* made by the Whiteman brothers at Furcy in Haiti. Furcy is south of the Cul de Sac trough that separates Hispaniola into northern and southern faunal areas — formerly separate islands.

It is not, of course, especially surprising that a form common in the northern faunal area should sometimes penetrate some distance or even extensively into the southern area. This seems a frequent phenomenon. What is surprising about the discovery of *aliniger* at Furcy, Haiti at ca. 1500 meters at the north margin of the Massif de la Selle is that this is not a lowland species, which could without special difficulty cross the dry and hot Cul de Sac Plain, but a creature of higher elevations, cooler temperatures and of quite different floral associations from those which are now seen in either the desertic or mesic habitats of the lowlands. Essentially, the discovery of *aliniger* at Furcy is analogous to finding a species of one island present on one cape of a neighboring island.

The ecology of *aliniger* appears to require that at some past time the Cul de Sac gap must have been climatically and floristically passable for the species: the passage from one montane island to the other must have been made at a time of much cooler temperatures — presumably the last cool-wet period of the Pleistocene.

The specimens from Furcy remain the only record of the species in Haiti. Doubtless in part this absence of record is an artifact of collecting. A spur of the Cordillera Central enters the northeast of Haiti, but little or no collecting has been done there.

At present the known localities for *aliniger* are: **Dominican Republic.** *La Vega Province.* Below Paso Bajito at about 900 m (type locality), Senckenberg 25825. Valle Constanza, MCZ 56912. Tireo near Constanza, MCZ 56913–15. Paraje La Palma, east of Constanza, MCZ 75140–41, 79341–43. El Rio, AMNH 44852–53. *San Juan Province.* Seven kilometers north of Carpintero,

MCZ 57463. *Dajabon Province*. Twelve kilometers south of Loma de Cabrera, ASFS V 1625. *Haiti. Departement de l'Ouest*. Furcy, MCZ 63444-45.

Over most of the southern island of Hispaniola — south of the Cul de Sac trough in both Haiti and Hispaniola — the absence of *aliniger* is plausibly accounted for by the presence of a closely related species — essentially *aliniger* without the axillary light and dark spots. This peculiar species is known from very few specimens, everyone of which is from a different locality. I have, therefore, called this new species by the Latin adjective which means "one at a time."

ANOLIS SINGULARIS new species

Holotype: MCZ 72043, adult male, Pourcine, Massif de la Hotte, Haiti, collected by François Vuilleumier, 31 December 1962.

Paratypes: MCZ 13778, La Gonave Island, Haiti, G. M. Allen coll. 1919; YPM 3229, Nan Cafe, La Gonave Island, P. Humphrey and Sarita Van Vleck coll., March 26, 1959; YPM 3194, Forêt des Pins, Massif de la Selle, Haiti, P. Humphrey and Sarita Van Vleck coll., February 19, 1959; AMNH 51728, Valle de Polo, Dominican Republic, W. G. Hassler coll., September 14, 1932; ASFS V 2608, 5 km NE Los Arroyos, 5800 feet (ca. 1750 meters) elevation, Pedernales, Dominican Republic, D. C. Leber coll., June 27, 1964; ASFS V 2985, 30 km N of Pedernales, 2680 feet (ca. 810 meters), Pedernales, Dominican Republic, hatched from an egg collected under a limestone rock in Cajetal, July 3, 1964, by R. Thomas; hatched July 16, 1964.

Diagnosis: An anole most closely allied to *A. aliniger* Mertens but differing in the absence of a scaleless, highly pigmented axillary area. Like *A. aliniger*, the new species differs from *A. chlorocyanus* and *A. coelestinus* in the greater enlargement of scales around the interparietal (Fig. 4), and in reduction of the dewlap in males.

Description: Head scales rather large, 6-8 scales across snout between second canthals. Frontal depression feeble, scales within it not smaller than those surrounding it. Five to seven scales border rostral posteriorly. Anterior nasal scale in contact with rostral. Three to four scales between supranasals.

