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ANOLIS INSOLITUS, A NEW DWARF ANOLE OF ZOOGEOGRAPHIC IMPORTANCE FROM THE MOUNTAINS OF THE DOMINICAN REPUBLIC

Ernest E. Williams

and

A. Stanley Rand [1]

ABSTRACT: *Anolis insolitus,* a new dwarf species occurring in the Cordillera Central of the Dominican Republic, is closely related to both *A. occultus* known from several montane localities in Puerto Rico and *A. darlingtoni* of the Massif de la Hotte in Haiti, but is closer to *A. darlingtoni,* a much larger species. The three species are basal members of the *carolinensis* group (*sensu lato*) in the West Indies, of which *A. occultus* is the most primitive known member.

INTRODUCTION

In the spring of 1963, the Museum of Comparative Zoology received from the Cordillera Central of the Dominican Republic a single small anole that was immediately recognized by E. E. Williams and by James D. Lazell, Jr., as a very distinctive and important new species. Even at that time the name *insolitus* — "strange or unusual" — was chosen for it.

Because, however, the new species was represented by a single specimen, its description was delayed, to wait upon more material. An attempt by Lazell, during the last week of December of 1963 and the first week of January 1964, to collect at the exact locality where the first specimen was taken failed because of bad weather.

Not until late summer of 1968 did E. E. Williams and A. S. Rand succeed in visiting the pertinent locality and in collecting a small series that fully confirms the "unusual" nature of the animal,

[1] Smithsonian Tropical Research Institute, Balboa, Canal Zone.

which also turns out to be of considerable phyletic and zoogeographic significance, its external indications of relationship verified by an osteological investigation made by Richard Etheridge (pers. comm.):

ANOLIS INSOLITUS n. sp.

Type. MCZ 60144, Paraje La Palma, Sección La Palma, Municipio Constanza, Provincia La Vega, República Dominicana, C. E. Ray and R. R. Allen coll. 19 March 1963.

Paratypes. (Same locality as type) MCZ 107014-18, A. S. Rand and E. E. Williams coll. 30-31 July 1968. (MCZ 107015 skeletonized, MCZ 107017-18 used unsuccessfully for chromosome study.)

Diagnosis. A dwarf anole related on the one hand to *A. darlingtoni* Cochran of southwest Haiti, from which it differs in size and in several features related to size, e.g. lamellae under fourth toe), and on the other to *A. occultus* of the mountains of Puerto Rico (which it resembles in size but from which it differs especially in

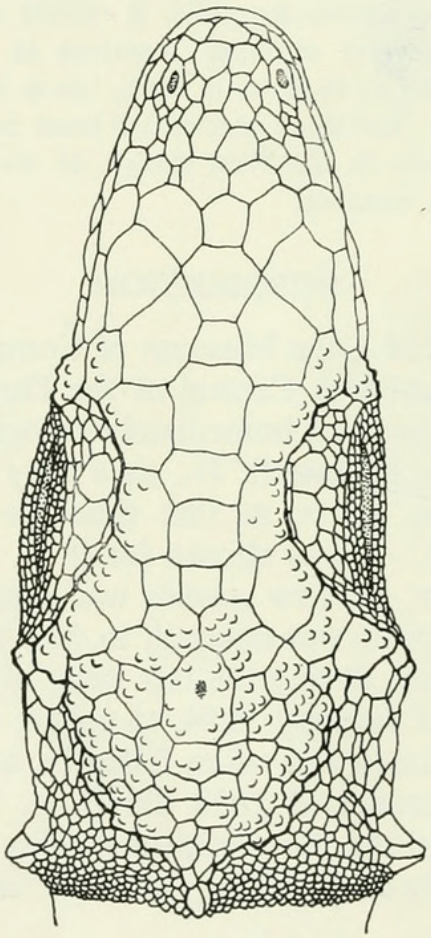

Fig. 1. *Anolis insolitus,* Type, MCZ 60144: dorsal view of head.

the much larger head scales). The new species differs from all known species of *Anolis* in the presence of small but distinct postorbital, supratemporal, and occipital spines, bony in nature and especially prominent in males (Fig. 1).

Description. Head: Narrow, elongate. Head scales large, smooth, smallest at tip of snout, three scales across snout between large second canthals. Nostril oval, nasal scale separated from rostral by a single oval scale. Rostral scale wide, low, in contact with five scales posteriorly.

Supraorbital semicircles large, weakly convex, rugose laterally, separated by a single row of scales as large or larger. A much less distinct row of seven large oval granules or scales on each side at the supraciliary margin, no elongate supraciliary. Posterior and internal to the supraciliary row, some smaller granules or scales. A single scale raised into a spine just beyond these smaller granules at the posterior end of each supraorbital semicircle. An elongate supraocular disk of ca. six to nine enlarged scales, two of them about one-third to one-half the size of the scales of the semicircles. Canthal ridge of six scales well defined, second canthal scale largest, diminishing in size anteriorly, anteriormost below nostril. Loreal rows three with some irregularity in size. A distinct supratemporal line of four to five enlarged scales, the fourth replaced by a spine. Temporal scales small, smallest at center, flat. Supratemporal scales above supratemporal line becoming larger toward a ridge of protuberant — almost spiny in ♂ — scales forming a U-shaped crest behind the interparietal region, in ♂ with a larger spine at base of U. Interparietal ovoid, much larger than the ear opening, separated by one flat scale on each side from the supraorbital semicircles. Scales surrounding interparietal large, flat, with some tubercles in ♂ (tubercles also on surrounding scales in ♂). Ear small, subround, placed far ventrally, directly behind the comissure of the mouth.

