

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS.

APRIL 12, 1962

NUMBER 155

NOTES ON HISPANIOLAN HERPETOLOGY

6. THE GIANT ANOLES

BY ERNEST E. WILLIAMS

INTRODUCTION

Mertens (1939) has called attention to the existence of geographic variation in the giant anoles of Hispaniola and has distinguished a typical western race, *Anolis ricordii ricordii* Duméril and Bibron, and an eastern race, *A. r. baleatus* Cope.

The distinction between these two forms is sharp and unequivocal; the situation is, however, more complicated than Mertens' limited sample (16 specimens) led him to believe. Study of the unreported series of Hispaniolan giant anoles in the American Museum of Natural History (AMNH) plus the specimens in the Museum of Comparative Zoology (MCZ) and the United States National Museum (USNM) (91 specimens in all) makes it clear that at least three vicariant forms are recognizable. The form occurring from Port-au-Prince *north* to Cap Haitien and Port-de-Paix is the one to which Mertens has shown that the name *ricordii* Dumeril and Bibron must be attached. Another, occurring in the north and east of the Dominican Republic, may be called, following Mertens, by Cope's name *baleatus* (*Eupristis baleatus* Cope 1864, Proc. Acad. Nat. Sci. Phila., p. 168, type locality "St. Domingo"). A third unnamed population occurs on the Barahona peninsula. A fourth population inhabiting the southwest peninsula of Haiti may be distinct. I list below the distinguishing characters of the three well-marked forms.

TABLE 1

<i>ricordii</i>	Barahona population	<i>baleatus</i> ¹
Very low nuchal and dorsal crests	Low nuchal and dorsal crests	A prominent nuchal crest, a variable but lower dorsal crest
Nuchal crest scales as long as or longer than high, and not or but little higher than the very low dorsal crest	Nuchal crest scales higher than long but <i>small</i> , not higher than the weakly developed dorsal crest	Nuchal crest scales much higher than long, always much higher than scales of dorsal crest
Head scales small, numerous (7-9 across snout at level of second canthal ²)	Head scales larger, fewer (4-6 across snout at level of second canthal)	Head scales large, few (2-5 across snout at level of second canthal)
In ♂♂ <i>deep black spots above shoulder</i> , sometimes also on occiput; no other evident pattern	Whole of body in both sexes with very <i>irregular small blotches and mottling</i>	Both sexes with no evident pattern or transverse <i>banding or reticulation</i>

CHARACTER ANALYSIS

The scales on the snout are swollen, bosslike in all Hispaniolan giant anoles. The differences are solely in the size of these bosslike scales. The contrast is extreme in this regard between the giant anoles of northern Haiti (*ricordii*) and those of the northern Dominican Republic (*baleatus*). The animals of the Barahona and southwestern peninsulas, however, are intermediate, overlapping in this regard the north Dominican (*baleatus*) and approaching the north Haitian populations. On this character alone it is not possible to separate every specimen of the north Dominican and the southern populations though there is a well-marked average difference.

Number of scales across the snout is a measure of a more general feature — general scale size — which is somewhat greater in *baleatus* than in *ricordii*. Mertens has cited a number of key regions, i.e. loreal region, base of the tail, etc., which show this.

¹ A. Salle, who collected the type of *Eupristis baleatus* worked both in the northern Dominican Republic and at the base of the Barahona peninsula (map of travels compiled by W. J. Clench). It was therefore necessary to confirm the application of the name by checking the characters of the British Museum type. Miss A. G. C. Grandison has courteously confirmed that the nuchal crest scales of the type are indeed significantly higher than the dorsal crest scales.

² I count the canthals forward from the anterior border of the orbit (see Fig. 1). The reverse count — from the anteriormost canthal back — is sometimes used, e.g. Oliver (1948). This, however, has the disadvantage that the scales here are small and variable and do not provide a stable starting point.

