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SOUTH AMERICAN *ANOLIS*: THREE NEW SPECIES RELATED TO *ANOLIS NIGROLINEATUS* AND *A. DISSIMILIS*

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ABSTRACT. Three new *Anolis* species are described from widely scattered localities in Colombia and Venezuela. Together with *Anolis nigrolineatus* and *Anolis dissimilis* they appear to represent a natural subgroup of the *punctatus* group of South American alpha anoles.

The lizard fauna of South America is poorly understood but more than that it is little known. It is, for example, very probable that there are many lizard species to be discovered in the continent's remoter and more obscure areas. The three new anoles here described are cases in point: they are from areas quite remote or obscure — one from a small river valley in Santander and the poorly known states of Tachira and Trujillo in Venezuela, another from a camp in remote Caqueta in Colombia, and still another from a mission in the delta at the mouth of the Orinoco.

More interesting, however, than the existence of new species in little explored areas is the close resemblance of these newly discovered, *perhaps* isolated anoles to species occurring at very great distances from them. The most extreme instance is the similarity of the anole from the mouth of the Orinoco to a form from Madre de Dios Province in Peru. However, the distances between the other forms that must be compared are relatively small only in the context of the immensity of South America.

Even in South America it is quite unusual to be compelled to describe related species from such small samples as are available for the three new forms (one, one and five), especially when these are spread over so wide an area with no series available for any locality. This may point to a special difficulty peculiar to small arboreal species. The fauna of open formations is usu-

ally obtainable in some appreciable numbers wherever it occurs. The species of forests are rarer or more difficult to obtain, but most probably both. Those elements of the forest fauna that occur well up in the trees or at least in thick vegetation are likely to be the last to be known. On morphology and affinity, although only for one is anything known directly of the ecology, the present three new species appear to belong to this most difficult group.

All three anoles are so close to *Anolis nigrolineatus* and *Anolis dissimilis* (Williams, 1965) that they, like these, must be assigned to the *punctatus* group of the alpha section of South American anoles.

A. nigrolineatus (Williams, 1965) was described from two specimens, both with questionable localities in southeastern Ecuador. Two additional specimens have since been discovered in the collections of the University of Michigan. These not only provide the first good locality for the species (Playas de Montalvo, Prov. Los Rios, Ecuador) but provide a better comparison with the new but very closely related species from eastern Colombia and western Venezuela which I call:

Anolis nigropunctatus new species

Holotype: ILS 21, an adult male.

Type locality: El Diamante, Norte de Santander, Colombia.

Paratypes (all adult females). ILS 20: Toledo, Norte de Santander, Colombia; MCNC 5395, Villa Paez, Edo Tachira, Venezuela; MCZ 136175, Quebrada Honda on road from Trujillo City to San Lazaro, Edo Trujillo, 4700 feet.

Diagnosis. Close to *A. punctatus* (cf. the slightly swollen snout in the male) but differing in color and squamation. Closer still to *A. nigrolineatus* but differing in wider head, apparently larger size (male 72 mm in snout–vent length rather than 46 mm), in the absence of the narrow middorsal black line and of the broad black spot in the dewlap. Nostril without a differentiated anterior nasal scale (Fig. 1). An apparently greater number of lamellae under phalanges ii and iii of the fourth toe (21–22 rather than 18–19).

Description. (Paratype variation in parentheses.) *Head:* Head scales flat, obscurely wrinkled. Seven scales (7–10) across snout between second canthals. Five scales (6–8) border rostral posteriorly. Circumnasal scale separated from rostral by one scale (or in contact). Four scales between supranasals. Snout