Suboculars in contact with supralabials, anteriorly grading into loreals, posteriorly grading into temporals. Seven supralabials to center of eye.

Mental large, semidivided, wider than deep, in contact with four granules between the infralabials. Two large infralabials on each side in contact with sublabials. Throat scales granular, smooth.

Trunk. Dorsal scales granular, smooth, subequal on flanks and middorsum except for a crest of small, triangular, swollen scales continuing middorsally from the U-shaped crest behind the interparietal to a point a little behind the insertion of the forelimbs.

Ventrals larger than dorsals, smooth, round, in transverse rows.

Gular fan. Moderately large; present in both sexes and well developed even in juveniles, lateral margins slightly inset, scales granular, smaller than throat scales, much smaller than ventrals; lateral scales about as large as edge scales in well-separated rows (♀) or less well-defined rows (♂).

Limbs and digits. Limbs short, tibial length ca = distance tip of snout to middle of eye. Fifteen to sixteen lamellae under phalanges ii and iii of fourth toe. Scales of limbs smooth, those of anterior thigh larger than those of ventrals. Supradigital scales smooth.

Tail. Round, with a distinct dorsal crest of a median row of enlarged, keeled scales, interrupted at intervals of two to four scales by paired paramedial scales, usually the most distal scale in any small series largest but with some irregularities. No enlarged postanals, but scales nearest vent larger in ♂ than ♀. Scales behind vent and round base of tail smooth, grading into keeled scales distally. Four ventral rows distinctly enlarged.

Color in life. The general body color is greenish or grey-brown, mottled, lichenate, with the dewlap, present in both sexes, blue-grey in front, orange behind. Detailed notes on two specimens follow: (1) ♀. Dull green with a dark grey middorsal zone enclosing a series of dark grey spots. Traces of a sacral butterfly pattern overlying a dull orange sacral spot. Blurred barring on tail, barring hardly visible on limbs. A light yellow streak under eye; reddish color on upper eyelid. Faint indication of a light streak from ear to arm. Flanks mottled. Dewlap blue-grey anteriorly, dull orange posteriorly, crossed by rows of white scales. (2) ♂. Dark butterfly-shaped blotches dorsally, less distinct on sides. One such blotch above shoulders, two on back, and one on sacrum. The sacral blotch crossed by a light orange spot. Tail and limbs crossbarred. A light yellow streak under eye; skin around eye reddish. A curved yellow streak from above ear to above base of arm. Sides and belly lightish cream, lightly speckled laterally with brown. Dewlap as above.

Field observations. (Compare with observations on *A. occultus* by Webster, 1969). Four of five specimens were caught asleep. One adult was taken about six feet from the ground on a broad, nearly horizontal leaf of a bush, its head facing toward the stem. Two other adults were found eight to ten feet apart, sleeping along slender, nearly horizontal twigs of bushes. One was about four and the other about five feet above the ground. Two juveniles were found at the edge of the forest about 15 feet apart, sleeping