Supraorbital semicircles separated by 1-2 scales, separated by one row of scales from supraocular disk. Seven to eleven smooth scales in the poorly defined supraocular disk which is separated from supraciliary by 2-3 rows of granular or sub-granular scales. One rather short supraciliary, flanked medially

by smaller scales and continued posteriorly by granules. Six to eight canthals, second and third largest, decreasing thence forward, anteriormost under rostral. Three to five loreal rows.

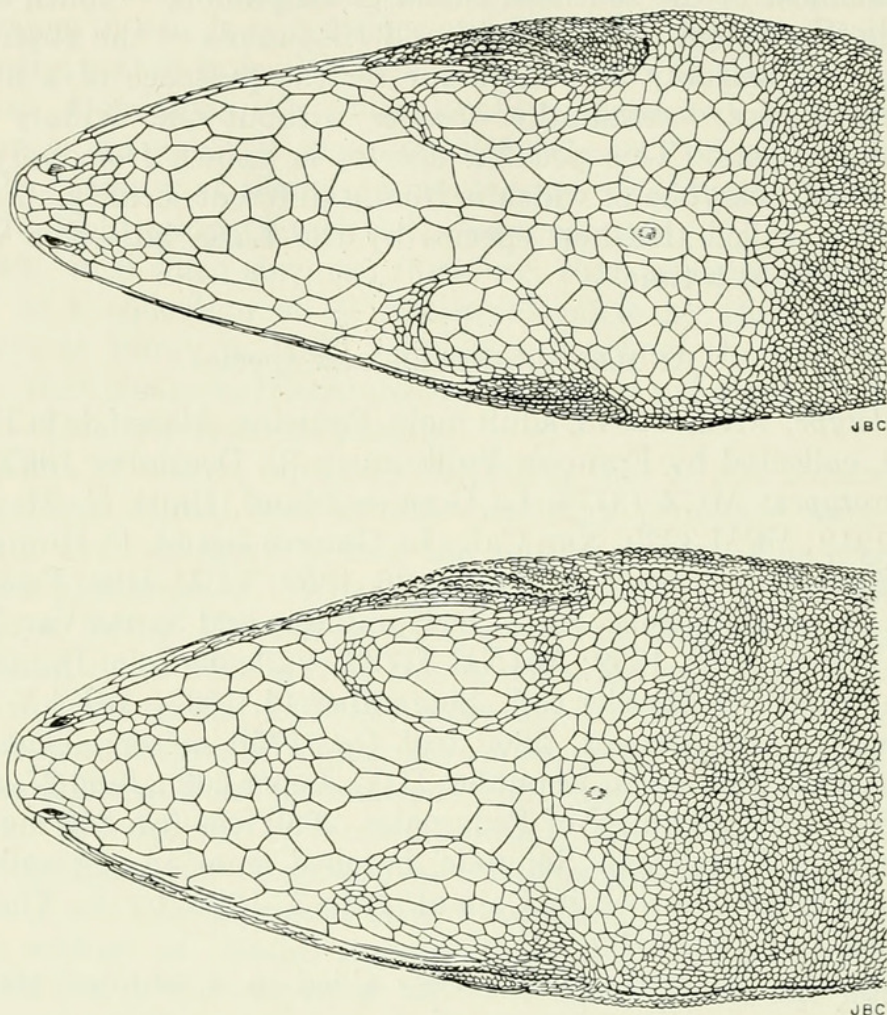


FIG. 4. Head squamation. Above: *A. singularis* Holotype, MCZ 72043; below: *A. coelestinus*, MCZ 74708. Both specimens from Pourcine, Massif de la Hotte, Haiti.

Temporal scales subgranular, smallest in center. A poorly defined intertemporal line. Supratemporals larger than temporals, increasing in size toward interparietal. Interparietal larger or slightly smaller than ear, separated from semicircles by 2-3 scales. Scales surrounding interparietal largest laterally but a very distinct zone of 5-6 rows of enlarged scales posterior to interparietal.

Suboculars broadly in contact with supralabials, anteriorly separated from canthal ridge by two scales, posteriorly merging into temporals. Seven to eight supralabials to center of eye.

Mentals broader than long, in contact posteriorly with 6-7 scales between infralabials (2 sublabials and 4-5 smaller scales); 5-7 sublabials in contact with infralabials. Central throat scales small, swollen, smooth.

