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THREE NEW SPECIES OF THE *ANOLIS PUNCTATUS* COMPLEX FROM AMAZONIAN AND INTER-ANDEAN COLOMBIA, WITH COMMENTS ON THE EASTERN MEMBERS OF THE *PUNCTATUS* SPECIES GROUP

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ABSTRACT. New species of the *Anolis punctatus* group are described from central and eastern Colombia: *A. vaupesianus* from Comisaría of Vaupés, *A. huilae* from the Departments of Huila and Tolima, *A. santamartae* from the south slope of the Sierra Nevada de Santa Marta. The characters useful in discriminating the eastern members of the *Anolis punctatus* species group are discussed and evaluated, and the species themselves are diagnosed.

INTRODUCTION

Important new collections from Colombia have yielded *Anolis* that require description. Those dealt with here are allied to *Anolis punctatus* of Amazonia and the Atlantic Forest of Brazil, and, like the other recently described members of the *punctatus* group (Williams, 1965, 1974), they occur in areas peripheral to the range of that central and widely dispersed species. The three new taxa thus fill in blank areas in the known range of the complex. However, like many others of the *punctatus* species group, excepting only the central widespread and best-known species *punctatus*, these are species almost without distributions or ecologies. There are so few localities from which they are known, so little is known about their biology, that they are question marks rather than known components of fauna. They testify primarily to our basic ignorance of South American lizards.

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I first describe the Amazonian taxa. Since the three best specimens are from the Comisaría of Vaupés, I call it:

Anolis vaupesianus, new species
(Figs. 1-5 and Map)

Type: MCZ 156309 (formerly UTA 3626), adult male.

Type locality: Timbo, a Cubeo village ca. 1 N 70 W on the Río Vaupés, E of Mitú, Vaupés, Colombia, William F. Pyburn coll., 24 July 1972.

Paratypes: COLOMBIA: **Vaupés**. UTA 6850, MCZ 154592 (formerly UTA 5051)¹ same locality as type. J. K. Salser, Jr. coll.; ICN 4542, Cano Ti near Pamopeta, W. W. Lamar coll.; UTA 10283, Wacara, Lois Lores and Marilyn Cathcart coll. *Amazonas*. MCZ 79655, lower Río Apaporis, I. Cabrera coll.; MCZ 112098, Tio Miriti-Parana, La Providencia, F. Medem coll.

Description (paratype variation in parentheses). *Head*: Head scales moderately sized, weakly (sharply) keeled toward tip of snout, smooth posteriorly. Ten (8-11) scales across snout between second canthals. Frontal depression distinct, scales within it smaller than those anterior to it (not or not conspicuously so). Eleven (9-10) scales border rostral posteriorly. Anterior nasal scale divided (not divided), it and inferior nasal scale in contact with rostral. Eight (6-7) scales between supranasals. Rostral area swollen, protuberant, rostral extending well beyond mental on male (not swollen or protuberant, rostral not extending much beyond mental in female).

Supraorbital semicircles separated by one minute scale (or by one or two larger scales or narrowly in contact), separated from the supraocular disk by one row of granules. Supraocular disk ill-defined (better-defined), grading into surrounding granular scales. One elongate supraciliary followed by minute granules. Canthus distinct, five (5-6) canthal scales, the second largest. Six (5-7) loreal rows counting down from the second canthal, the ventralmost largest.

Temporals and supratemporals granular, the latter grading into larger scales around the interparietal. An ill-defined and tapering double intertemporal row of somewhat enlarged scales. Inter-

¹This is a specimen referred to as *A. punctatus* by Greene (1977).

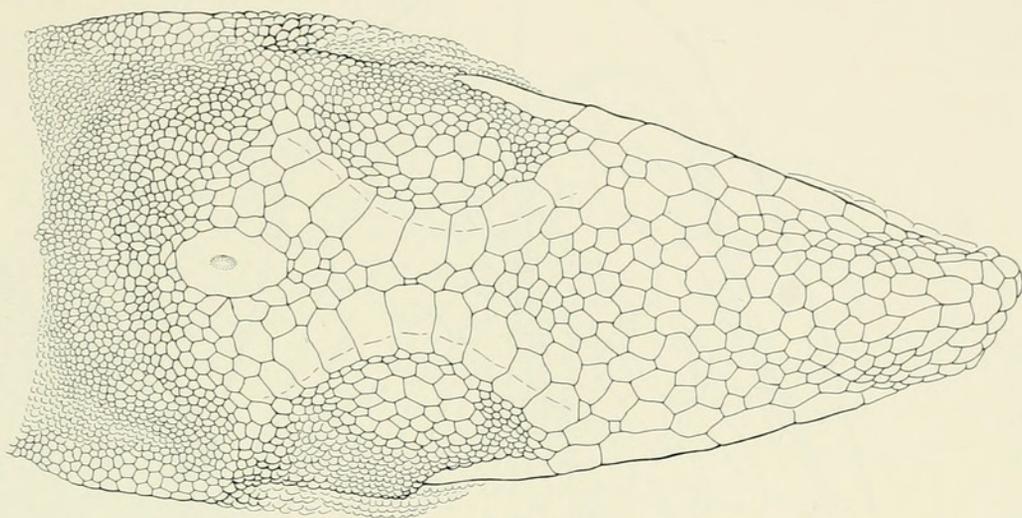


Figure 1. *Anolis vaupesianus*, n. sp. Type ♂, MCZ 156309. Dorsal view of head.

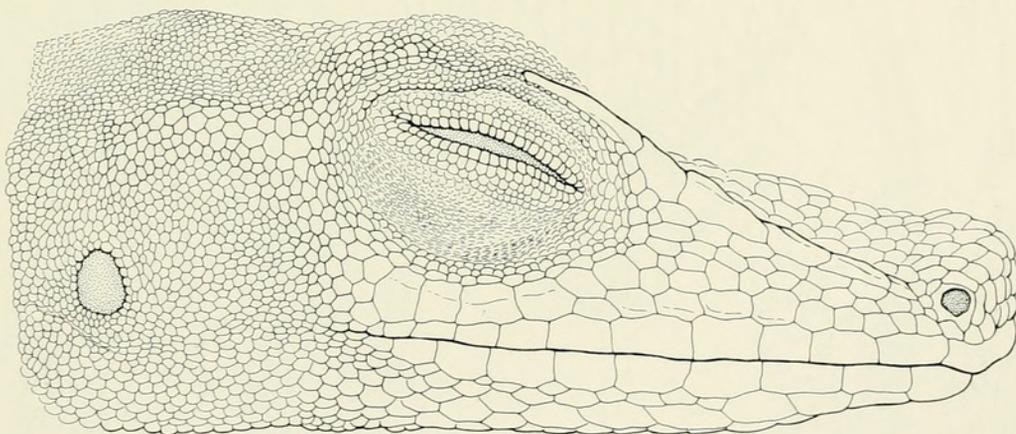


Figure 2. *Anolis vaupesianus*, n. sp. Type ♂, MCZ 156309. Lateral view of head.

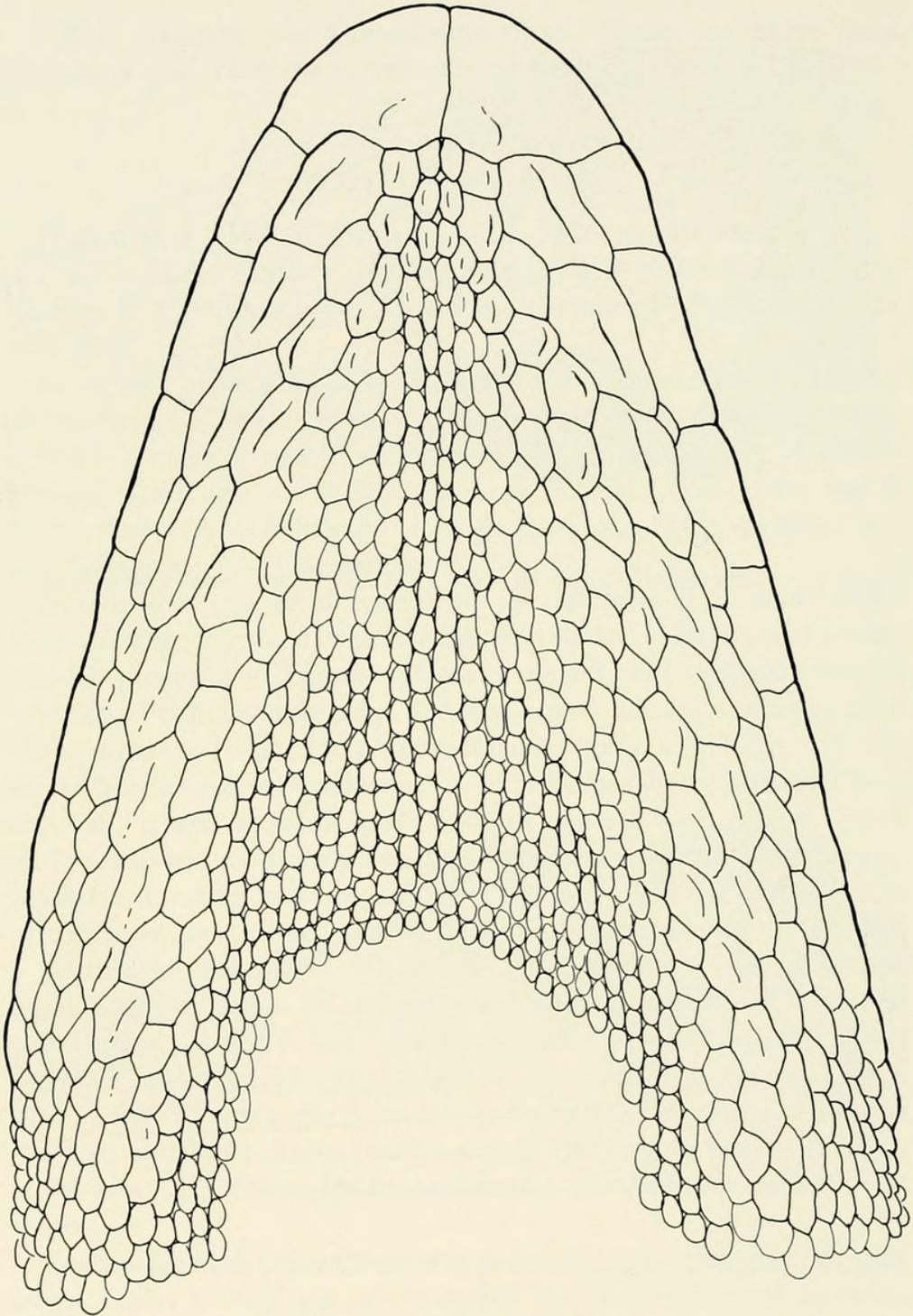


Figure 3. *Anolis vaupesianus*, n. sp. Type ♂, MCZ 156309. Ventral view of head.