The snout, however, provides the clearest expression of this general feature and one which can be reduced to a simple count with an adequate numerical range (2-9). Mertens has used a similar transverse count but makes it directly in front of the eyes. I have chosen a transverse count somewhat further forward because this transverse line, anterior to the supraorbital semicircles seems to me more suitable as a place for a standard count utilizable for all species of *Anolis*.

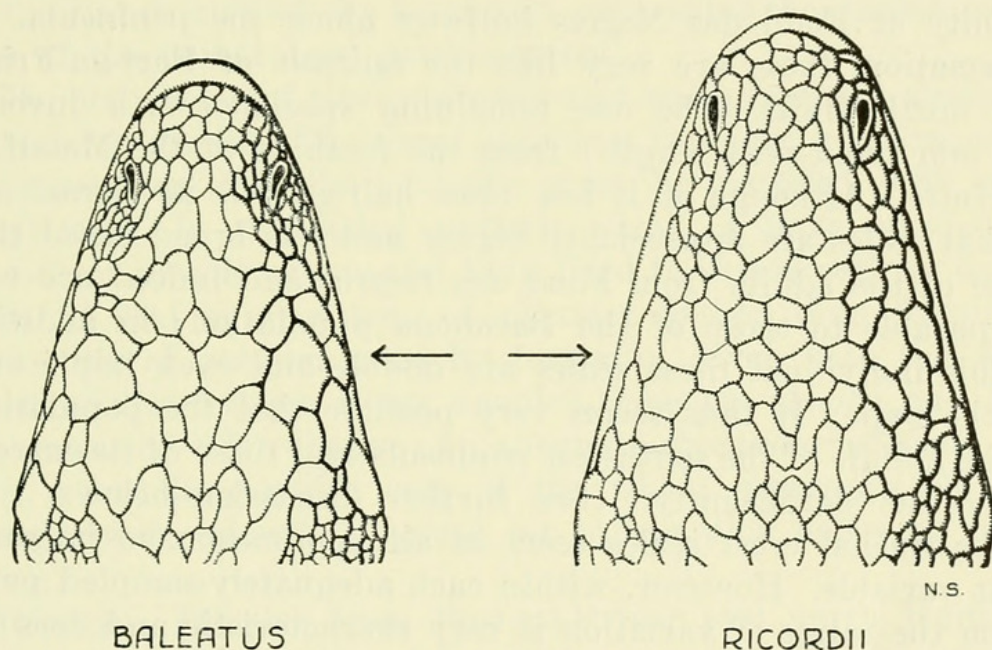


Fig. 1. The two extremes of anterior head squamation in *Anolis ricordi* subspecies. The arrows indicate the place at which the count across the snout is to be made.

The pattern of geographic variation of nuchal crest scales is not so simple. Again, the populations of Port-au-Prince and northern Haiti and northern Dominican Republic show the extremes, the crests of Port-au-Prince and of north Haiti populations very low with a long anteroposterior base, while those of north Dominican Republic populations are tapering, high, short based anteroposteriorly. The southern populations could again be described as intermediate but on careful examination this is not quite accurate. Both the north Haitian and southern populations have a reduced nuchal crest as compared with the north Dominican population but the nature of the reduction is different. The nuchal crest scales of north Haitian animals are long-based, low, rounded scales, not at all tapering; they are

sometimes shorter but usually slightly higher than the very low, long dorsal crest scales. In the giant anoles of the Barahona peninsula the nuchal scales are, in contrast, still short anteroposteriorly, relatively high, tapered, but *very small*, not appreciably higher than the tallest dorsal crest scales and notably smaller in area than the largest dorsal crest scales.