Dewlap: Hardly differentiated, only indicated as a longitudinal fold; scales larger than throat scales, smaller than ventrals.

Trunk: Middorsals hardly enlarged, grading very gradually into flank granules. Axilla with normal granular scales. Ventrals larger, smooth, quadrate, juxtaposed, transverse. Postanals enlarged in male. Scales posterior to vent smooth.

Limbs: Largest forelimb scales smaller, largest hindlimb scales larger or smaller than ventrals, both weakly unicarinate. Supradigital scales smooth; 21-23 lamellae (27 in one hatchling) under phalanges ii and iii of fourth toe.

Tail: Verticils with four scales above, three below. Scales subequal.

Color in life: YPM 3194, Forêt des Pins, Haiti: Emerald green labials and limbs. Yellow eyelids, olive head and back, yellow green venter, last quarter of tail black with yellow tip.

YPM 3229, Nan Cafe, La Gonave Island, Haiti: Head silvery grey mottled with turquoise and brown, the latter extending to the shoulder. A brown spot just behind shoulder. Back silver gray mottled with turquoise. Tail and limbs very pale buff, tail banded with sky blue. Underparts pale turquoise becoming lemon on femora and at vent.

ASFS V 2608. 5 km NE Los Arroyos, Dominican Republic: Dorsal ground color gray to brown, a pattern of dark chevron-shaped middorsal blotches and smaller, roughly triangular lateral blotches. Light lateral stripes. Venter faint rust, speckled with greenish.

ASFS V 2985 (hatchling). 30 km N Pedernales, Dominican Republic: Dorsal ground color green with longitudinal darker stripes, especially middorsally.

Species status. On present evidence, *A. aliniger* and *A. singularis* are wholly allopatric. The question of species or subspecies status does therefore arise. My decision to describe *singularis* as a species is based upon two considerations: (1) a high valuation placed upon the axillary differences in pigmentation and squamation, which I assume to imply behavioral differences; (2) the presence of typical *aliniger* at Furcy appears to imply a capacity

to invade the territory of an allied taxon — a feature more probable for a species than a subspecies. Both these points require further elaboration.

(1) It is frequent in *Anolis* for the most conspicuous and taxonomically useful differences between very closely allied species to be in structures such as the dewlap that are involved in species recognition and intraspecies agonistic behavior. Thus, in subgroup 1 of the present paper, the southern island form *A. coelestinus* has a dewlap with pale skin and small scales while the northern island species *A. chlorocyanus* has a dewlap with pigmented skin and greatly enlarged scales. *A. semilineatus* and *A. olssoni* differ in an exactly similar way, *A. semilineatus* having the dewlap skin pale, the dewlap scales small, *A. olssoni* having pigmented dewlap skin and greatly enlarged dewlap scales. (In the latter case there are other strong differences.)

Dewlap color, however, does vary intraspecifically in *Anolis* (e.g. in *A. distichus*, *A. brevirostris*, *A. cybotes*) and sometimes individually, as, of course, body pattern may do also. To what extent such color variation disturbs species recognition is quite unknown, and equally unknown are any differences in display behavior between allied full species such as *A. coelestinus* and *A. chlorocyanus* or *A. semilineatus* and *A. olssoni*.

In the present case, I have chosen to infer that the orange axillary spot of *aliniger*, attended as it is by loss of normal squamation in that area and contrasted with the unmodified axilla of *singularis*, is comparable to the species recognition marks that distinguish species pairs and not to the simpler color variations that may occur intraspecifically.

(2) The species pair *A. coelestinus*-*A. chlorocyanus* may be the only instance in which the geographic boundary between species is exactly that area of the island which at one time, as an open seaway, divided Hispaniola into northern and southern parts. It is certain that this seaway has been profoundly important for origin of many widely distributed Hispaniolan species; Mertens (1939) early recognized its importance. (See also Williams, 1961.) But it is in fact very unusual for allied species which have originated north and south of this important zoogeographic boundary to be precisely limited by it now that the seaway has become dry land. The situation which I described in the species pair *A. semilineatus*-*A. olssoni* is commoner: one or the other or perhaps both members of the species pair interpenetrate the range of the other to a greater or lesser extent. Usually, it would appear, there is,

as in *A. semilineatus*-*A. olssoni*, sufficient ecological difference between the members of a species pair to permit this, but in the case of *A. coelestinus*-*A. chlorocyanus* the ecologies are too similar to permit anything but a stand-off, with a very narrow, perhaps fluctuating zone of sympatry.