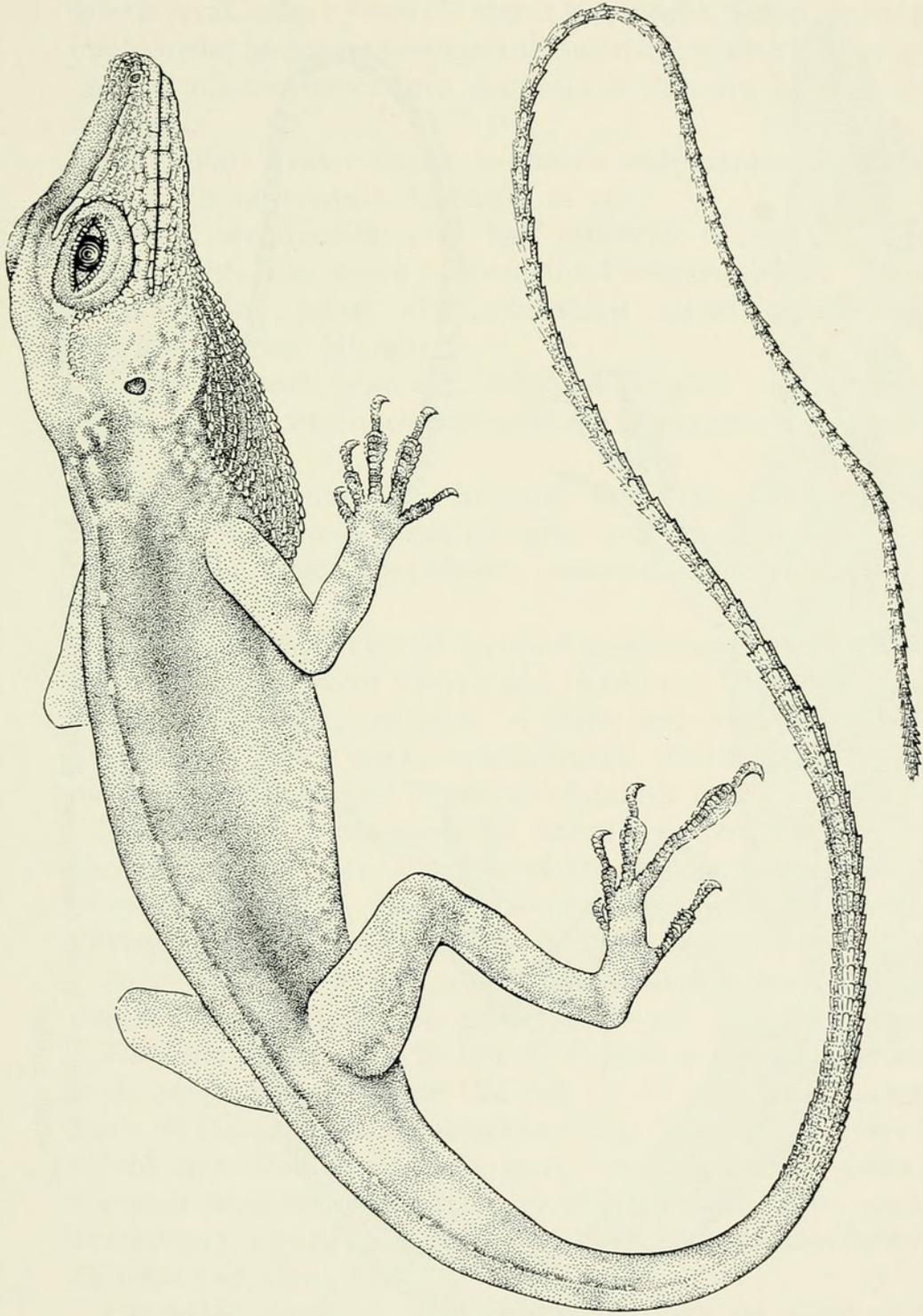


Figure 4. *Anolis vaupesianus*, n. sp. Type ♂, MCZ 156309. Lateral view of whole animal.

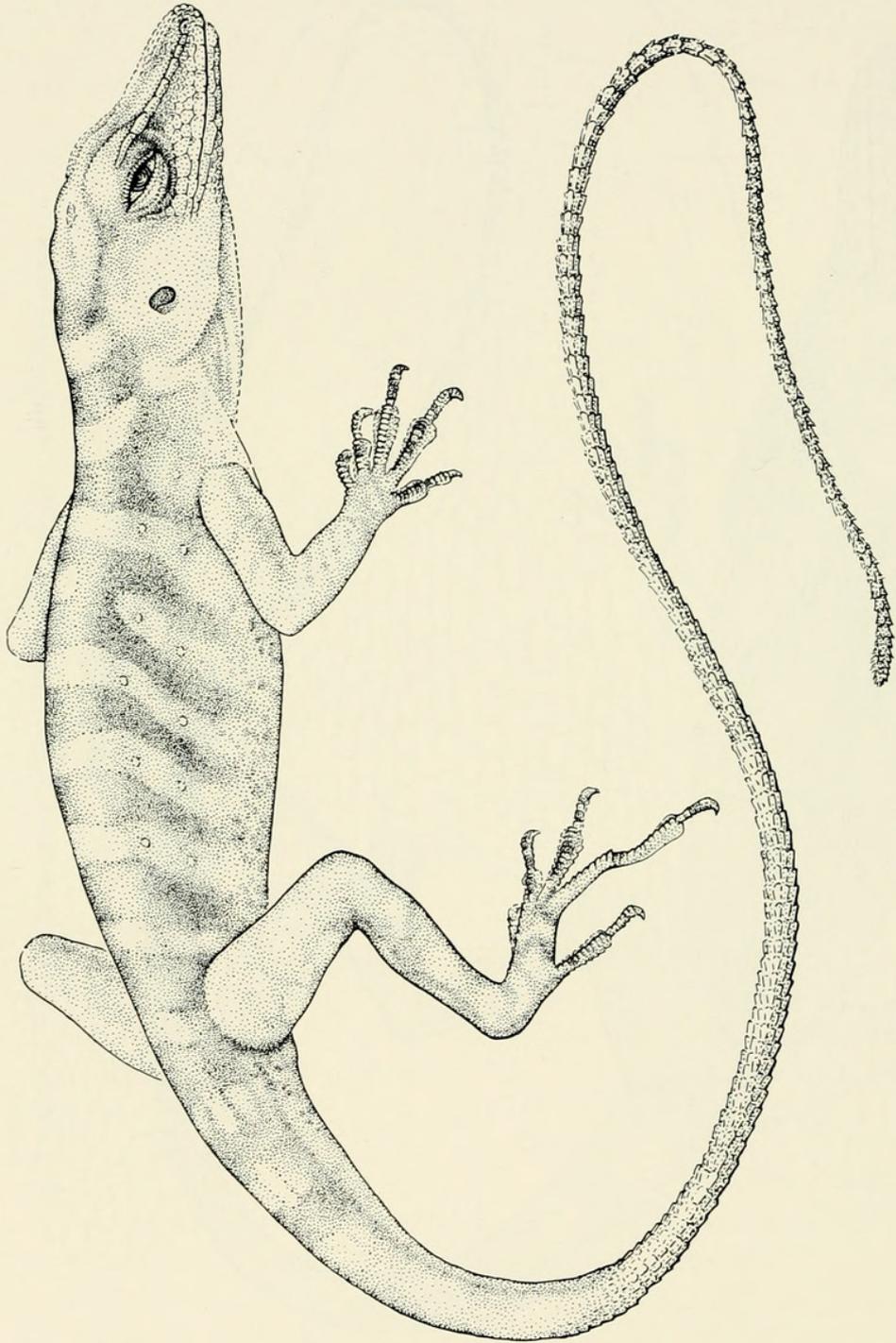


Figure 5. *Anolis vaupesianus*, n. sp. Paratype ♀, MCZ 112098. Lateral view of whole animal.

parietal much larger than ear (larger), separated from the supra-orbital semicircles by two (3) rather large scales. Scales surrounding interparietal largest anterolaterally, posteriorly grading through an area of minute scales into the dorsals that are as large as the temporals.

Suboculars weakly keeled, in contact with supralabials. Seven to eight (7-9) supralabials to center of eye.

Mental semidivided, each half distinctly wider than long, in contact with four scales between the keeled sublabials. Three (5) sublabials in contact with infralabials. Gulars small, smooth, increasing in size laterally.

Trunk: Dorsals granular, subequal, smaller than the weakly keeled ventrals which are subimbricate (juxtaposed), in transverse rows.

Dewlap: Moderate in male, not extending posteriorly much beyond axilla. Lateral scales elongate, larger than ventrals, in close-packed rows. Edge scales shorter, crowded, subimbricate. Vestigial in female.

Limbs: Largest scales on forelimb unicarinate, on digits weakly multicarinate. On hind limbs scales in front of thigh and lower leg weakly unicarinate, on back of thigh and lower leg granular. Supradigital scales weakly multicarinate. Twenty-five (22-26) lamellae under phalanges ii and iii of fourth toe.

Tail: Weakly compressed. No dorsal crest. No verticils. Scales above weakly carinate. A double middorsal row. Scales behind vent at most very weakly carinate, becoming distinctly so posteriorly. Postanal scales not well defined in male, absent in female.

Size: Male type: 82 mm snout to vent; largest male paratype: 78 mm snout to vent. Female paratype: 75 mm snout to vent.

Field notes and color in life: F. Pyburn presents the following notes on the male holotype: "24 July 1972 I collected a dark green anole on the base of a small tree in village (Timbo) about one hour before dark. Dorsum of head, body, legs dull uniform green with scattered blue flecks; venter grey; dewlap skin black; scales of dewlap grey. Lizard turns dull brown when handled. Has fleshy keel on nape and along back."

For MCZ 154592, a male, the notes below are abridged from those of J. K. Salsler, Jr.: "*Anolis* sp.; Timbo (Vaupés), Colombia; March 20, 1974: very hot noon-time; caught in an aged avocado tree

- scaled tree and jumped from its top in attempt to escape. . . Blue dots dorsolaterally placed in stripes from vertebra down, angling down to lower sides; changes from dark green to green-brown mottled very quickly; eyes golden, eyelid border yellow. . ."

For the female paratype, MCZ 112098 (Fig. 5), from the Río Miriti-Parana, Federico Medem has provided the following information: "Caught 8:30 a.m. on underbrush, one meter high, in open country. . . Gular sack small, greenish. Iris golden. Intense green on body with lateral small blue spots. Middorsally 16 squarish sand-colored spots. Dark transverse bars on tail. Venter light gray with dark vermiculations."

For MCZ 79655, a male, Medem reports the color as: "Dorsally green with lateral blue spots; dewlap 'morado' - violet, mulberry-colored."

Comparisons: Very few specimens of *A. punctatus* are recorded from Colombia. The nearest to any of the type series of *A. vaupesianus* are two recently collected specimens in the Paris Museum (MHNP-1978-3086-87) from Hameau Kuira, Río Agara Parana, a tributary of the Río Putumayo, in Amazonas Territory. Both are males with strongly keeled ventrals, dorsum an unpatterned dark purplish and dewlap with light skin with minute dispersed melanophores and purplish scales.

The *A. vaupesianus* most nearly adjacent to these is MCZ 79655 from La Providencia, Río Miriti-Parana, a tributary of the Río Caquetá, also in Amazonas. It is unfortunately a female. MHNP-1978-3086 has therefore been compared with the topotypic paratype UTA 6850, which is of the same size and sex. The dewlap in the paratype contrasts strongly with the Amazonas *punctatus* in its intensely black skin and white scales, and the ventral scales in *vaupesianus* are smaller and decidedly more weakly keeled. No other scale differences are evident, but the color and pattern of the Mitu paratype as preserved are strikingly different from anything observed in *punctatus*: it is brown, strongly blotched with darker, the dorsal blotches tending to form transverse series across the back. Anteriorly, a dark V, the apex backward, formed of somewhat irregular blotches, reaches the middle of the orbit on each side. A less well defined V in medial to this, reaching to the tops of the orbits.