The few specimens from the southwestern peninsula do not permit adequate analysis of the populations of this important geographic area. The four adults examined all come from the vicinity of Fond des Negres halfway along the peninsula. In squamation, these are very like the animals of Port-au-Prince and north Haiti. The one remaining specimen is a juvenile (78 mm snout-vent length) from the foothills of the Massif de la Hotte. Although it is less than half-grown, its dorsal and nuchal scales are appreciably higher and less broad based than those of the adults from Fond des Negres and indeed are very comparable to those of the Barahona population; in addition, in this individual these scales are double and even triple even on the nape. It thus seems very possible that the populations of the middle of the southwest peninsula and those of its extreme end differ significantly. (See further discussion below.)

The nuchal crest scales seem in all populations to be somewhat variable. However, within each adequately-sampled population the range of variation is very characteristic and does not blur the distinctions tabulated above. Despite statements by Boulenger (1885) and by Mertens (1939), I do not find a clear correlation with sex; females, for example, of *baleatus* do not consistently have lower nuchal crest scales than male *baleatus* of the same size. There is, however, clear ontogenetic change; the smallest individual of *baleatus* at hand (AMNH 28651 from San Juan Bay, Samana, 41 mm snout-vent length) has the nuchal crest scales only incipiently enlarged and could not be recognized as a member of the *baleatus* population on that character. However, in *baleatus* the characteristic, tapering, spinelike nuchal scales develop very early and even specimens little more than half grown (e.g. MCZ 57719, Santiago, ♂, 83 mm snout-vent length; MCZ 5445, Samana Peninsula, ♂, 88 mm snout-vent length) are very readily recognizable.

Dorsal crest scales are more variable than nuchal crest scales, and variable in a peculiar fashion: there is sometimes a regular alternation of relatively high triangular single scales and pairs

of much lower, more quadrangular scales.¹ However, such a regular alternation occurs — if present at all — on only a portion of the back and there is present between nuchal crest and dorsal crest, on the one hand, and dorsal and tail crests, on the other, various irregular conditions with double and single crests erratically intermingled and scale types somewhat intermediate and rather irregularly so. In *ricordii* itself with a very low dorsal crest the double condition with all low scales is most frequent; in *baleatus* the situation is individually very variable; in the Barahona and the southwest peninsulas the double condition of the dorsal crest predominates.

The body color of live specimens and well-preserved alcoholics is probably useful. The usual specimen, however, requires much interpretation and its evidence must be received with some skepticism. In tabulating pattern, above, I have ignored all ill-defined discolorations and have tried to assess pattern on the basis of real aggregations of pigment rather than fortuitous darkening of random areas by formalin. Even with this qualification the problem is not simple: these are *Anolis* and have the power of color change; an adequate discussion of their pattern would be possible only if the whole repertoire of color changes were known. I record my information below by population.

Ricordii: Females from Port-au-Prince and north Haiti appear to be plain green above with no markings of any sort. Males from Port-au-Prince are also mainly green (as preserved they may show an obscure, very fine brown reticulation) but are distinguished by a large, very characteristic patch of black above the shoulder but of ill-defined shape and varying extent. There may also be irregular black patches extending onto the back of the head. There may also be a white patch at the corner of the mouth. A Cap Haitien male (Senckenberg 10445) is quite similar to Port-au-Prince specimens. Of three males newly received from Ti Guinin a little to the east of Cap Haitien (MCZ 66147-9) two have almost no black at the shoulder (only small and inconspicuous spots) and none at all on the head. The other male is as devoid of black spotting as any female. All show fine brown reticulation quite like that of similarly preserved Port-au-Prince males.

¹ In the tabulation above I have compared the nuchal crest scales with the highest crest scales at midbody.

Baleatus: Schmidt (1921, p. 10) records specimens from Sanchez and Villa Rivas as "usually green with dark-edged transverse bands of light greenish yellow." Preserved specimens which have any definable pattern show this transverse banding which is present on dorsum, limbs and tail; it appears to be most persistent on the tail. It is very conspicuous in a specimen near hatchling size (AMNH 28651). There are frequently numbers of small spots on the sides of the belly and on the venter. The MCZ Santiago series, though preserved in a light phase, show very irregular light banding much invaded by dark reticulations, but the bands are very prominent on limbs and tail.