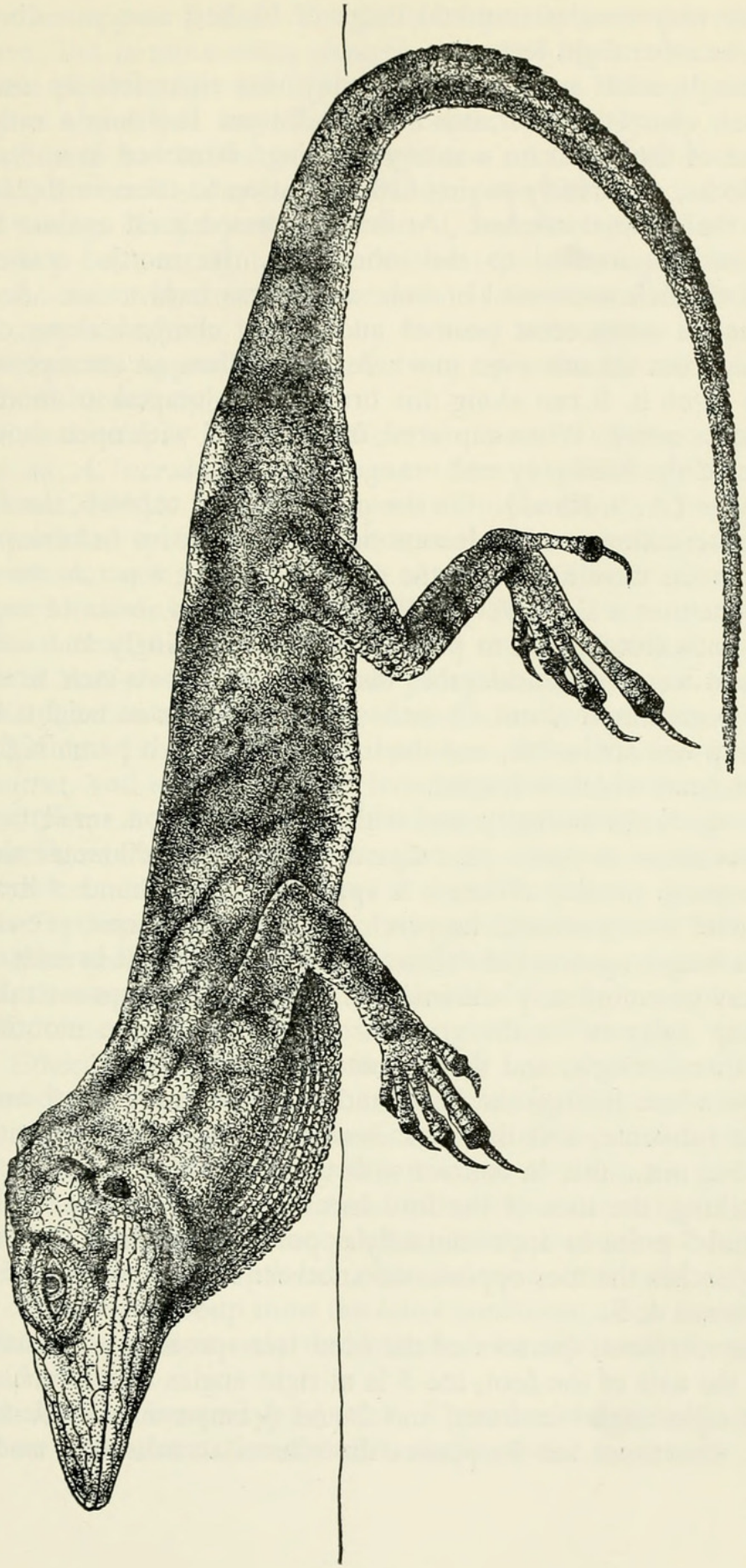

Fig. 2. *Anolis insolitus*, Type, MCZ 60144: lateral view.

along the very slender terminal twigs of bushes; one was about six and the other eight feet up.

The single adult seen during the day was eight feet up on a horizontal, quarter-inch branch of a small tree. It was in a rather open part of the forest on a sunny morning. It moved in and out of sun flecks, apparently paying little attention to them in the few minutes that it was watched. At first it pressed itself against the branch and squirrelled to the other side. Its mottled pattern matched the lichen-covered branch, and it was hard to see. Soon it resumed a more erect posture and slowly climbed along one branch and out on one even more slender. When an attempt was made to catch it, it ran along this branch and jumped to another a few inches away. When captured, it threatened with open mouth and erected the blue-grey and orange dewlap.

Behavior (A. S. Rand). On the morning after capture, the following observations on the locomotion and defensive behavior of two specimens were made: on the ground or along a perch, movement was either a slow, very deliberate walk or a series of rapid hops. Jumps from perch to perch were made willingly and accurately, and were of considerable distances for a two-inch lizard. One jump measured about 12 inches with little loss in height; another jump was six inches, and the lizard landed on a perch higher than that from which it started.

A lizard climbs willingly and without difficulty on small twigs but seems more at home on twigs of about body diameter than on those much smaller. When it is approached by a hand, a lizard will squirrel slowly around its perch, even a slender one, pressing its whole length against the substrate. On a horizontal branch the lizard may go completely underneath. Very closely approached, it may jump away or to the ground. When seized, the mouth is opened threateningly, and there is an attempt to bite.

Except when hiding, the head and shoulders are raised away from the substrate, and the neck is straight, whereas the vent is almost, but not quite, in contact with the substrate.

In walking, the toes of the fore feet are spread widely so that toes 1 and 5 point in approximately opposite directions. On very slender perches the toes oppose one another: 1, 2 versus 3, 4, 5 or 1, 2, 3 versus 4, 5.

On flat surfaces, the toes of the hind feet spread so that toe 4 extends the axis of the foot, toe 5 is at right angles to this behind, toe 1 at right angles in front, and 2 and 3 between. On slender perches, sometimes toe 5 opposes the others, sometimes 1 and 5

together oppose 2, 3, 4. The tail is frequently carried in an upright curve, but is more often straight and rests against the substrate. While climbing, the tail is frequently used as a sliding hook. Usually at about half way along its length, the tail hooks in a semicircle over and behind some projection. As the lizard moves forward, the hook slides backwards along the tail until the tip of the tail reaches the projection, crosses it, and drops off. The tail may be used on a straight branch without projections by being bent to one side and around the branch. If the branch is shaken, the tail may strengthen its hold by forming a complete loop around the branch. Apparently only the very tip is flexible enough to grip a small branch tightly.