The case of *A. aliniger*-*A. singularis*, which is surely another example of a northern island-southern island pair, differs from that of *A. coelestinus*-*A. chlorocyanus* in that these are inhabitants of cooler upland areas and should now be quite separated by the whole extent of the hot Cul de Sac Plain and by much of the mesic woodlands on either side. That any *A. aliniger* occurs on the south side of the Cul de Sac Plain indicates, as I have suggested above, the former existence of a zone of passage right across the Cul de Sac for species now characteristic of cool upland climates. At such a period *A. aliniger* invaded the southern island and may well have met *A. singularis*. If contact occurred, certainly no merging of populations resulted. The Furcy *aliniger* are quite unmodified, as typical as any from Valle Constanza. Perhaps there was a slight ecological difference with *A. singularis* living at higher elevations than *A. aliniger*. (The known true south island records of *A. singularis* would fit this pattern but the Gonave records would not.) Or perhaps *A. aliniger* displaced *A. singularis* in part of the latter's range.

Too little is known about either taxon to permit any but the most provisional hypothesis. It does, however, seem plausible to regard the invasion of the southern island by *aliniger*, without any indication of compromise of its characters, as evidence that it and *singularis* have indeed achieved species status and to infer that *A. aliniger* and *A. singularis* are, like *A. coelestinus*-*A. chlorocyanus*, too similar ecologically to occur together.

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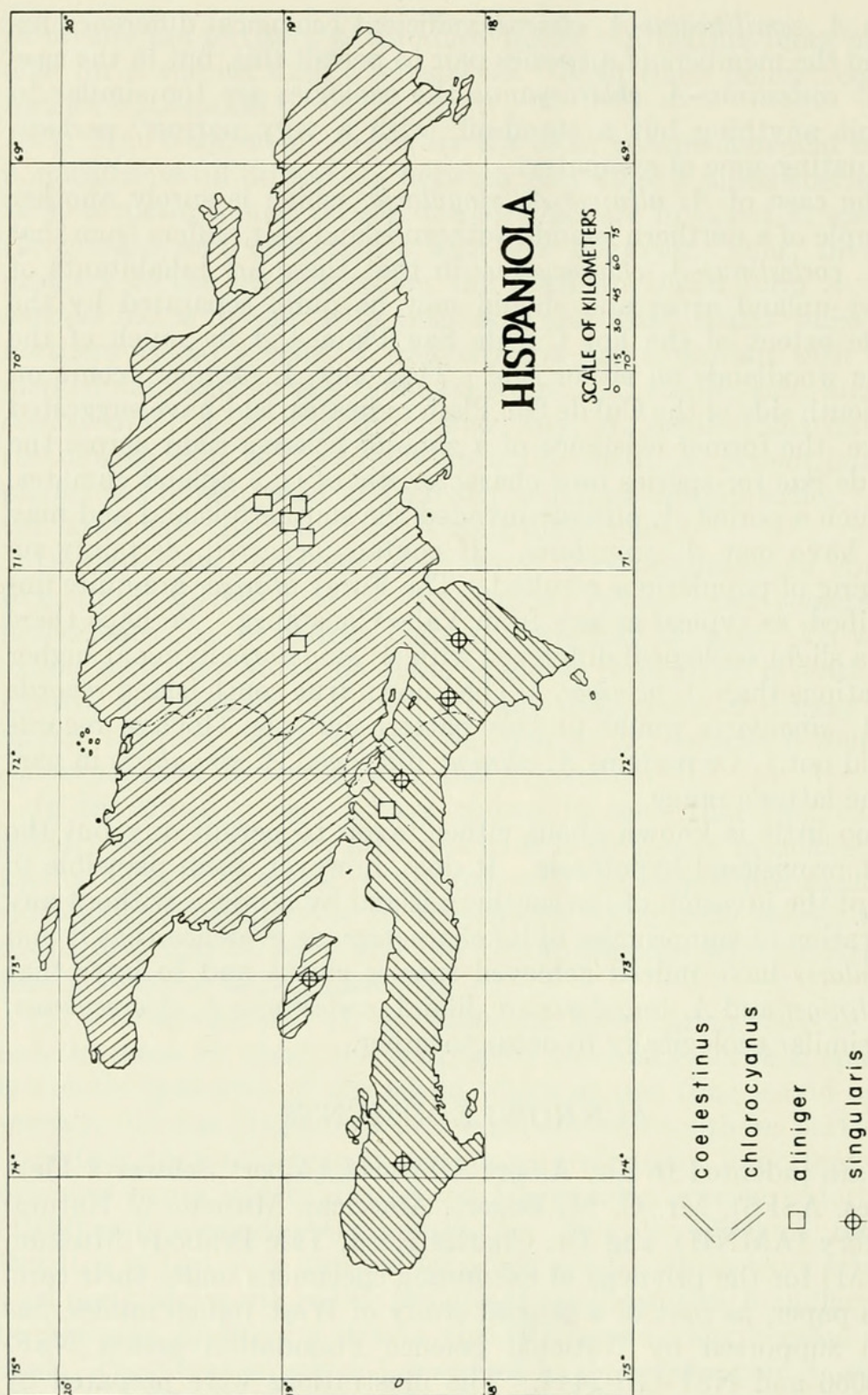