Barahona Population: I have unfortunately been unable to find any description of Barahona giant anoles in Hassler's notes. I must therefore rely entirely on the preserved specimens, which, however, are unusually consistent, though from several localities and with very different collection dates. Collected by Hassler, they differ strikingly from the *baleatus* specimens, most of which were also collected by Hassler. All Barahona specimens, and most clearly those from Valle de Polo, show irregular small blotches, very variable in tint and extent, scattered over the entire dorsum. The closest approach to this condition is seen in those *baleatus* which show reticulation. There are never in the Barahona specimens the large shoulder spots of *ricordii*, *sensu stricto*.

One specimen (AMNH 51241 from Enriquillo) does show transverse banding, but more obscurely than in *baleatus*. The small blotches are also very obscure in this specimen, which therefore could not in this phase be recognized as a member of the Barahona population on its color. The nuchal and dorsal crest scales are, however, typical *barahonae*, and the hypothesis which I have adopted is that the blotching so characteristic of most preserved specimens is characteristic only of one of the phases of the color repertoire possible to this population.

Population of the Southwest Peninsula of Haiti: Again the material is inadequate for proper analysis, the more evidently so since the few available specimens suggest that this is not a unit sample. The juvenile from the Massif de la Hotte is, as preserved, reddish or purplish brown with indistinct broken dark longitudinal lines on head and nape and more evident narrow brown transverse bands on the back, six between shoulder and groin, in pairs with very slightly lighter reddish-brown between each pair. The tail is obscurely annulate.

In contrast, the three adult females from the vicinity of Fond des Negres are essentially patternless (MCZ 66016 is dark and obscurely vermiculate, and USNM 72631, 72633 are plain light green except for a subocular half ring of scales that is conspicuously white). The single male is similarly nearly patternless but has also the subocular half ring of white and, in addition, a series of small black spots above the shoulder, very like a vestige of the large black shoulder spot of Port-au-Prince animals and very like those of the two Ti Guinin males.

TAXONOMIC EVALUATION

There appear to be at least three distinctive populations of giant anoles, all readily separable by nuchal crest development and body color, less sharply separable by the size of the scales on the snout. These populations are allopatric and thus may be species or subspecies.

The differences between typical *baleatus* and typical *ricordii* are such that they could well imply specific distinction. However, all the populations south of the Cul de Sac Plain, both the rather distinctive Barahona animals and the very poorly known populations of the southwest peninsula, are to some degree intermediate between the two northern extremes although presenting some features that are their own. In thus bridging the morphological gap between the extremes, they strongly suggest that the Hispaniolan giant anoles belong to a single species.

The giant anoles are scarce and local. It is not to be expected that intergradation between the several populations will be easy to demonstrate; specimens from many of the critical intermediate areas are conspicuously lacking.

The Fond des Negres and Ti Guinin specimens, on the other hand, may be intergrade populations. The vestigial shoulder spots present in the two Ti Guinin males and the single Fond des Negres male suggest this conclusion, as does, in the latter case, the combination of nuchal and dorsal squamation most like typical *ricordii* with somewhat lower scale counts across the snout. No giant anoles are at hand from the northwest Dominican Republic. This is the area in which intergradation between *ricordii* and *baleatus* is to be expected. It is thus not at all surprising to find the first suggestion of loss of characters of the typical race just to the east of Cap Haitien.

On the southwest peninsula, the Fond des Negres area is one in which such intermediate populations are to be expected, as recent collections from the area show. Thus, *Dromicus parvifrons parvifrons* and *D. parvifrons protenus* appear to meet in this area and several anole races (to be reported later in this series) show intergradation at just this point.

I thus interpret the Fond des Negres giant anoles as intergrades between typical *ricordii* and a population to the west occupying the tip of the southwest peninsula. This western population I infer to be represented at present by the single juvenile specimen collected by P. J. Darlington in the foothills of the Massif de la Hotte.