Relationships. Anolis insolitus is almost as distinct in Hispaniola as *A. occultus* is in *Puerto Rico* (Williams, Rivero, and Thomas, 1965): it is quite impossible to confuse it with any other Hispaniolan species. However, it does have resemblances in two directions, with *A. darlingtoni* of western Hispaniola and with *A. occultus* of the mountains of Puerto Rico. These resemblances indicate that it is an annectant rather than an isolated form.

It is best placed in its proper group on osteological characters. Table 1 records the pertinent comparisons (information provided by Richard Etheridge — pers. comm. — from X-rays of *occultus, insolitus,* and *darlingtoni* and from dry skeletons of *occultus* and *insolitus*). According to the informal groupings suggested by Etheridge (1960), *A. occultus* emerges as a very primitive (and somewhat aberrant) member of the *carolinensis* group (those with "T-shaped" interclavicles; compare Etheridge's 1960, fig. 4) of alpha anoles (those without caudal transverse processes) . The primitiveness of *occultus* is manifested by a high number of attached inscriptional ribs ("parasternals" of Etheridge 1960, but see Etheridge 1965). *A. darlingtoni* is a somewhat less primitive member of the same group (fewer attached inscriptional ribs), but is peculiar in the specialized character of non-autotomic caudal vertebrae. *A insolitus* is again a member of the same group, but, like *A. darlingtoni,* is specialized in having non-autotomic caudals; it is, however, more advanced than *A. darlingtoni* in having only three attached inscriptional ribs and one free one. (Most of the *carolinensis* group show the latter condition; a few are still more advanced and have only two attached inscriptional ribs and two free.)

A. insolitus has pterygoid teeth. These are absent in *A. occultus,* and we lack information about *A. darlingtoni.*

The occurrence of pterygoid teeth (primitive for lizards in general) in *Anolis* is somewhat erratic. They are usually absent in dwarf species. At least in the West Indies, however, they are frequently present in the more primitive members of any group. In the *carolinensis* group, their presence can be verified in *A. chlorocyanus, A. coelestinus, A. aliniger, A. equestris, A. allisoni,* and *A. carolinensis* among the more primitive species, and in *A. lucius* among more specialized forms. The presence of pterygoid teeth in *A. insolitus* is presumably to be regarded as primitive and is so recorded in Table 1.

A. darlingtoni and *A. insolitus* are unique among Hispaniolan anoles in having non-autotomic caudals, and, indeed, are the only West Indian members of the genus *Anolis* that lack tail autotomy. (*Chamaeleolis* and *Chamaelinorops,* the only other West Indian anoles to lack tail autotomy, are very distinct genera.) Though loss of autotomy has occurred several times in anoles, its occurrence in the West Indies only in two species on one island suggests affinity; it does not, of course, demonstrate it.

The enlarged plate-like head scales of *A. insolitus* and *A. darlingtoni* (compare Fig. 3 and Fig 2) provide the most obvious external resemblance between the two species. This character, however, is not unique to these species even within the West Indies. In fact, *A. darlingtoni* and *A. valencienni* were formerly united in the genus *Xiphocercus* solely on the basis of similar large plate-like head scales. *A. darlingtoni* and *valencienni,* however, belong to