This very distinctive color and pattern are not, however, seen in the remainder of the type series of *vaupesianus* which, as preserved,

are not strikingly dissimilar to *A. punctatus*. At best the distinctive pattern of UTA 6850 represents an element of the pattern repertoire of *A. vaupesianus* not present in *A. punctatus*. It clearly will not serve to distinguish most specimens.

Habitat: The few notes on *vaupesianus* available give little indication of its ecology, except that it is associated with trees. The fact that the type was caught in a village probably indicates that it is an edge animal, not characteristic of the dark forest.

The second species was first discovered in the Departamento del Huila. It has therefore been called:

Anolis huilae, new species
(Figs. 6-9 and Map)

Type: ICN 3725, an adult male, collected by Helen Chin, October, 1976.

Type locality: Herberto Herrera's coffee plantation, Palestina, Huila, Colombia.

Paratypes: COLOMBIA: **Huila**. KU 169830-31, Parque Arqueológico San Agustín, 3 km SW San Agustín, 1750 m; ICN 3726, MCZ 159121-22: Palestina; MCZ 156305: Quebrada La Casajosa, Parque Nacional Natural La Cueva de los Guácharos (northern boundary); INDERENA R-0297, -0562, -0665, MCZ 156306, 156316: Parque Nacional Natural La Cueva de los Guácharos; ICN 4461-62: 62 km (by road) NW San Isidro de Isnos, 1940 m. **Tolima**. ICN 3732: Amaine; ICN 3727-31, 3733, INDERENA (numbers not now available, formerly UVMP 4400, 4404), MCZ 159112-117: Cajamarca; Cali (Univ. Valle, Depto. Biol.) UVC 38, 191, ICN 3735-36, MCZ 159119-120: Juntas; ICN 3734, MCZ 159118: Llanitas, 10 km N Ibagué.

[Referred specimen: Meta: ICN 4541 ca. 3-4 km NNE of Manzanares.]

Description (paratype variation in parentheses). *Head*: Most head scales smooth, slightly concave, a few convex, obtusely keeled. Ten (8-11) scales across snout between second canthals. A few narrow scales in the frontal depression much smaller than surrounding scales. Eight (7-9) scales border rostral posteriorly. Anterior and inferior nasal scales in contact with rostral. Seven (6-7) scales dorsally between nasals. Snout not protuberant in male.

Supraorbital semicircles broadly in contact with each other and with the supraocular disks. Supraocular disks with few (several)

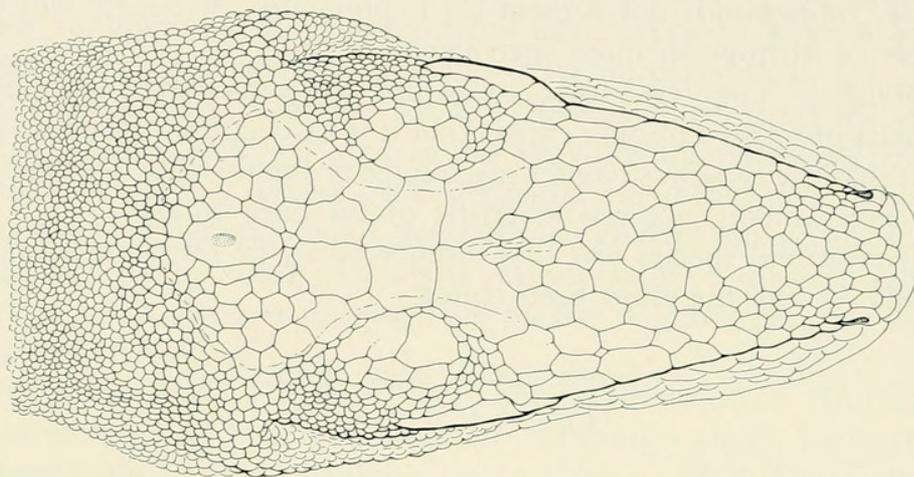


Figure 6. *Anolis huilae*, n. sp. Paratype ♂, MCZ 159015. Dorsal view of head.

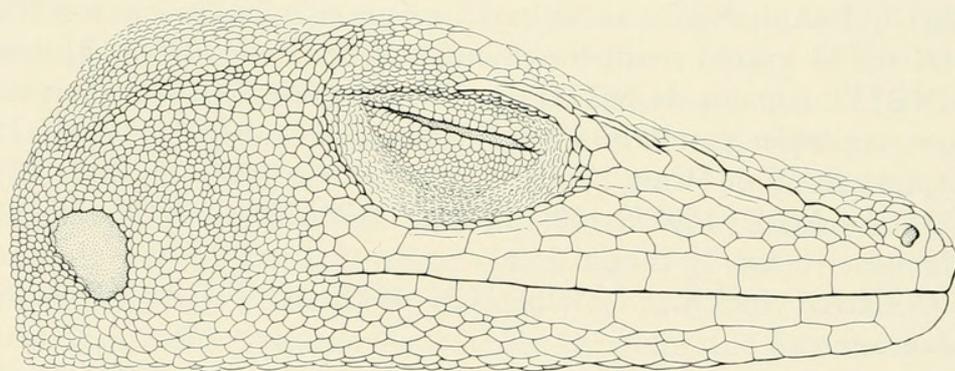


Figure 7. *Anolis huilae*, n. sp. Paratype ♂, MCZ 159015. Lateral view of head.

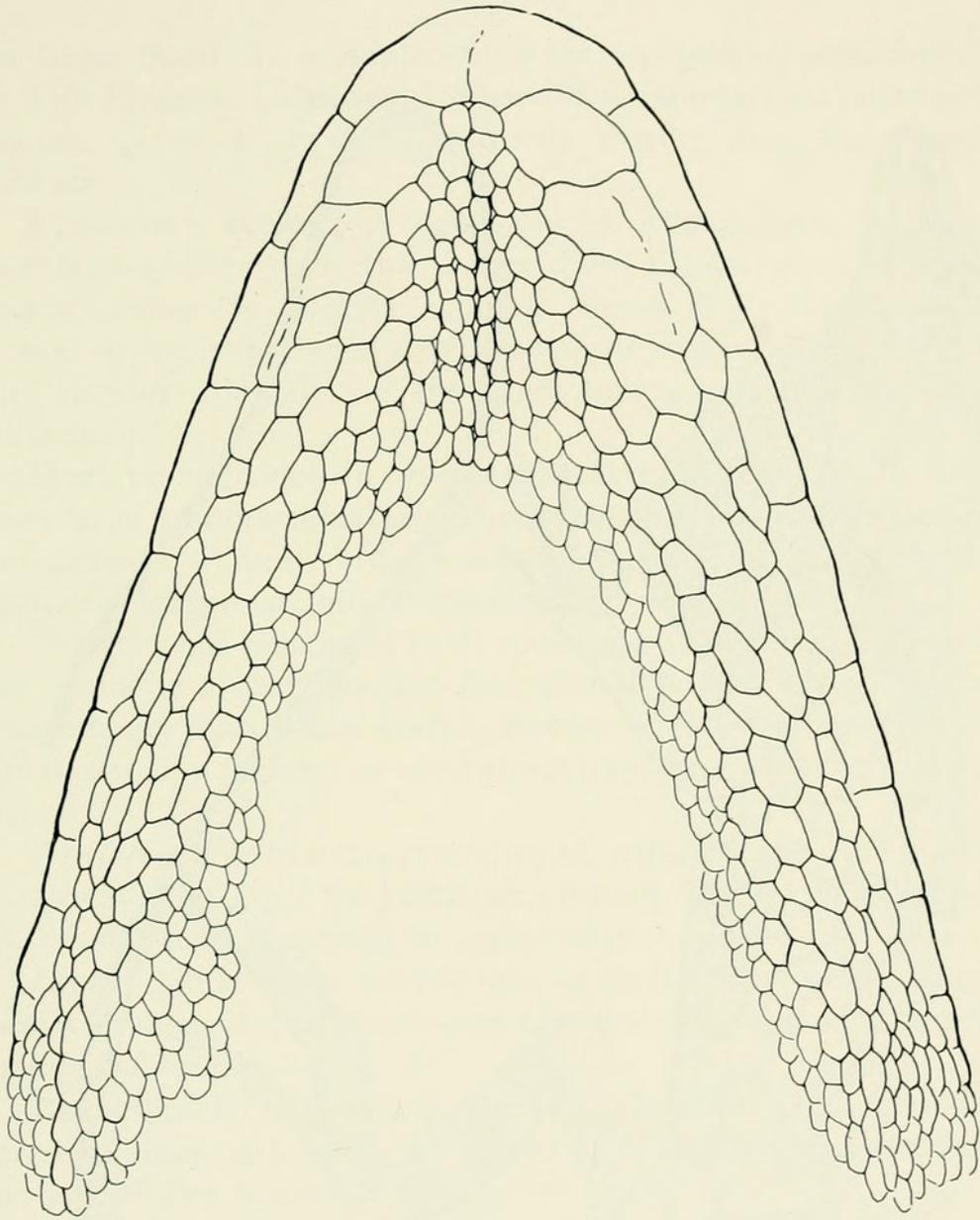


Figure 8. *Anolis huilae*, n. sp. Paratype ♂, MCZ 159015. Ventral view of head.

large smooth scales. One elongate supraciliary on each side followed by granules. Canthus blunt, ca. 8 canthal scales, the second and third largest. Five (4–5) loreal rows, counting down from the second canthal, subequal.