The wide-banded specimen from Enriquillo in Barahona is reminiscent of the banded color phase in typical *baleatus*, but in squamation it is not intermediate and it is geographically quite unsuitable as a member of an intergradient population. Nevertheless, the presence of this color phase hints at a closer relation with *baleatus* than otherwise could be inferred.

The absence of other evidence or hint of intergradation is easily accounted for by the gaps in the distributional record, and, granted the desirability of further evidence, recognition of subspecies status seems justified for typical *ricordii*, for *baleatus*, for the Barahona population and probably also for a population at the west end of the southwest peninsula of Haiti. The latter two populations are currently nameless. That from the southwest peninsula is at the moment very insufficiently known, and it would not now be appropriate to describe it. The Barahona population, on the other hand, is well recorded and may be formally named:

ANOLIS RICORDII BARAHONAE new subspecies

Type: MCZ 43819, Polo, Valle de Polo, Barahona, Dominican Republic, an adult female collected by W. G. Hassler, September 1932, J. C. Armstrong donor.

Paratypes: Valle de Polo, MCZ 56141, AMNH 51036, 51235-6; Herman's Finca near Paradis, AMNH 51231-3; Barahona, AMNH 50255-6, 50261; Halfway between Trujin and Enriquillo, AMNH 51230; Enriquillo, AMNH 51241.

Diagnosis: A subspecies of *ricordii* distinguished from the typical form and from *baleatus* Cope by the nature of the nuchal crest (formed by small but slender tapering scales not or very

little higher than the highest scales of the dorsal crest), by the size of the scales of the snout (4-6 across snout between second canthals), and by a characteristic phase of coloration in both sexes in which small blotches are present, irregular in shape and of varying intensity.

List of Specimens Examined: A. r. barahonae (17 specimens). DOMINICAN REPUBLIC. *Polo, Valle de Polo*: MCZ 43819; *Valle de Polo*: AMNH 51036, 51235-7, MCZ 56141; *Barahona*: AMNH 50255-6, 50261; *Herman's Finca near Paradis*: AMNH 51231-3; *Halfway between Trujin and Enriquillo*: AMNH 51230; *Enriquillo*: AMNH 51241; locality uncertain: AMNH 51229, 51234, 51240.

A. r. ricordii (12 specimens). HAITI. *Port-au-Prince*: AMNH 49501; *Diquini*: MCZ 8619, USNM 118902, 123988; *Source Leclerc, Morne Decayette, near Port-au-Prince*: MCZ 65729-31; *Petionville*: MCZ 60013-4; *Marcaco*: USNM 69437; *Port-de-Paix*: MCZ 63338; *Ti Guinin near Cap Haitien*: MCZ 66147-9. [Records by Mertens: *Port-au-Prince*, 4 specimens; *Cap Haitien*, 1 specimen.]

A. r. baleatus (57 specimens). DOMINICAN REPUBLIC: *Peña, near Santiago*: MCZ 57713-9; *Santiago*: MCZ 7831; *Las Bracitas*: AMNH 41465-6; *El Rio*: AMNH 41294, USNM 62104-5; *Rio San Juan*: USNM 74940-1; *Samana Peninsula* (various localities): MCZ 5445, AMNH 28651, 39807-15, 39817-23, 39825-9, 39837, 40224-30, 40387-90, 42285, 42775, 44841-4; *La Romana*: MCZ 16321. [Records by Mertens: *Santiago*, 5 specimens; *Moca*, 4 specimens; *Finca Arbol Gordo near Villa Altogracia*, 1 specimen.]

A. r. subsp. nov. (1 specimen). HAITI: *Foothills, Massif de La Hotte*: MCZ 38277.

A. r. subsp. nov. x *r. ricordii*. *Pemel near Fond des Negres*: MCZ 66015-6; *Fond des Negres*: USNM 72631, 72633; also 72632, skeletonized.