FIG. 5. Distribution of the Hispaniolan green anoles.

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(Received 10 May, 1965.)

TABLE 1.
Scale characters of the Hispaniolan green anoles

	<i>coelestinus</i>	<i>chlorocyanus</i>	<i>aliniger</i>	<i>singularis</i>
scales across snout	6-10	4-7	6-9	6-8
loreal rows	4-7	3-5	3-4	3-5
scales between supraorbital semicircles	1-3	0-2	0-1	1-2
scales between interparietal and semicircles	2-6	1-5	2-4	2-3
lamellae	23-32	27-34	21-24	21-23 ¹

¹ 27 in one hatchling, ASFS V 2985

TABLE 2.
Scale characters differentiating the Hispaniolan green anoles

<i>coelestinus</i>	<i>chlorocyanus</i>	<i>aliniger</i>	<i>singularis</i>
scales behind interparietal grading rather gradually into dorsal scales	as in <i>coelestinus</i>	Scales behind interparietal <i>not</i> grading into dorsals but several rows abruptly larger	as in <i>aliniger</i>
size of scales of dewlap <i>ca.</i> = ventrals	size of scales of dewlap > > ventrals	dewlap vestigial, size of scales of dewlap area < ventrals	as in <i>aliniger</i>
supradigital scales multicarinate	as in <i>coelestinus</i>	supradigital scales smooth	as in <i>aliniger</i>
axillary area with normal granular squamation	as in <i>coelestinus</i>	axillary area <i>without</i> granular scales	as in <i>coelestinus</i>

TABLE 3.

Color characters differentiating the Hispaniolan green anoles

<i>coelestinus</i>	<i>chlorocyanus</i>	<i>aliniger</i>	<i>singularis</i>
a white line on supralabials pro- duced posteriorly to above the shoulders (absent in Ile Vache popu- lation)	never any white markings on side of head or neck	as in <i>chlorocyanus</i>	as in <i>chlorocyanus</i>
axillary area with vertical black and light bars or unpatterned	as in <i>coelestinus</i>	axillary area with a light spot (orange in life) followed by an ink-black blotch of larger or smaller extent — both concealed by normal position of arm	as in <i>coelestinus</i>
dewlap scales blue, skin olive-gray	dewlap scales white to blue, skin with black or (<i>cyanostictus</i>) cadmium yellow basal spot	dewlap skin and scales greenish	as in <i>aliniger</i>



Williams, Ernest E. 1965. "The species of Hispaniolan green anoles (Sauria, Iguanidae)." *Breviora* 227, 1–16.

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