Temporals slightly smaller than the supratemporals, both granular. No differentiated intertemporal line of enlarged scales. The scales surrounding the interparietal abruptly larger, those anterior and lateral largest (not so in female). Interparietal equal to (smaller

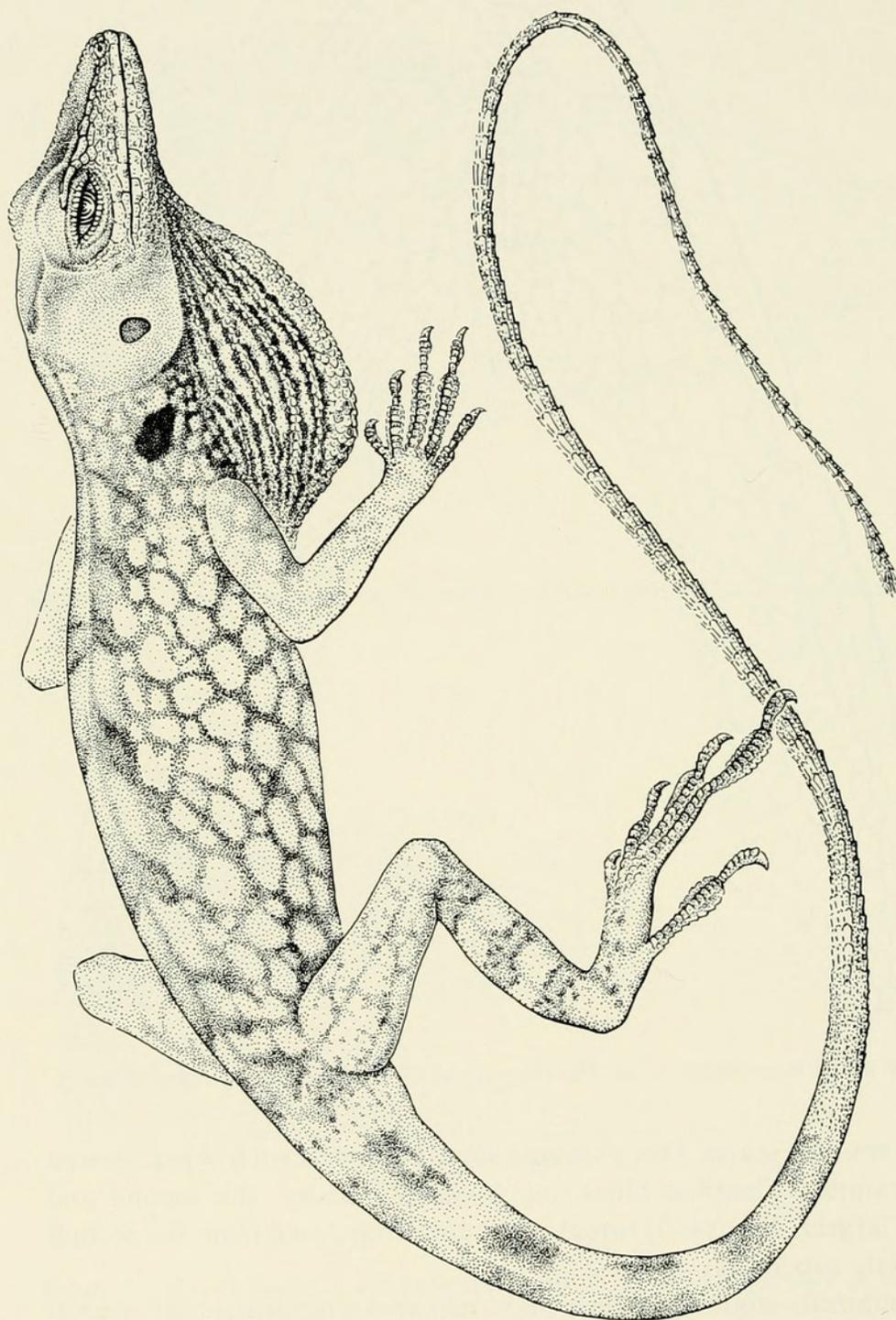


Figure 9. *Anolis huilae*, n. sp. Paratype ♂, MCZ 159015. Lateral view of whole animal, dark phase.

or larger than) ear, separated from the supraorbital semicircles by 2-3 (0-2) scales. Large scales posterior to interparietal followed by minute granules on nape, distinctly smaller than the granular dorsals.

Suboculars keeled, in contact with supralabials, continued posterior to the eye by two distinct (less distinct) rows of smaller scales, anteriorly meeting canthals. Seven (5-7) supralabials to center of eye (supralabial five is much the longest in one paratype, an obvious anomaly; in the type, the supralabials are nearly subequal).

Mental semidivided, in contact with three (1-4) scales between the very large, smooth sublabials. Three sublabials (1-4) in contact with infralabials. Central throat scales small, swollen, oval, becoming abruptly longer laterally alongside the sublabials.

Trunk: a few middorsal (2-4) rows indistinctly enlarged, weakly or distinctly keeled, grading into granular flank scales. Ventrals much larger than largest dorsals, smooth, imbricate or subimbricate (juxtaposed in female), not in distinct transverse rows (in transverse rows).

Dewlap: Large in male, extending to midbelly (absent in female). Scales at edge larger than ventrals, smooth. Lateral scales smooth, in double rows separated by naked skin.

Limbs: Limb scales weakly uni- or multicarinate. Supradigital scales multicarinate. Twenty-one (22) lamellae under phalanges ii and iii of fourth toe.

Tail: Slightly compressed, without crest. Enlarged postanals present (absent in female). A double row of keeled scale middorsally on tail. Scales behind vent smooth.

Size: The male type is 75 mm in snout-vent length. The largest male reaches 82 mm.

Color in life: Helen Chin reports topotypic animals as 'parrot green' in the trees. Her color transparencies show tan and reticulate animals after capture.

Color notes are available for two MCZ specimens. MCZ 156405, a male: "Dorsum bright green with yellow spots (seven large spots along the spine). Tail banded green and black. A white dot inside a black ring on side of neck behind the ear. Eyelid yellow, iris grey. Chin grass-green. Dewlap yellow with six green stripes, these bordered by numerous black dots. Rest of underparts greyish."

MCZ 156306, a female: "Dorsum with wide tan stripe from back

of head to halfway down tail, at which point it becomes speckled with black dots. Rest of back grey-green, darker next to tan stripe, and lighter with dark patches on the sides. Legs banded black and light green. Head light green with dark around eyes. Tip of tail bronzy. Venter yellow with few small black spots."

Both these specimens are near-topotypes. Palestina is a settlement at the beginning of the 22 km trail leading to the Parque Nacional Natural La Cueva de los Guácharos.

The colors in life of the Kansas specimens from Parque Arqueológico de San Agustín are described rather differently (although not in the same detail): "At night - dorsum pale green with brown reticulations. Dewlap cream with grey-bordered white streaks. Iris creamy-grey. Tongue orange."

Notes are at hand also for two females collected by Pedro Ruiz and J. D. Lynch near San Isidro de Isnos (notes by Lynch):

ICN 4461: "Sleeping on leaf in forest near stream. Iris yellowish. Ground color dull green with brown barring; greenish cream spots on flanks; tail barred brown and medium brown with cream edges; venter dirty cream with brown spots. Throat the same but with greenish cast."

ICN 4462: "Sleeping on Ortega, 3 m above stream at edge of corn field. Iris grey brown. Tongue pale orange yellow."

Dennis M. Harris has provided notes on the series from Tolima:

"*Male*: Dorsum pale leaf-green, spotted most vividly on the sides by 1-2 mm diameter circular dots of greenish-yellow. Head slightly brownish. Eyelid yellow. Nape with a lateral spot of blue-green to black, sometimes surrounded by a yellow area, sometimes with a light center. Tail barred or not with bands equal in width to the green. Venter white to grayish. Dewlap skin pale yellow, scales cream, in rows that are edged with black spotting.

Male may change to a deep brown with vivid yellow spots. It does so when handled and possibly as a response to another male. The one brown male seen in the field was never a green one, and had a vertically flattened body and extended dewlap. (The cream scales of the dewlap may become drab greenish in the brown-phase male.)

Female: Banded or striped, light or dark brown. The stripe is crayola brown with dark brown flecks. There is no color change except for minor tone changes."

Color notes have been made available by W. W. Lamar for the single animal from Manzanares, Meta: "Dorsum dark gray with

numerous light gray-green spots. Mid-dorsum brighter than rest of the back. More green toward the center of the flanks. Tops of forelegs gray-green with lighter yellow-green elbows and feet. Hind legs with 3 light bands above knee. Three broken bands below knee. Tail pale green with 11–12 dusty bands. A black spot with an aquamarine center on the side of the neck. Yellow eye ring and snout aqua-blue-green, darker between the eyes. Venter pale yellow with dark gray spots on the sides, brighter yellow near vent, broad portion of tail, and inguinal area. A patch of aqua-blue on tail 10–25 mm from vent, rest of tail dark gray. Dewlap an overall aqua green-blue striped with pale green and dotted with black. Spaces between stripes are pale yellow. Nostril yellow. Tongue yellow.”

Comparison of these notes for the Meta specimen described shortly after death with the detailed account from Huila and Tolima shows various discrepancies. Color differences in *Anolis*, however, may be described differently by different individuals or by the same person at different times. This, plus the capacity for color change, suggest caution in attributing taxonomic significance to color differences of the sort seen here. (See also comment below.) *There are no scale differences.*

Color as preserved: Most male *A. huilae* are strikingly distinctive because of the bold lateral spotting, plus the lines of dark spots on the dewlap. Some specimens display a more muted spotting. This is especially true of the individual from Manzanares, Meta. The latter seems at first distinguishable because the spotting on the dewlap is not in lines but quite random. Some specimens from Tolima, however, have the spotting on the dewlap irregular also. The Meta animal does not, on present evidence, fully match the type series; since it is also geographically peripheral (on the east side of the Andes, rather than in the Magdalena Valley) I have not made it a paratype. With only one specimen and no structural differences it is not permissible to describe it taxonomically.

Habitat: Dennis Harris reports: “found on relatively smooth bark tree *trunks* usually, between 1 and 7 meters. Males almost exclusively there, females sometimes on bushes nearby, 1 m high. Usually only single male/tree trunk (25 cm+ diameter). Shrubs seem to be only *peripheral* environments. Not found on very smooth-bark guayaba (guava) trees. Not found on trunks with heavy moss growth. Common right in town of Cajamarca and along edges of road. Males more frequently seen and more of them

caught. Only time male and female seen together on tree trunk they were copulating. Usually seen head down, out (like *frenatus*) on trunk. At Anaime *Prionodactylus argulus* found at same site. At Llanitas, 10 km from Ibagué, *Anolis antonii* and *A. huilae*; at Juntas, much higher, *Phenacosaurus* and *A. huilae*."

MCZ 156316 was found below a cave-hole of *Rupicola rupicola* among defecated seeds. Apparently a food item, it was in relatively good condition and quite recognizable.

Comparisons: *A. huilae*, although obviously a member of the *punctatus* species group, is not obviously closely related to any other presently described member. The color pattern of males is highly distinctive.

A third species comes from the southern slopes of the isolated Santa Marta range. It is to be called:

Anolis santamartae, new species
(Figs. 10-13 and Map)

Type: CAS 113922, adult male.

Type locality: San Sebastián de Rábago, Sierra Nevada de Santa Marta, Cesar, Colombia (10° 4" N, 73° 16" W), Borys Malkin coll., 1-10 April, 1968.

Paratypes: same data as type: CAS 113924, MCZ 156311.

Description (paratype variation in parentheses). *Head:* Moderately elongate. Head scales rather large, smooth, flat except for smaller bluntly keeled or swollen scales at tip of snout. Six (4-5) scales across snout between second canthals. Frontal depression distinct, the scales within it larger (some smaller) than those anterior to it. Anterior and inferior nasal scales in contact with rostral. Four (5-6) scales dorsally between supranasals. Rostral area protuberant in male, overhanging lower lip (not so in female).