BEHAVIOR

The giant *Anolis* of Hispaniola is infrequently seen by collectors and consequently our information on its ecology and habits is limited. Such information as is available is summarized below by A. S. Rand. Quotation marks refer to Rand's personal observations.

A. ricordii ricordii, Morne de Cayette, near Port-au-Prince, Haiti (A. S. Rand and J. Lazell). "A large individual was seen about 15 feet up on a branch of a 30-foot high tree on the edge of a patch of brush on the hillside. It remained sitting quietly in sight for about half an hour until we climbed the tree to attempt to capture it. It then climbed out among the small branches where, despite an intensive search, we were unable to locate it again."

Port-de-Paix, Haiti (A. S. Rand and J. Lazell). "A female was seen sitting head down on the trunk of a large tree about 4 feet from the ground. The tree was one of a series forming a fence row. The lizard allowed us to approach and noose it."

A. ricordii baleatus, Pena near Santiago, Dominican Republic (C. E. Ray and A. S. Rand). "Local people who brought in a series at this locality reported that they lived among the upper branches of the larger shade trees in the coffee plantations."

Finca Arbol Gordo, Dominican Republic. Mertens reports that the single specimen collected by him jumped to the ground from the trunk of a palm tree. Mertens kept this animal in captivity for some time and wrote that it was active only in the late afternoon. When approached it squirreled around to the other side of its perch. It slept exposed on small branches with its hind legs flexed.

A. ricordii subsp., Camp Perrin, Haiti (A. S. Rand and J. Lazell). "A small boy guided Rand to a stand of coffee where a crowd of Haitians had treed a large individual. The lizard was about 20 feet up in a small tree. It was too high to noose and the tree too small to climb so we attempted to scare the lizard to a more favorable situation by poking it with a long pole. After considerable fuss the lizard ran out along a small branch to the next tree, down that to the ground, across the ground to hide among the roots of a large Cieba tree. After considerable prodding among the roots we dislodged the lizard which avoided the herd of assistants successfully and climbed the Cieba out of both sight and reach."

Above Maceline, near Camp Perrin (A. S. Rand and J. Lazell). "In a small stand of coffee we saw a single animal about 15 feet up in one of the large trees on a large branch. When Lazell climbed the tree it squirreled about the branch concealing all of itself except one eye. It then climbed up and out among the small branches and disappeared from view."

Mertens speculates that the giant anoles of Hispaniola were originally inhabitants of the lowland rain forest and have adapted to cultivated areas by living in the crown of the taller trees. The observations of Rand and Lazell tend to support this conclusion.

INTRASLAND ZOOGEOGRAPHY

The portion of Hispaniola south of the Cul de Sac Plain, including the southwest and Barahona peninsulas and the La Selle and La Hotte ranges, has, as Mertens has emphasized, a number of endemic species and even genera. I have recently (Williams, 1961) stressed the importance of this area, which I have called the "southern island," in the initial differentiation of forms now widespread in the portion of the island north of the Cul de Sac Plain.

Barahonae as an isolate in "southern island" easily fits this pattern. *Baleatus* and typical *ricordii* do not.

This is merely the first of many examples to be discussed in this series which will show that not all the patterns of differentiation in Hispaniola can readily be explained by the simple hypothesis of "southern" and "main island" isolates. As in the present case so in a considerable number of others, there appear to be additional loci of differentiation, e.g. northern Haiti, which are not so evidently marked off by present or recently past barriers to distribution.

These cases of subsidiary loci of differentiation are not at present well analyzed. Hispaniola has not been really well collected, and it is now evident that the differentiation of local populations that occurs within it is finer grained than the sporadic collecting of the past could reveal. For many of the instances of minor loci of differentiation, data are just now being gathered.