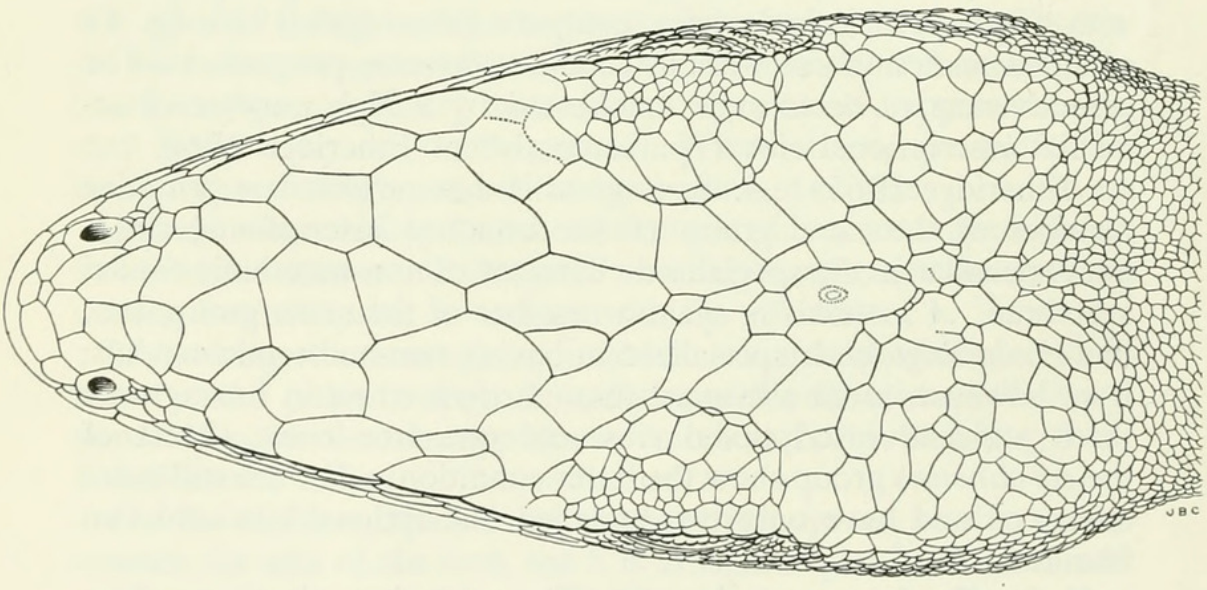

Fig. 3. *Anolis darlingtoni,* MCZ 38251: dorsal view of head.

two different sections of the genus *Anolis* as analyzed by Etheridge (1960), alpha and beta respectively, and the character of plate-like head scales is now recognized as having arisen many times within the anoles. Again, therefore, this resemblance is not proof of affinity between *darlingtoni* and *insolitus,* but the presence of so special a character in two species of one island is suggestive.

It would be a possible argument against the close affinity of the two species that *darlingtoni* (72 mm) is approximately twice the snout-vent length of *insolitus* (33 mm). Differences in size between closely related species, particularly if they are sympatric, are not unusual, but as far as is known, these two species are widely allopatric, and the size difference is extreme.

However, a number of external characters suggest not only an affinity between *darlingtoni* and *insolitus* but also suggest relationships with *occultus:* (1) the simple annular nasal scale separated by one round scale from the rostral (=prenasal not fused with nasal); (2) the small, round, ventrally-placed ear; (3) the long head and short limbs; (4) the low number of loreal rows; (5) the smooth ventrals.

Table 2 lists not only those characters in which all three species are similar but also all other pertinent external characters. The significant resemblances between any two or among all three species are italicized. It is easily seen that *insolitus* occupies a key position. In many critical and sometimes quite special characters (e.g. absence of an elongate supraciliary scale; presence of a *slotted* gular fan in both sexes), *insolitus* resembles sometimes *darlingtoni,* sometimes *occultus.*

It is clear, of course, that *insolitus* is not just an intermediate between the two species. It has very striking specializations of its own. The small spines and rugosites on the head are the most remarkable feature; these are as visible on the skull as they are externally. The crest of enlarged scales on the nape and the peculiar tail crest are almost as singular. In another regard, *insolitus* is not intermediate; the inscriptional ribs show a condition more advanced than that shown by either *occultus* or *darlingtoni.* However, such a complex of primitive and advanced adaptations is just what we should expect of the surviving representative of the stock that was at one time intermediate between the ancestral grade now represented by *occultus* and the more advanced grades represented by *darlingtoni* and by other still more advanced members of the *carolinensis* group. The importance of *insolitus* as an annectant form phyletically and zoogeographically is not diminished by admission of its specializations.

Figure 6 shows the known localities for *A. darlingtoni* (still known only from the unique type from Roche Croix, Massif de la Selle, Haiti) and *A. insolitus* (known now from six specimens from La Palma in the Cordillera Central of the Dominican Republic). Such a map reflects more ignorance than knowledge. Though Hispaniola has recently been assiduously collected, it is obvious that the fund of new information and of new taxa is not nearly exhausted, and the need for further collection and study is abundantly clear. The genus *Anolis* is only one fraction — even though an important one — of the herpetofauna of Hispaniola. The current count of species (including *insolitus*) is 21. Of these, no less than seven have been described in the last ten years (*christophei* Williams; *koopmani* Rand; *cochranae* Williams and Rand; *whitemani* Williams; *singularis* Williams; *rimarum* Thomas and Schwartz; *insolitus* Williams and Rand). In Table 3 we list the known species with comment on degrees of distinctness and on geographic variation (the latter may in some cases conceal valid species). We confess to a lack of belief that the list is complete. An asterisk marks those species that are especially inadequately known.

Certainly the most plausible assumption based on current evidence is that *darlingtoni* and *insolitus* are geographic representatives — south island and north island respectively — of one stock. This assumption, however, leaves the extreme size disparity of these allopatric species without easy explanation. A discussion of this point and of the possible history of Hispaniolan anoles is deferred to a future paper.

A. darlingtoni has not previously been adequately figured. Cochran (1941, pl. 11) provided only a photograph, which showed little more than general shape. Figures 3 and 4 permit comparison with the similar figures of *A. insolitus*.

Figure 5 diagrams the probable relationship of *A. insolitus* within the *carolinensis* subsection of alpha *Anolis*. It and *A. darlingtoni* appear to be the earliest radiation of this stock within Hispaniola. Three further radiations have occurred within Hispaniola, one of these, that of the Hispaniolan grass anoles, being the result of a back invasion from the complex radiation of the *carolinensis* group in Cuba (Williams, 1961).