Supraorbital semicircles broadly in contact with each other and with the supraocular disks. Supraocular disks well defined, comprised of 8 to 10 smooth scales. Remainder of supraocular area with large granules. Canthus distinct, four or five canthal scales, the second and third (or first and second) largest. Five (4-5) loreal rows, the lowermost largest. Temporal and supratemporal scales granular, larger at the angle of the mouth than at the angle between temporal and supratemporal regions. Scales surrounding the interparietal rather abruptly larger, largest laterally, grading into dorsals

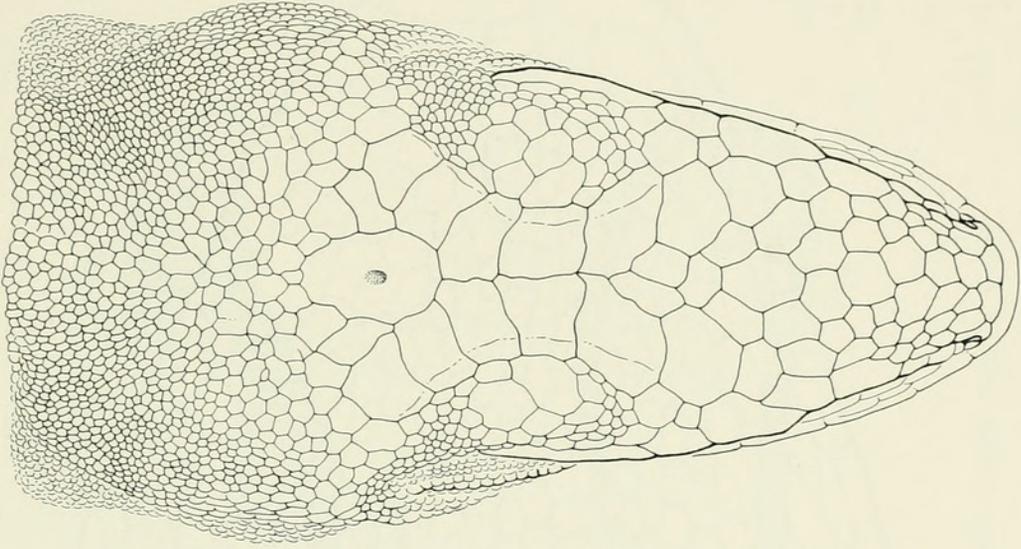


Figure 10. *Anolis santamartae*, Type ♂, CAS 113922. Dorsal view of head.

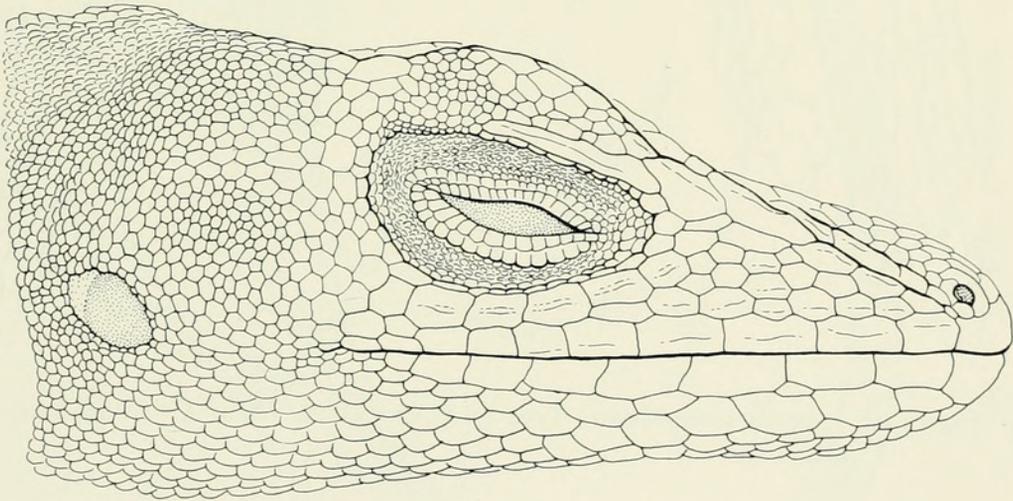


Figure 11. *Anolis santamartae*, Type ♂, CAS 113922. Lateral view of head.

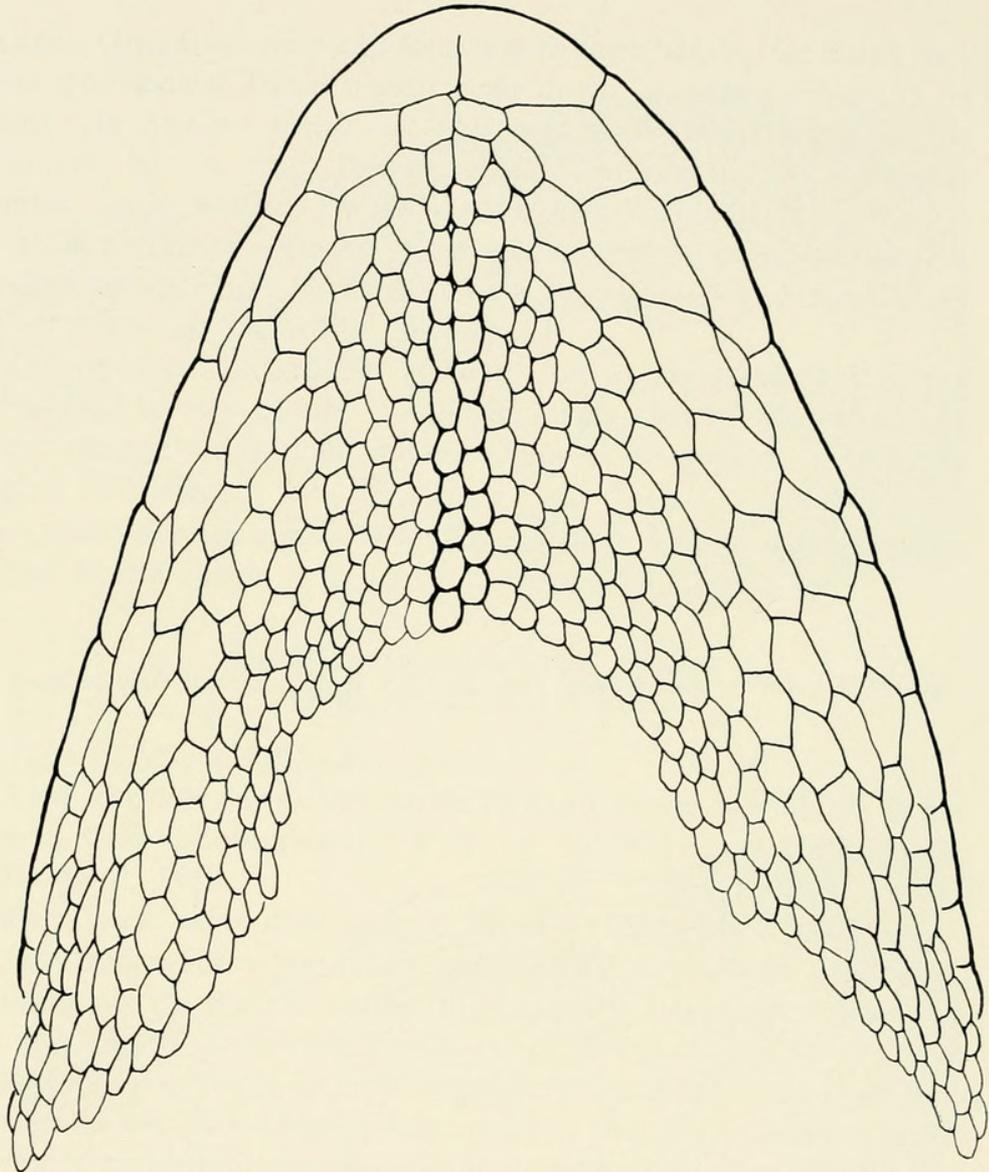


Figure 12. *Anolis santamartae*, Type ♂, CAS 113922. Ventral view of head.

posteriorly. Interparietal much larger than ear, broadly in contact with the supraorbital semicircles.

Suboculars weakly keeled, in contact with supralabials, anteriorly separated from the canthal ridge by two (1-2) scales, posteriorly grading into the temporals. Seven supralabials to the center of the eye.

Mental semidivided (mental region abnormal in MCZ 156311), in contact with two large scales between the well-developed sublabials.

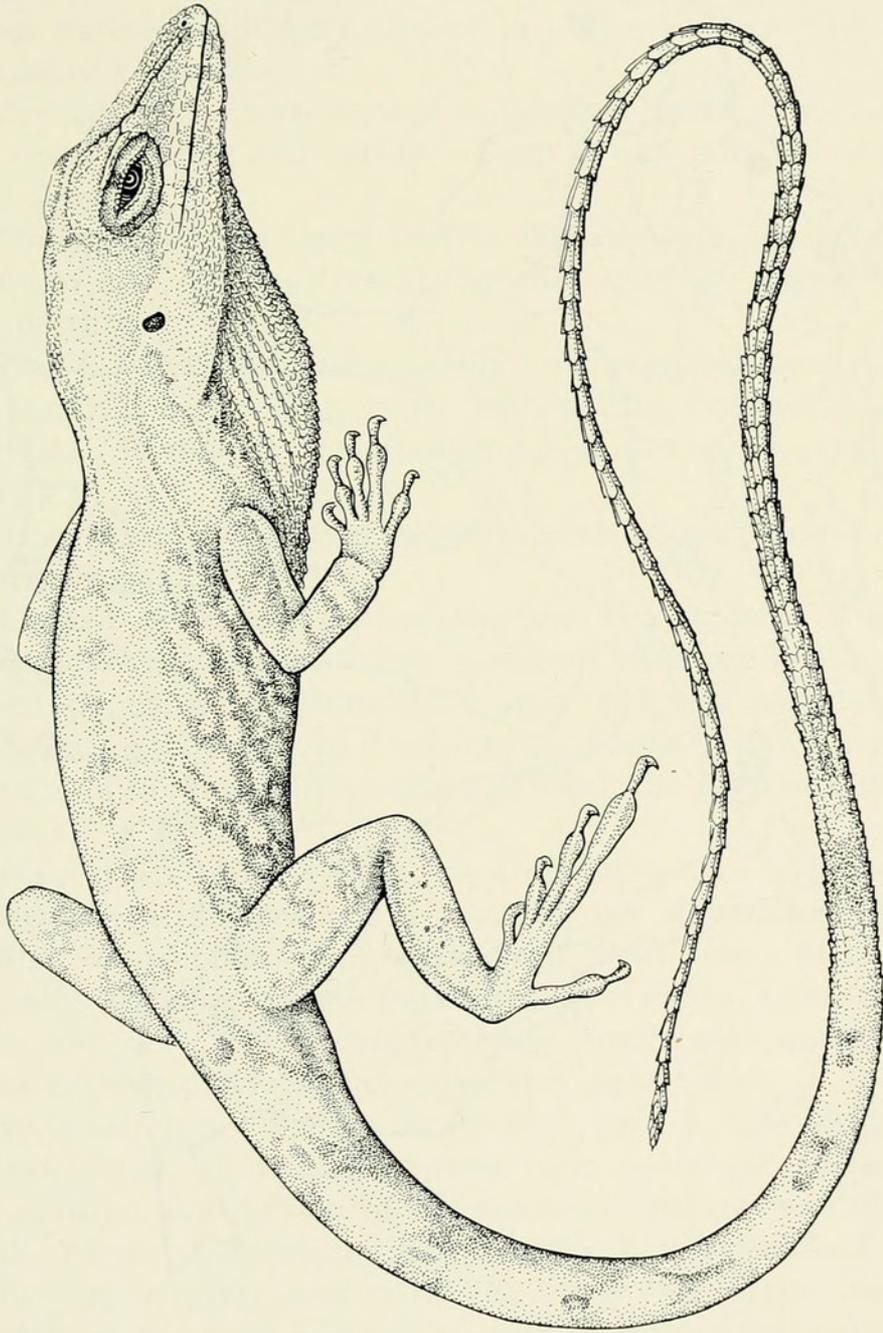


Figure 13. *Anolis santamartae*, Type ♂, CAS 113922. Lateral view of whole animal.