RELATIONSHIPS OF *RICORDII* AND THE OTHER WEST INDIAN GIANT ANOLES

Anolis ricordii clearly belongs to the series of giant anoles that includes *equestris* of Cuba and *cuvieri* and *roosevelti* of the Puerto Rican-Virgin Island complex. *Anolis garmani* of Jamaica seems, even on externals, to show no features, except size, which specially link it to this group, and Richard Etheridge in an unpublished thesis (University of Michigan) has shown that osteologically it belongs to quite a different section of the genus.

No full study has ever been made of the Greater Antillean giant anoles as a group, though they clearly merit such a study.¹ I do not intend to attempt this here, but in order to place the races of *ricordii* within a frame of reference which might add to our understanding of them and of their origin I have compared all of the species for a number of mostly qualitative characters which were simple to determine and to evaluate. Table 2 presents the results of this comparison.

It is sufficiently clear even from the limited evidence presented by Table 2 that we are dealing with four good species. The Hispaniolan populations are a unit as compared with the forms of the neighboring islands and, as in the case of the other polytypic giant anole, *A. equestris*, the intransland differentiation has involved primarily scale size and color pattern.

There is one unusual zoogeographical feature in the distribution of the giant anoles — the occurrence of *A. cuvieri* and *A. roosevelti* on the same island bank, *cuvieri* on the mainland of Puerto Rico, *roosevelti* on Culebra in the Virgin Islands. These two are very distinct species. Their differences are at another level than those between *ricordii* and *baleatus*, and their occurrence on what must at various times during the Pleistocene have been a single land mass provides a special problem in accounting for their origin and dispersal.

ACKNOWLEDGMENTS

This paper was in part made possible by collections made under National Science Foundation Grants NSF G-5634 and G-16066 and grants from the American Philosophical Society and the Society of Sigma Xi. Assistance given by the governments and people of the Haitian and Dominican Republics is also gratefully acknowledged. I am indebted also to Charles M. Bogert and Doris M. Cochran for loans from the collections under their care. Dr. Norman Hartweg permitted examination of the second known specimen of *Anolis roosevelti* Grant. Dr. W. J. Clench provided information on the areas visited by A. Salle in the Dominican Republic.

¹ For further information on the non-Hispaniolan species see Stejneger (1904), Grant (1931), Schwartz (1958).

TABLE 2

Character	<i>equestris</i>	<i>ricordii</i>	<i>cuvieri</i>	<i>roosevelti</i>
Head scales	Swollen, very rugose	Swollen, keeled or wrinkled	Relatively flat, keeled	Swollen, keeled
Scales across snout	2-5	2-9	6-8	6-8
Frontal depression	None	Shallow	Shallow	Deep, bounded by ridges
Interparietal from supraorbital semicircles	4-5 Scales swollen	4-6 Scales swollen	3-5 Scales with multiple tubercles	2 Scales smooth, flat
Sublabials	Sublabial row well differentiated, scales smooth	Sublabial row well differentiated, scales smooth	Sublabial row <i>not</i> differentiated, scales often multicarinate	Only anteriormost sublabial on each side differentiated, scales smooth
Postanals	Present in ♂	Present in ♂	Present in ♂	<i>Not</i> present in ♂
Scales under base of tail	Smooth	Smooth	Keeled	Smooth
Scales on side of base of tail	Small, quadrate arranged in regular vertical rows	Small, quadrate arranged in regular vertical rows	Rather large, irregular in shape and arrangement (Cf. figs. 87 and 88, Stejneger, 1904)	Small, quadrate arranged in regular vertical rows
Scales on limbs and digits	Smooth	Keeled	Keeled	Keeled
Lamellae under 4th toe (approximate)	45	31	33	33
Snout-vent length, adult ♂	157 mm	137 mm	135 mm	160 mm