ACKNOWLEDGMENTS

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Fig. 4. *Anolis darlingtoni*, MCZ 38251: lateral view.

TABLE 1

	occultus	*insolitus*	*darlingtoni*
angular	absent (SPECIALIZED)	same	? same
splenial	absent (SPECIALIZED)	same	? same
pterygoid teeth	absent (SPECIALIZED)	present	?
interclavicle	T-shaped (SPECIALIZED)	same	same
inscriptional chevrons	5-6 attached; 0 free (PRIMITIVE)	3 attached; 1 free (SPECIALIZED)	4 attached; 0 free (INTERMEDIATE)
caudal vertebrae	1. without transverse processes	same	same
	2. autotomic (PRIMITIVE)	non-autotomic (SPECIALIZED)	non-autotomic (SPECIALIZED)

TABLE 2

occultus	*insolitus*	*darlingtoni*
34 mm snout-vent length	33 mm snout-vent length	72 mm snout-vent length
9-13 scales across snout	3 scales across snout	5 scales across snout
nasal scale separated from rostral by a single scale	*nasal scale separated from rostral by a single scale*	*nasal scale separated from rostral by a single scale*
supraorbital semicircles weak, separated by 2-4 scales	supraorbital semicircles strong, separated by one row of *wide* scales	supraorbital semicircles strong, separated by one row of narrow scales
No differentiated supraciliaries	*A distinct supraciliary row, but no scale elongate*	*A distinct supraciliary row, but no scale elongate*
no postorbital, supratemporal, or occipital spines	postorbital, supratemporal, and occipital spines, especially prominent in males	no postorbital, supratemporal, or occipital spines
no distinct supratemporal line of enlarged scales	a distinct supratemporal line of large scales *ending in a spine*	no distinct supratemporal line of enlarged scaled
Ear small, round, low	*Ear small, round, low*	*Ear small, round, low*
interparietal small, round, ca = ear, separated from semicircles by 2-6 scales	*interparietal ovoid, much larger than ear, separated from semicircles by one large scale*	*interparietal ovoid, much larger than ear, separated from semicircles by one large scale*
canthal ridge weak, barely differentiated	canthal ridge strong	canthal ridge strong
loreal rows 2-6	*loreal rows 3*	*loreal rows 3*
suboculars in contact with supralabials	*suboculars in contact with supralabials*	*suboculars in contact with supralabials*
10-11 supralabials to center of eye	7 supralabials to center of eye	7 supralabials to center of eye
mental in contact with 4 scales between sublabials, no differentiated infralabials	mental in contact with 4 scales between well-differentiated infralabials	mental in contact with 2 scales between well-differentiated infralabials

occultus	*insolitus*	*darlingtoni*
middorsal scales smooth, flat, subequal	a low crest of triangular enlarged scales on the nape to a little past insertion of arms	scales on nape somewhat smaller than middorsally
ventrals > dorsals, smooth, juxtaposed in transverse rows	ventrals > dorsals, smooth, juxtaposed in transverse rows	ventrals ca = dorsals, smooth, subimbricate in transverse rows
gular fan large, present in both sexes; inset, scales in rows in females, not in row in males	*gular fan moderately large in both sexes, inset, scales in distinct rows in females, rows less distinct in males*	gular fan large, not inset, scales evenly distributed in males
limbs short, tibial length ca = distance snout tip to center of eye	*limbs short, tibial length ca = distance snout tip to center of eye*	*limbs short, tibial length less than distance snout tip to center of eye*
14-20 lamellae under phalanges ii and iii of 4th toe	15-16 lamellae under phalanges ii and iii of 4th toe	24 lamellae under phalanges ii and iii of 4th toe
scales of limbs smooth, always smaller than ventrals	scales of limbs smooth, of anterior thigh larger than ventrals	scales of limbs weakly carinate, of anterior thigh larger than ventrals
supradigital scales smooth	*supradigital scales smooth*	supradigital scales multicarinate
tail round without dorsal crest	tail round with dorsal crest	tail round without dorsal crest
no enlarged postanal scales in male	*no enlarged postanal scales in male*	enlarged postanal scales in male

TABLE 3

The Anoles of Hispaniola

Species	*Distribution*	*Distinctness*	*Geographic differentiation*
ricordii	islandwide	in a separate species group	Several described subspecies, some of which are sharply enough distinct to raise the question of possible species status
**insolitus*	known from one north island locality	very sharply distinct, but apparently the north island representative of *darlingtoni*	unknown
darlingtoni	known from one south island locality	amply distinct, the south island representative of *insolitus*	unknown
coelestinus	south island	distinct, overlapping its north island representative *chlorocyanus* in a very limited fashion in the Port-au-Prince region, perhaps at other points of contact	present but not strongly marked
chlorocyanus	north island	almost parapatric to its south island representative *coelestinus* but with limited overlap	present but not strongly marked