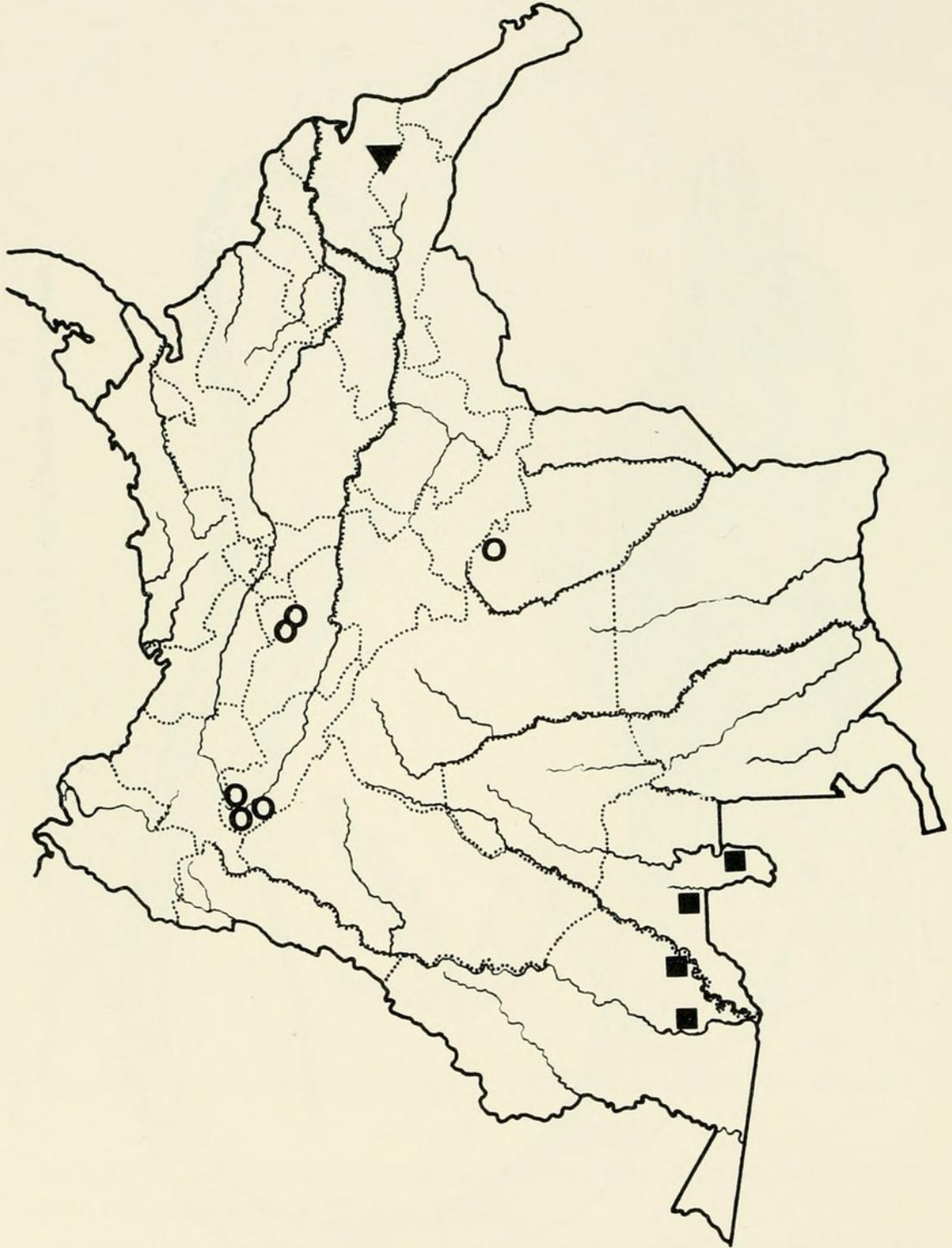


Figure 14. Distribution of the species described herein. ▼: *Anolis santamartae*; ○: *Anolis huilae*; and ■: *Anolis vaupesianus*.

Four (3) sublabials in contact with infralabials. Gulars rather large, swollen, increasing in size laterally and anteriorly.

Trunk: Ca. four to six middorsal rows flat, weakly keeled, subimbricate, much larger than flank granules but grading into them. Ventrals still larger, smooth or obtusely keeled. Chest scales distinctly keeled.

Dewlap: Large in male, only indicated in female. Scales in close set rows, elongate and narrow, except at edge where they are flat and smooth.

Limbs: Scales on limbs uni- to multicarinate, those on digits multicarinate. Eighteen (19–21) lamellae under phalanges ii and iii of fourth toe.

Tail: Compressed. Scales weakly to strongly carinate. A double middorsal row. No tail crest. No verticils. Scales behind vent carinate. Post-anals large (broken up on one side type, absent in female.)

Size: Male type: 50 mm, snout to vent. Male paratype: 55 mm. Female paratype: 53 mm.

Color as preserved. Female paratype: Gray-brown. A light line from suboculars to above ear. A narrow dark interorbital bar. A series of ovoid or rhomboidal dark blotches paravertebrally. Irregular oblique dark streaking on flanks. Limbs irregularly banded. Tail very weakly banded. Throat and belly smudged with darker.

Male type: Gray. A light line from suboculars to above ear. Another light line from lower edge of ear along lateral edge of dewlap onto underside of upper arm. Weak traces of blotching dorsally. Irregular oblique dark streaks on flanks. Limbs and tail with very weak and obscure markings. Underneath smudged with brown. Dewlap skin white, scales very light brown.

Male paratype: A dark interorbital bar. A light stripe from suboculars to above ear, another from below ear to shoulder. Middorsum and dorsum of tail obscurely marked with light and dark. Flanks with oblique dark streaks. Limbs smudged above. Belly with irregular dark markings. Throat with vaguer markings.

Habitat: San Sebastián is at the border between the Departments of Cesar and Magdalena, and the specimens may have been collected in either Department. The elevation is at, or above, 2,000 m. There are no ecological notes.

DISCUSSION

Comparison of *santamartae* and the other two new species of the *punctatus* complex with each other and with the other already-described members of the complex could be made in tabular form, as in Williams (1974). Here, however, I prefer to discuss and evaluate the characters on which I recognize the several species. I begin with the color differences.

Color in Life

For this purpose the few detailed descriptions of color in life of *Anolis punctatus* must be quoted.

Hoogmoed (1973) has a description for *A. punctatus* '*punctatus*'¹ from Surinam: "Color in life grass-green above with sky-blue dots, eyelids purplish with a yellow rim. Chin bluish, throat greenish. Belly white to purple-green. In bright sunlight the lizards are purple with sky-blue dots. Dewlap in males yellow ochre with rows of white scales; in females the scales on the dewlap are yellow. Iris orange-brown."

A parallel description is provided by Dixon and Soini (1975) for *A. punctatus* '*boulengeri*' from the Iquitos area in Peru: "The dorsal coloration of adults is leaf-green with six to seven very narrow white cross-bands confined to the upper body. The lower sides are spotted with minute white dots, and the limbs are spotted with minute dark brown spots. Occasionally specimens are deep purple dorsally, especially after being in captivity for a few hours. The white cross-bands and white spots are very distinct when the latter color prevails. Male dewlaps are orange to reddish-orange with the enlarged lateral scale rows light yellow."

P. E. Vanzolini has provided me with a translation of the unpublished field description of Helmut Sick of an *A. punctatus* '*punctatus*' from the Atlantic Forest in Brazil (Río Itaunas, Espírito Santo): "General body color alive: grayish sepia, dewlap chrome yellow. Freshly killed: moss green, eyelid yellowish green, dewlap chrome yellow with stripes composed of whitish green spot, chin whitish-green. Underparts greenish-white. Digits and tail with

¹Western specimens of *punctatus* with keeled ventrals are usually called *boulengeri* O'Shaughnessy whether as subspecies or species. See Williams and Vanzolini (1980) for evidence that '*boulengeri*' is a morph and not a valid taxon.

vestiges of dark brown crossbands. Posterior two-thirds of tail grayish sepia. Flanks with lines of white spots. . . .” Vanzolini himself describes dewlap colors for two additional specimens: (Santo Amaro dos Brotas, Sergipe): ‘pure yellow’; (Lago Mapori, Rio Japura, Amazonas): ‘rusty orange.’

No color descriptions from living specimens are available for *A. santamartae*, *A. caquetae*, *A. deltae*, or *A. nigropunctatus*. The color descriptions of *A. vaupesianus* and *huilae* have been given above.

There are serious problems in the comparisons of color and pattern in the members of this complex. The few good reports are for the local populations of widely scattered regions or for individual specimens. This would be a difficulty in any taxonomic group. In *Anolis* an additional problem exists: color repertoire may be extensive and tends to be especially so in the green species. In the latter, the difference between light and dark phases may be extreme, and there may be in life intermediate patterns or colors that are only briefly or occasionally seen. (This may have been true, for example, of the Meta specimen referred to *A. huilae* above.) Preserved specimens compound the dilemma already posed. Pattern or lack of pattern may be due entirely to the preservative, or to its strength. Specimens done in strong formalin tend to a muddy uniformity; many of the older specimens in collections are of this type. It is fortunate that none of the specimens considered in this paper are of so inferior a quality. Nevertheless, they have been preserved by different individuals with different preferences in technique. The preserved specimens are therefore only minimally comparable.

But even the available descriptions of color in life are imperfectly comparable. They were not made to be checked against one another, and they therefore do not stress quite the same details. They were never checked against the same color standards.

Yet it is quite clear that enough information exists to assure us that differences exist. While no possibility exists of entirely avoiding error, some plausible conclusions may be drawn.

Color in anoles is best discussed by breaking it into components. It is a fact about *Anolis* in general that dewlaps are least modified by color change and most readily interpretable in preserved specimens. This fact quite accords with the view (e.g., Rand and Williams, 1970; Williams and Rand, 1977) that the dewlap is an intra- and interspecific signal which should have high constancy in order

always to convey the same message. (A caveat: this rule may have less validity in mainland *Anolis* than it appears to have in the species of the islands.)

In the present case we have the following evidence of dewlap color:

punctatus punctatus (Surinam)

- yellow ochre with white scales (Hoogmoed). The other reports from the range of subspecies (Sergipe, Espirito Santo) stress a yellow color also.

punctatus 'boulengeri'

- orange to reddish-orange (Dixon and Soini). Clearly a deeper shade than in *punctatus punctatus*, but not sharply different. Preserved specimens of both taxa show only light skin and scales.

vaupesianus

- 'black' (Pyburn); 'mulberry red' (Medem) presumably on the authority of the collector: 'greenish' in the female; Medem, in this case himself the collector. There is an obvious discrepancy here, but we are evidently dealing with a dark dewlap, and the dewlap skin in all preserved specimens is darkly pigmented.

From these notes it is clear that *vaupesianus* is sharply distinct in dewlap color from the animals that in size and morphology it most resembles, western *A. punctatus*, and from *A. huilae*. The dewlap of the latter, with dark spots placed in lines or randomly, is quite unlike any of the others. Insufficient information exists for any really useful discussion of dewlap color in the other taxa.