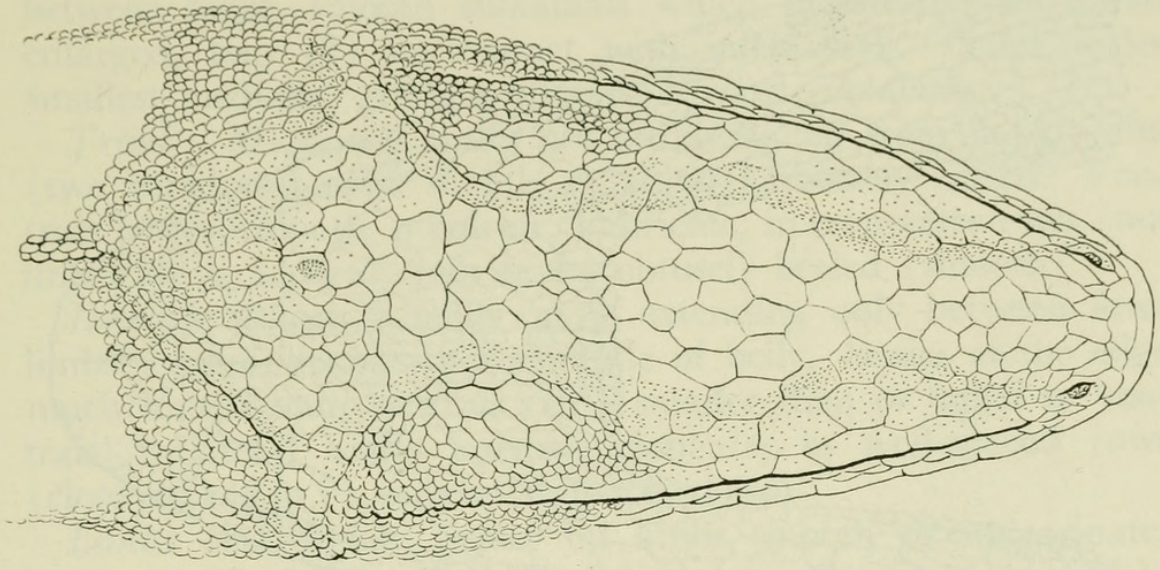

Figure 1. *Anolis nigropunctatus* Holotype. Dorsal view of head.

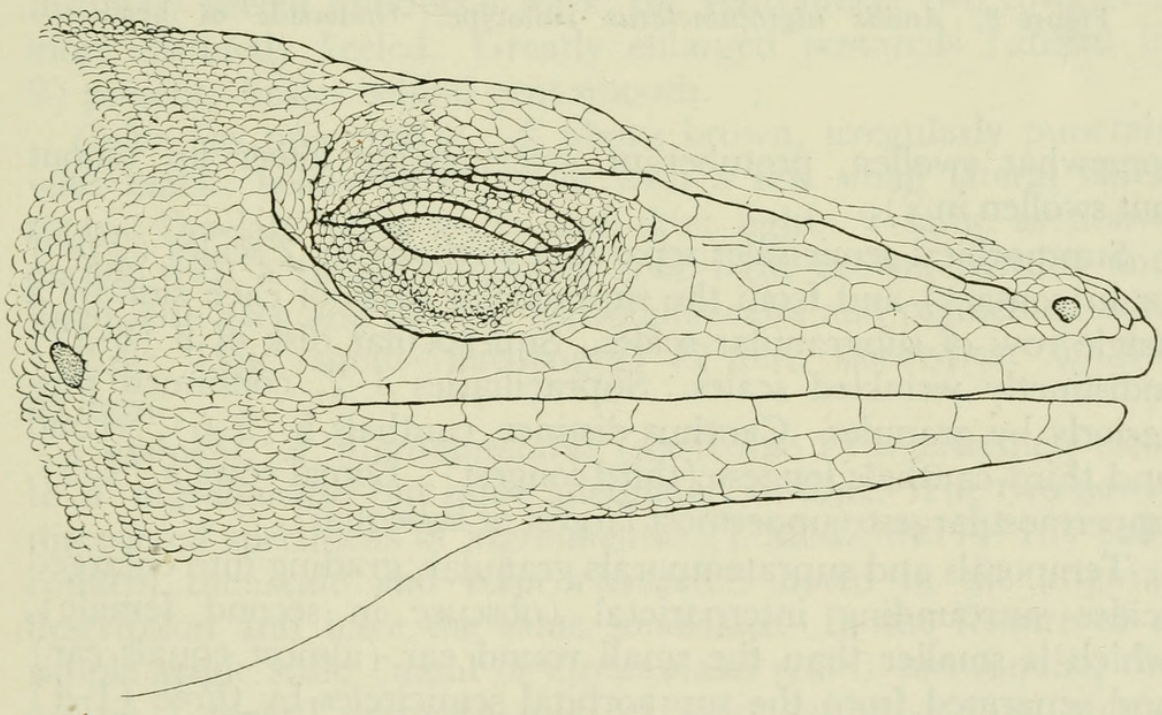

Figure 2. *Anolis nigropunctatus* Holotype. Lateral view of head.