Species	*Distribution*	*Distinctness*	*Geographic differentiation*
aliniger	north island with one known incursion into south island	amply distinct from both sympatric *chlorocyanus* and its closer relative *singularis*	unknown
singularis	south island and Gonâve	amply distinct both from sympatric *coelestinus* and its closer relative *aliniger*	unknown
cybotes	islandwide except peaks of the Cordillera Central and some of the arid plains	distinct, one of a group of climatically differentiated species	mostly not strongly marked but some distinct altitudinal (*armouri*) and peripheral races (*haitianus*). Some still unanalyzed local populations
whitemani	certain extreme arid areas of both north and south islands	distinct, the arid country representative of *cybotes*	unknown
shrevei	peaks of the Cordillera Central	distinct, the representative of *cybotes* at extreme altitudes, structurally close to *whitemani* but very distinct ecologically	unknown
distichus	most of the island, usually in mesic situations	distinct, but closely related to its arid country representative *brevirostris*	striking color races, especially remarkable diversity in dewlap color

brevirostris	arid portions of north and south islands and Gonâve	distinct, climatically separate from its close relative *distichus* but with some marginal sympatry	dewlap races present
hendersoni	south island	sharply distinct, related to *chlorocyanus-coelestinus* but not closely	strong color races
christophei	north island (montane broadleaf forest)	sharply distinct, related to *monticola-rimarum* but not closely	unknown
etheridgei	north island (montane broadleaf forest)	sharply distinct, related to *monticola-rimarum* but not closely	unknown
monticola	south island (montane broadleaf forest)	distinct, but the south island representative of *rimarum*	two color races
**rimarum*	known from a single north island locality (montane broadleaf forest)	distinct, but obviously close to *monticola*	unknown
**koopmani*	known from one south island locality (montane broadleaf forest)	amply distinct, related to *monticola* but not closely	unknown

Species	*Distribution*	*Distinctness*	*Geographic differentiation*
semilineatus	islandwide	distinct, the mesic climatic representative of arid area *olssoni* to which it is partly sympatric	no indication of geographic differentiation
olssoni	islandwide but not known from the south coast of the south island	distinct, the dry country representative of mesic area *semilineatus*	no indication of geographic differentiation
**cochranae*	higher elevations of the Cordillera Central	distinct; an altitudinal derivative of the *semilineatus* group	unknown

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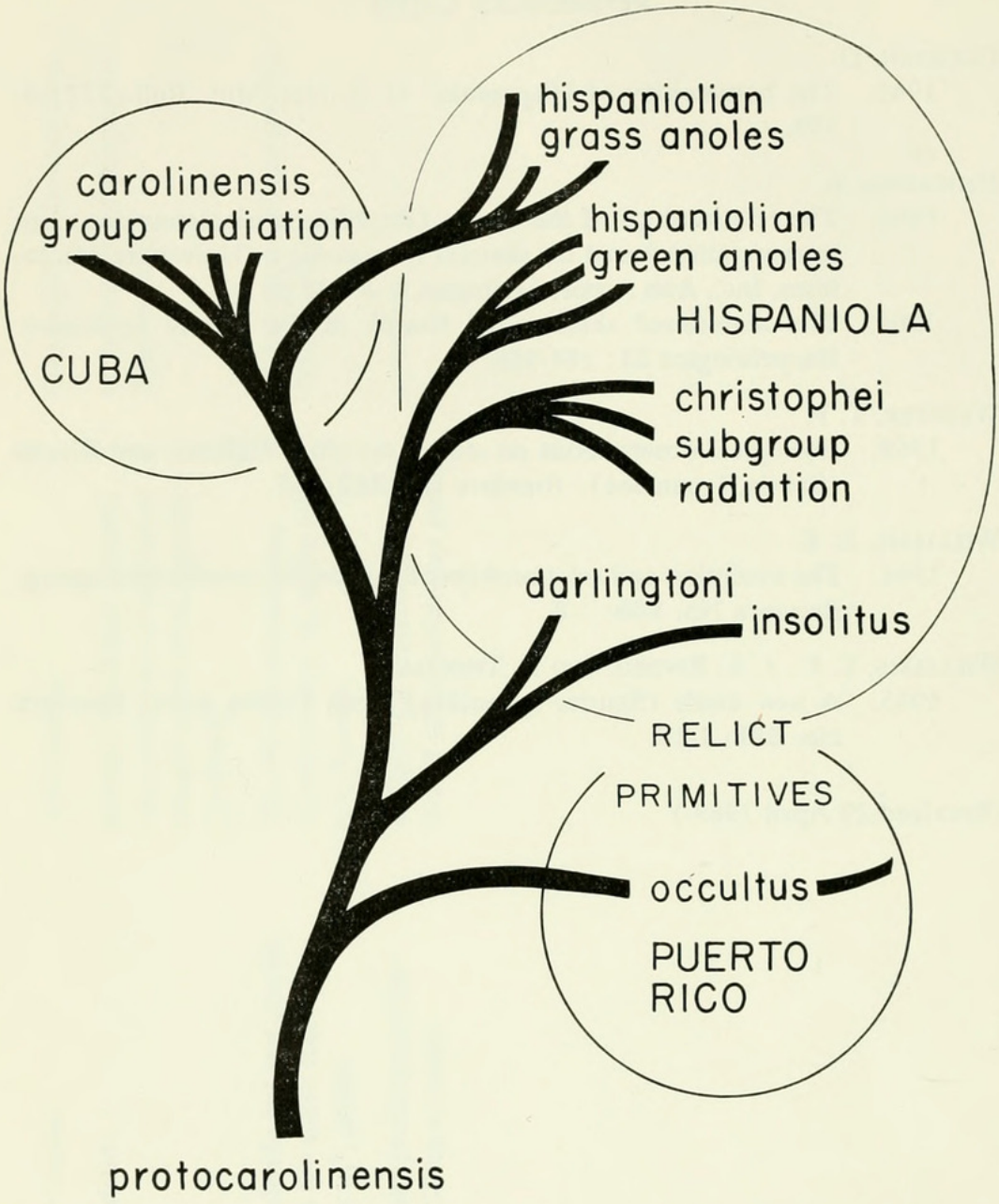