As regards body color, I am very uncertain what can be inferred. From the descriptions of Hoogmoed for Surinam and of Dixon and Soini for Peru, it would appear plausible that a purple phase exists in western *A. punctatus* which does not occur in *A. vaupesianus*, but Vanzolini has not noticed such a purple phase in the *punctatus* of Amazonia and eastern Brazil *punctatus* that he has caught. Absence of purple may therefore not be fully diagnostic for *vaupesianus*. Other aspects of the color of *vaupesianus* involve tints and special aspects of its color repertoire which again are of uncertain value. Size, body, and dewlap color seem safer guides to identification. For *A. huilae* we do not know enough about color repertoire to evaluate the colors in life that we do know. The bold flank spotting seen in *huilae* may be useful, like the nape spot, but neither are obvious in females and are not mentioned in some of the descriptions of colors

in life. See above for discussion of the specimen from Meta. For *nigropunctatus*, *caquetae*, *santamartae*, and *deltae*, discussions of preserved body color are of very dubious value. Are the spots of preserved *nigropunctatus* surely of diagnostic value? There is at present no way to tell. The light line in *santamartae* from suboculars to ear seems distinctive. It is less evident in the type than in the other darker specimens. It may or may not be readily visible in life. For these last four species body color cannot be disregarded but determination of specimens must depend upon size, scale characters, and *locality*. Let us look at these features in sequence.

Size

A. vaupesianus, *A. huilae*, and *A. nigropunctatus* are all within the size range of *A. p. punctatus* (70–80+ mm snout to vent length). *A. dissimilis*, *A. caquetae*, *A. santamartae*, and *A. deltae* are, on present evidence, smaller (50–60 mm) (Table 1). (I include in these tables and discussions all described members of the *punctatus* group east of the Pacific slopes of the Andes.)

Table 1. Size of *punctatus* group anoles from east of the Andes and from the inter-Andean valleys.

	Maximum male snout to vent length (in mm.)
<i>punctatus</i>	85
<i>transversalis</i>	83
<i>vaupesianus</i>	82
<i>huilae</i>	82
<i>jacare</i>	73
<i>nigropunctatus</i>	72
<i>deltae</i>	58
<i>caquetae</i>	57
<i>dissimilis</i>	56
<i>santamartae</i>	55

Scale characters

The more significant of these may be examined one by one:
Ventrals: In *Anolis* it is probable that smooth ventrals are

primitive, keeled ventrals the derived condition. (The argument derives from the apparently more frequent correlation of smooth than keeled ventrals with other characters considered primitive; this is not a strong argument.) Most *punctatus* group species have smooth ventrals, but a few have strong keels on the venter. Table 2 again lists the conditions of the several species east of the Andes or in the inter-Andean valleys.

Table 2. Ventral scales in *punctatus* group anoles from east of the Andes and from the inter-Andean valleys.

<i>punctatus</i>	smooth or weakly to strongly keeled
<i>vaupesianus</i>	weakly keeled
<i>transversalis</i>	smooth
<i>huilae</i>	smooth
<i>jacare</i>	smooth
<i>nigropunctatus</i>	smooth
<i>deltae</i>	smooth
<i>caquetae</i>	weakly keeled
<i>dissimilis</i>	smooth
<i>santamartae</i>	smooth or weakly keeled

Nostril-rostral relationship: This character is somewhat variable within species, but within a narrow range. The *punctatus* group shows only a fraction of the possible range, and each species shows only a segment of this restricted range. The relevant conditions and the species in which these are seen are listed below:

- 1) *Circumnasal scale (=nasal) directly in contact with rostral:* *nigropunctatus, jacare.*
- 2) *Circumnasal scale separated from rostral by a small round undifferentiated scale:* *nigropunctatus, dissimilis.*
- 3) A differentiated *anterior nasal* scale present and in contact with rostral (the anterior nasal is characteristically triangular and overlaps posteriorly part of the *circumnasal*): *deltae, huilae.*
- 4) *Anterior plus an inferior nasal* in contact with rostral: *punctatus, boulengeri, transversalis, vaupesianus, caquetae, huilae, santamartae.*

It is noteworthy that, while a species may exhibit two of these four categories, these are always adjacent ones and no species is

known to range the full gamut. This character will *assist* in discriminating species.

Snout protuberant or not in males: This character, well known in *A. punctatus*, is clearly present in *A. vaupesianus*, less obvious in *nigropunctatus*, and absent in the other taxa. It again *assists* in identifying species.

Scales across the snout between second canthals: The range in the *punctatus* group is moderate, most species ranging between 6 and 9, *transversalis* including, however, values as low as 4, and *caquetae*, *nigropunctatus* and *vaupesianus* reaching 10. Very low counts here may point to *transversalis*. Counts otherwise are not diagnostic.

Scales between the semicircles: the minimum number between the semicircles is 0, usually implying broad contact. In the species set as a whole the modal conditions are 0 and 1; a count of 2 is relatively infrequent. This character cannot be relied on to distinguish species.

Loreals: The maximum number of loreals (counted down from the second canthals) may be as low as 3 (*transversalis*) or as high as 7 (*vaupesianus*). More frequently the count ranges from 4 to 6. Again, a very low number of loreals may point to *transversalis*, but in general loreals are not diagnostic.

Interparietal: A very large interparietal in contact with the semicircles is a distinguishing feature of the unique type of *caquetae* and of the type series of *santamartae* and of *dissimilis* and *deltae*. An interparietal smaller than the small ear is characteristic of *nigropunctatus* (clearly so only in the type). For the other members of the *punctatus* group the interparietal is not diagnostic.

Number of supralabials to the center of the eye: The exceptional number of 11 is distinctive for *A. dissimilis*. A range of 6 to 9 is characteristic for all the other species and hence does not discriminate among them.

Lamellae under phalanges ii and iii of fourth toe: Number of toe lamellae in *Anolis* correlates with two factors—perch and size. In the known cases, *punctatus* group anoles tend to high perches—usually in the crown—and should have high lamellar counts for their size. Correspondingly, the better-known, larger species, known to correspond to expectations in perch—*punctatus*, *vaupesianus*—have counts in the mid- to upper 20s. *A. nigropunctatus*, *A. jacare*, and *A. huilae* have relatively low counts for *punctatus* group animals of their size (20–24).

Tail crests: Two species—*dissimilis* and *deltae*—have tail crests and hence are unique in the group. Others have a double row without a crest.

Species Diagnoses

What combinations of characters diagnose the *punctatus* group species I have described herein and the others previously described? (See also Tables 3 and 4.)

- 1) *Vaupesianus* is distinctive in its *black dewlap, strongly protuberant snout* in males, *weakly keeled ventrals*, and *moderate size*. (Distribution: Vaupés and Amazonas.)
- 2) *Huilae* is distinctive in its spotted or streaked dewlap, and (usually) in the *vivid mottling* of its flanks and in its *moderate size (ventrals smooth)*. (Distribution: the upper Magdalena valley in Huila and Tolima, perhaps at high elevations on the eastern slope of the Andes in Meta [Manzanares].)
- 3) *Santamartae* is distinctive in the large *interparietal broadly in contact with the semicircles*, plus *smooth* or *weakly keeled ventrals*, *small size*, and a *light line from supralabials to ear and from ear to upper arm*. (Distribution: south slope of Santa Marta mountains.)
- 4) *Caquetae* is diagnosed by its *large interparietal broadly in contact with the semicircles*, plus *keeled ventrals*, *small size*, and no light line from suboculars to ear. (Distribution: known only from the Upper Apaporis in Caquetá, Colombia.)
- 5) *Nigropunctatus* stands out by its *small interparietal, smaller than the small ear*, an irregularly and weakly punctate pattern on the flanks (in males on middorsum also), *snout protuberant in males*, and by *moderate size (ventrals smooth)*. (Distribution: from Norte de Santander in Colombia to Táchira and Trujillo in Venezuela.)
- 6) *Deltae* has the *large interparietal broadly in contact with the semicircles* and *small size of caquetae* but has *smooth ventrals*, a *tail crest* and a *short, blunt head*. (Distribution: Delta of the Orinoco in Venezuela.)
- 7) *Dissimilis* has a very *large interparietal in contact with the semicircles*, *small size*, *smooth ventrals* and *tail crest* like those of *deltae*, but a *strikingly elongate head*. (Distribution: Madre de Dios in Peru.)

- 8) *Jacare* is distinctive in *moderate size*, male without a *protuberant snout*, with an *immaculate yellow dewlap* and a *strongly reticulate body pattern* with often an *oblique light streak* from the throat to above the shoulder; *female* with *unspotted body* and *unmarked throat* (ventrals smooth). (Distribution: the Sierra Madre de Mérida in Venezuela.)
- 9) *Transversalis* is like *jacare* in *moderate size* and the *lack of a protuberant snout in males*, but the male has a *yellow dewlap with streaks and spots*, and a *body pattern of oblique light lines enclosing rows of black spots*; and females with *bold transverse bands on the body* and the *throat vividly cross-marked with black* (ventrals smooth). (Distribution: western Amazonia.)
- 10) *Punctatus* has *moderate size* and a *strongly protuberant snout* in males and a *yellow or orange dewlap*. (*Ventrals smooth or keeled*). (Distribution: Amazonia, the Guianas, and the Atlantic Forest of Brazil.)

The Geography of Difference

The species of the *punctatus* group that have been discussed here are all those thus far reported that are east of the Andes or inter-Andean. (For convenience, *santamartae* is counted in this group; it lies in an eastward-looking valley in the southern part of the isolated Sierra Nevada de Santa Marta.) This assemblage, as it turns out, is, if not a natural group, clearly as natural as a group which also includes taxa west of the Andes, currently referred to the *punctatus* species group. None of the western species are demonstrably close to the species here considered.¹

¹I no longer consider *A. nigropunctatus* to be especially close to *A. nigrolineatus* (Williams, 1965). *A. nigropunctatus*, as will be suggested below, is probably closer to *A. jacare*, and *A. nigrolineatus* may be a strict synonym of *A. festae* Peracca (syntypes examined). Both nominal species have the same highly peculiar dewlap with an elongate dark spot. There are no scale differences. There is variability in head shape. The sole known differences between southern Ecuadorian specimens (Machala, El Oro) known from recent large collections by Fitch, Echelle and Echelle, and northern populations (Pichincha) known from equally large collections made by Kenneth Miyata are smaller size in the northern populations (Miyata, personal communication) and a blue iris in the north (Miyata) as compared with the yellow iris reported by Fitch *et al.* (1976) for southern animals. No recently collected animals—live or preserved—show the narrow dark middorsal line believed diagnostic for *A. nigrolineatus*.

Table 3. Scale variation in *punctatus* group anoles—inter-Andean or east of Andes.