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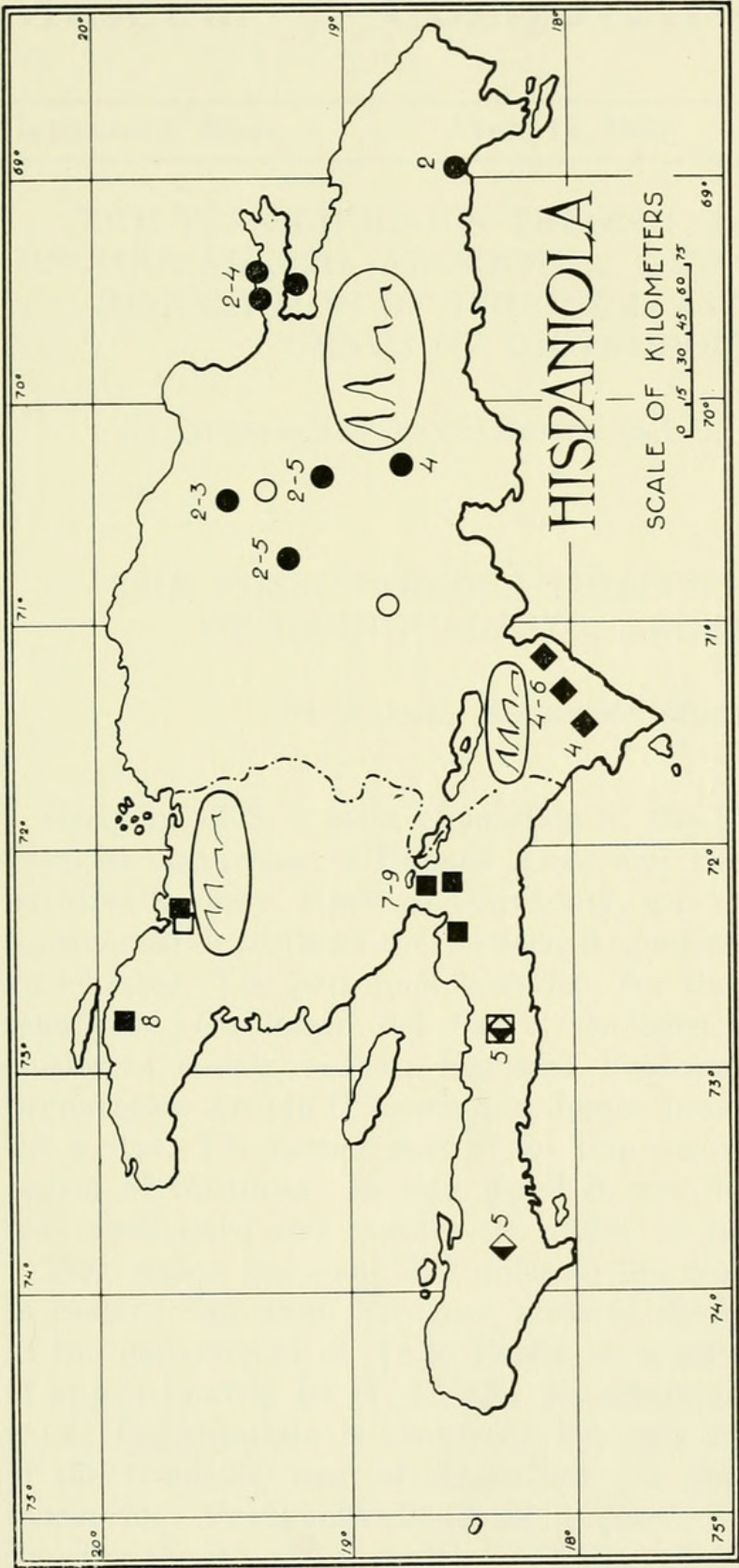
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Distribution of *Anolis ricordii* subspecies. Hollow symbols for *ricordii* and *baleatus* are Mertens' records. In each oval is represented, left to right, the outline of two nuchal scales and two of the lower dorsal scales. Numbers are counts of scales across snout in populations indicated by adjacent symbols.



Williams, Ernest E. 1962. "Notes on Hispaniolan herpetology. 6. The giant anoles." *Breviora* 155, 1–15.

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