Fig. 5. Diagram of relationships within the *carolinensis* subsection of alpha *Anolis*. *A. darlingtoni*, *A. insolitus*, and *A. occultus* are primitive relicts within this subsection.

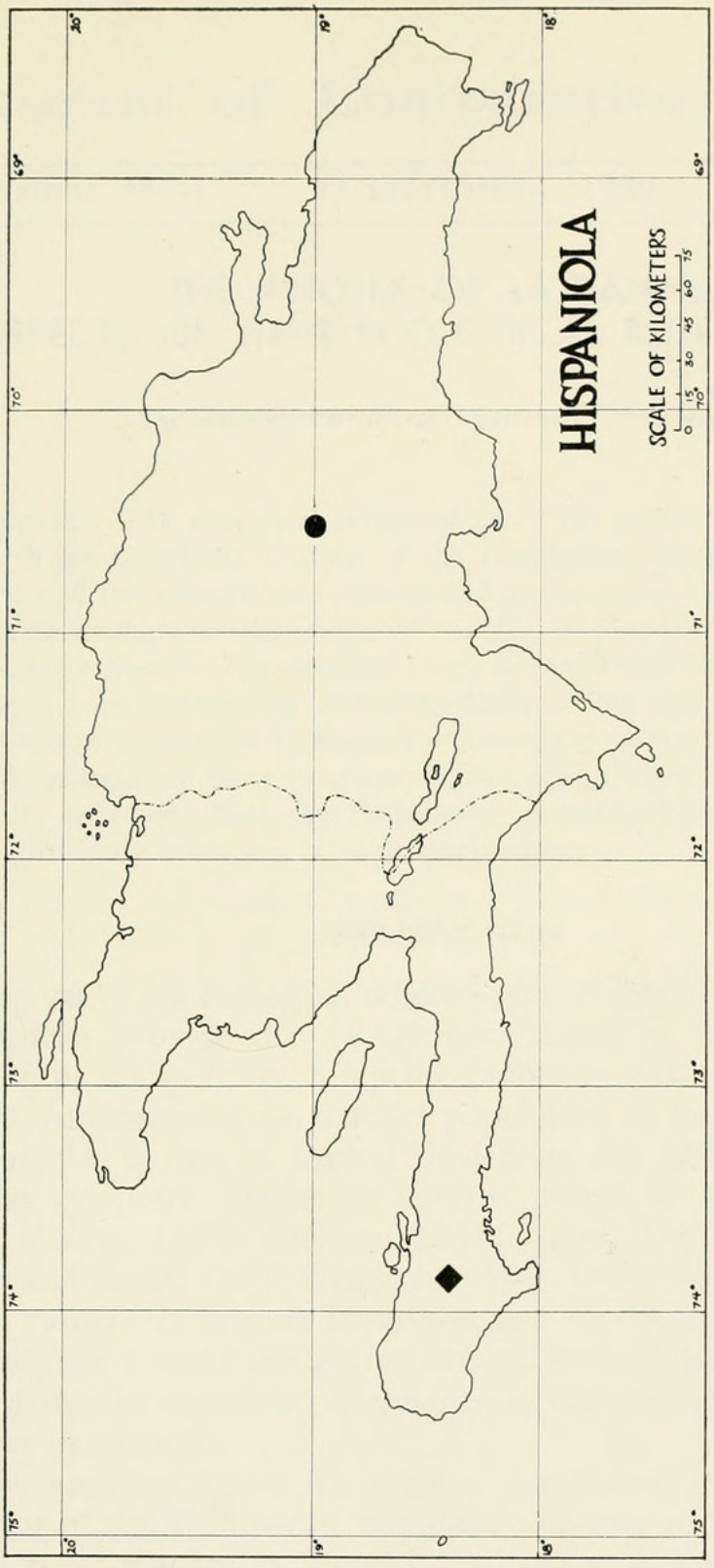

Fig. 6. Map of the distribution of *A. insolitus* and *A. darlingtoni*.