	<i>transversalis</i>	<i>punctatus</i>	<i>vaupesianus</i>	<i>huilae</i>	<i>jacare</i>
sample size	N = 38	N = 157	N = 6	N = 17	N = 24
dewlap in ♀	+	-	-	-	-
snout swollen in ♂	-	+	+	-	-
scales across snout	4-8	7-14	8-10	8-11	6-8
nasal/rostral	anterior and inferi- or nasal in con- tact with rostral	anterior and inferi- or nasal in con- tact with rostral	anterior and inferi- or nasal in con- tact with rostral	anterior and inferi- or nasal in con- tact with rostral	circumnasal in con- tact with rostral
scales between semicircles	0-1	0-3	0-2	0	0-2
loreal rows	3-6	4-8	5-7	4-5	4-7
interparietal/ear	>>	>/<	>/>>	>/<	>
scales between interparietal and semicircles	0-3	(0)-(5)	2-3	0-3	1-3
scales between sub- oculars and supra- labials	0	0	0	0	0
supralabials to center of eye	6-9	6-10	7-9	5-7	7-9
lamellae under fourth toe	22-27	22-30	22-25	20-24	19-25
ventrals	smooth	keeled or smooth	weakly keeled	smooth	smooth
tail crest	-	-	-	-	-
size	83	85	80	82	73

Table 3 (continued)

	<i>nigropunctatus</i>	<i>santamartae</i>	<i>caquetae</i>	<i>deltae</i>	<i>dissimilis</i>
sample size	N = 4	N = 3	N = 1	N = 1	N = 1
dewlap in ♀	-	-	?	?	?
snout swollen in ♂	(+)	+	+	-	-
scales across snout	7-10	4-6	10	8	7
nasa/rostral	circumnasal in contact with rostral or separated by 1 scale	anterior and inferior nasals in contact with rostral	anterior and inferior nasals in contact with rostral	anterior nasal in contact with rostral	circumnasal separated from rostral by 1 rounded scale
scales between semicircles	0-2	0	1	0	0
loreal rows	4-6	4-5	5	4	4
interparietal/ear	<	>>	>>	>>	>
scales between interparietal and semicircles	1-4	0	0	0	0
scales between suboculars and supralabials	0	0	0	0	0
supralabials to center of eye	7	7	7	7	11
lamellae under fourth toe	21-22	18-21	22	24	17
ventrals	smooth	smooth or obtusely keeled	weakly keeled	smooth	
tail crest	-	-	-	+	+
size	72	55	57	58	56

Table 4. Scale variation in *Anolis punctatus*.

	Colombia N = 4	Ecuador N = 38	Peru N = 46	Bolivia N = 6	Guyana N = 8	Surinam N = 7	Brasil N = 48
scales across snout	8-11	7-12	7-14	9-13	9-11	8-11	7-14
scales between supraorbital semicircles	0-2	0-2	0-2	1-3	1-2	0-2	1-2
loreal rows	5-8	4-7	5-7	5-8	4-6	5-6	5-7
interparietal/ear	>	>	>/<	≈	>/<	≈	>/<
scales between interparietal and semicircles	2-4	1-4	(0)-(5)	2-4	2-4	1-3	1-3
supralabials to center of eye	6-8	6-9	6-9	8-10	7-10	7-10	6-9
lamellae under fourth toe	24-25	24-29	22-29	25-29	23-26	24-25	22-30
ventrals	keeled	keeled	keeled or smooth	smooth	keeled or smooth	smooth	keeled or smooth

The eastern and inter-Andean assemblage is, itself, clearly morphologically heterogeneous, showing several levels of differentiation. Yet it is a striking fact that only one of the 11 forms here called species is widely sympatric with any of the others: *A. transversalis* occurs within the range of *A. punctatus* and *A. vaupesianus*. It is abundantly distinct not only from the two taxa with which it is sympatric, but from *all* other *punctatus* group species. It differs not only in the striking color characters emphasized in the section immediately above, but it stands at one extreme in scale characters also (low counts of loreals and scales across the snout).

None of the other nine described forms is known to co-occur. Two of them, however, are in their own way sharply distinct. *A. dissimilis*, as its name implies, seemed very distinct when it was first made known, but the tail crest, otherwise unique within the *punctatus* group, has since been found in widely allopatric *deltae* (which differs, however, *inter alia*, in its much shorter head).

The remaining taxa are allopatric; they do, however, divide into low-land and high-land forms, and this, while it is not *prima facie* evidence against conspecificity, makes it a little less likely.

The low-land species are *punctatus*, *vaupesianus*, and *caquetae*. Here it is clear that as regards the first two I have relied on color in life. The difference, however, is sharp, and, if there are any intermediate populations, we can specify where they must be: in Amazonas between the Ríos Putumayo and Caquetá.

It is, of course, crucial to the final allocation of all allopatric taxa that are phenetically similar that, when possible, we endeavor to discover whether there is a contact zone and to determine what happens there. I have expressly chosen not to call distinctive populations subspecies merely because they are related. Unless variation is clinal and the relevant characters not congruent—in which case taxonomic description is not warranted—the alternative to the hypothesis of allospecies, which I am using here, is subspecies, a highly restrictive hypothesis according to which distinctive populations with congruent characters meet in well-defined zones of intergradation. I agree with the long-expressed opinion of Wilson and Brown (1953) that these restrictive conditions are rarely met. *A. punctatus* and *A. vaupesianus* are, indeed, distinctive populations but closest relatives that are either allospecies, the ends of a cline, or subspecies. There is not present evidence of clinal change or of

intergradation. My decision therefore is to tentatively regard the two populations as allospecies.

The case of *A. caquetae* is different. It is a single specimen peculiar in some aspects of color and squamation—in combination *outside* the known limits of other forms. As a single specimen, it is not clearly representative of any distinctive population. None of its characters is individually unusual within the broad variation of the *punctatus* group. The *large* interparietal in contact with supra-orbital semicircles is not at all usual in the *punctatus* species group, but see *A. santamartae*. The color *as preserved* is distinctive but suffers the difficulty of preserved color in *Anolis*, discussed at some length above. Clearly, acceptance of *A. caquetae* as a valid species involves risk of error. But if it were to be synonymized, what would it be synonymized with? *A. punctatus* or *A. vaupesianus*? Or would both sink into a variable species to be called *A. punctatus*? The large interparietal in contact with semicircles is rare in *A. punctatus* (one known case in 157 specimens), unknown in *A. vaupesianus* (but the sample is too small for a secure statement). It is closer to *A. vaupesianus*, but it would seem erroneous on present evidence to synonymize *A. vaupesianus* with *caquetae*. The case here is one of inadequate evidence, and, above all, of inadequate search for evidence. The fauna of Ríos Vaupés, Caquetá, and Putumayo and their tributaries is very poorly known.

The remaining taxa with which we are concerned—*jacare*, *nigropunctatus*, *huilae*, and *santamartae*—are all animals of high elevations. Of these, only *jacare* is an old name, and *huilae* and *santamartae* have been described herein.

Santamartae is the most distinctive of these. In the tendency to keeling of the ventrals and the light line from the labials toward the ear it is unlike the others. It seems also to be smaller.

The other three, it must be confessed, are primarily distinctive in coloration. *A. huilae* seems to stand out in this series. The bold light spotting and nape spot in males, as well as the contact of differentiated anterior and inferior nasals with the rostral, contrast with the dark spotting of *nigropunctatus* and the vermiculation of *jacare* and with the primitive circumnasal scale characteristic of both the latter.

Between *jacare* and *nigropunctatus* there are no conspicuous scale differences other than the smaller interparietal of *nigropunctatus* (but this is sharply evident only for the male type of *nigropunctatus*,

the only known male). They differ, however, in color; the sparse dark spots of *nigropunctatus* are quite unlike the bold vermiculation of male *jacare*. I am reinforced in my confidence of this color character by examination of a series of 11 specimens of *jacare* from three localities in the state of Merida made available to me by James R. Dixon. The males seem clearly distinctive; the females are not as readily assigned. Between these two, however, and even between *nigropunctatus* and *huilae*, there might be a contact zone. The appropriate intermediate regions remain uncollected.

I have not here gone beyond a minimal analysis of the phenetic similarities of the 10 species of the eastern *punctatus* species group. I do not attempt any history or even any dendrogram of relationship. It seems to me totally premature to do so.

Of the 10 species only three—*punctatus*, *transversalis*, and *jacare*—have been known for more than 15 years. Of these, only *punctatus* is widespread and relatively common. *A. transversalis* is widespread but rather scarce in collections, although the collections of Pekka Soini (Soini and Dixon) indicate that it must be moderately common, at least in the Iquitos region. *A. jacare* is known only from the Merida region in Venezuela where, from the experience of Carlos Rivero Blanco and Williams (Williams *et al.*, 1970, and the recent collections by James Dixon), it is commoner than the infrequent sightings of it and the meager collections indicate.

Anoles of the *punctatus* group are animals usually of the canopy and appear rather infrequently on the trunks or near the ground (*A. huilae* *fide* Dennis Harris may be an exception since it is, according to his report, more of a trunk-ground adapted species like *A. frenatus* [cf. Scott *et al.*, 1976 for the latter]). Most of them are, therefore, not conspicuous lizards, whatever their real abundance.

Other species may be genuinely rare, rare enough that the question of intraspecies and interspecies, even intergeneric competition, becomes moot. It is difficult, however, to demonstrate that failure to observe is equivalent to real rarity. Many species of *Anolis* also are highly cryptic and behaviorally highly adapted to crypsis, almost never visible unless they move. Some, readily capturable while sleeping and therefore known to be at least locally common, are rarely seen in the daytime, and their diurnal activity and ecology are therefore almost unknown.

However, quite apart from any characteristics of the animals that may make acquisition of knowledge about them difficult, a primary and evident difficulty is failure to explore and to collect. *Anolis huilae* is not only a species just now described, but only very recently collected. Dennis Harris is the collector of all the Tolima specimens—23 obtained in one 10-day trip which did not specialize in *Anolis* but sought lizards of all kinds. Such a collection in a brief span implies that prior sampling of this area, which has not been totally neglected—it is the type locality of *Anolis tolimensis* and *A. ibague*—has nevertheless been quite inadequate.

If this is true of areas from which there is moderately good representation in old collections, what may still be coming from areas that are still altogether or nearly untouched?

The Department of Nariño is one such area. Collections by even Ayala's group have been only in the low-lands near Tumaco; there is no reason to believe that even near Tumaco there is not much more to find.

An undescribed species is known from the west side of the Sierra Nevada de Santa Marta, and one on the south side has been described herein. What occurs on the east side? Are the new species the only ones on the west and south sides? Is the fauna of the Chocó completely known, of Cauca, Antioquia, Bolívar, Santander, and Norte de Santander? One can, in fact, call the roster of the Departments of Colombia and it will not be possible to say even of the relatively well collected areas that the herpetofauna is completely known. We in fact do not know enough to estimate the fraction that is unknown. (However, to shirk the frustrating effort of dealing with incomplete and inadequate evidence would be to acquiesce in the perpetuation of ignorance. Our obligation is, while not avoiding these thorny thickets, to explore carefully and to leave the paths that we pursue plainly marked.)

What has been done in this paper is to attempt—and I do not vouch for more than an attempt—to answer the first and most elementary (but most fundamental) of biological questions: *who?*—i.e., what is the cast of characters? After we have answered this first question we may begin to ask the question *where?* On the way we may begin to answer other questions: *what does it do? with whom does it interact?* Much later, when the picture is much clearer, we can try to answer historical questions: how did this *system* come about. On the evidence before us the picture is too incomplete, the

unfilled places in the evidence too blatant and glaring, to begin an analysis of species group history or even, in any serious sense, of inter-group relationship. We do not yet know enough to ask the right questions.

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