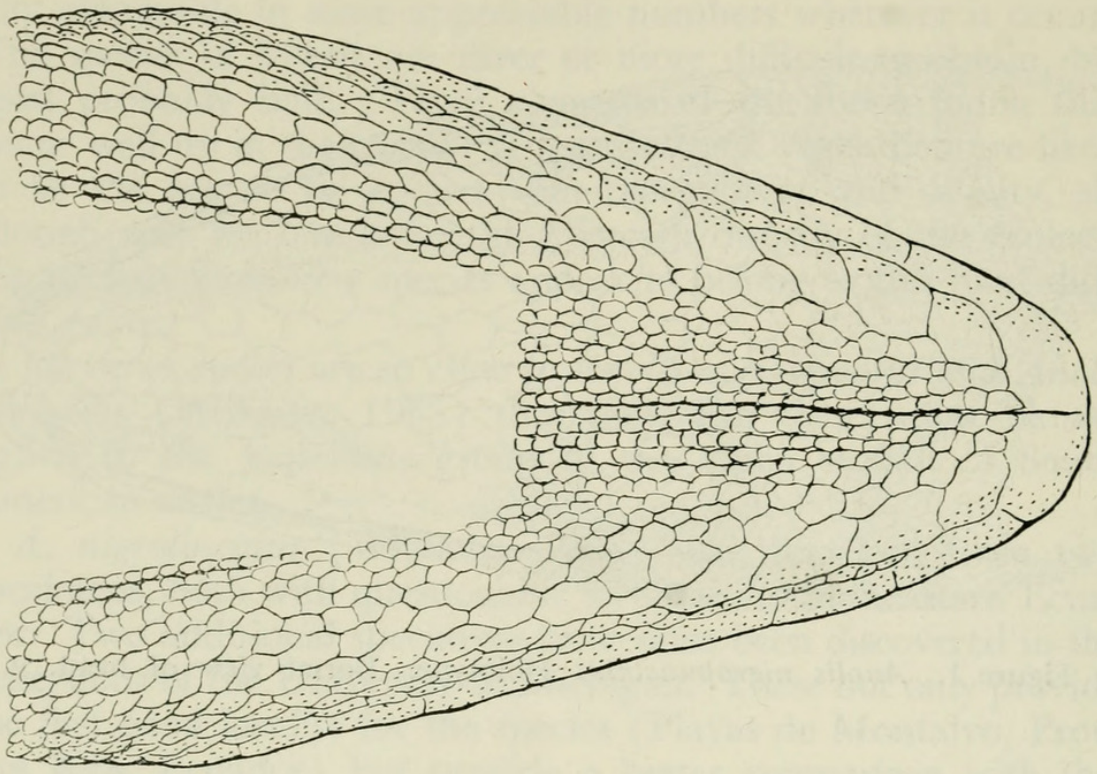

Figure 3. *Anolis nigropunctatus* Holotype. Underside of head.

somewhat swollen, protuberant, overhanging lower lip (snout not swollen in ♀).

Supraorbital semicircles separated medially by 2 scales (2 or 1 or in contact) and from the supraocular disks of each side by a single row of subgranular scales. Supraocular disk of 9 (8–12) indistinctly wrinkled scales. Supraciliaries 1–2, continued posteriorly by granules. Canthus distinct, canthals 5 (5–6), second and third canthals longest (third longest). Loreal rows 5 (4–5), uppermost largest (uppermost largest or subequal).

Temporals and supratemporals granular, grading into enlarged scales surrounding interparietal (obscure in second female), which is smaller than the small round ear (almost equals ear) and separated from the supraorbital semicircles by three (1–4) scales. Several of the scales surrounding interparietal larger than that scale (or 2/3 that size). Scales posterior to interparietal grading gradually into dorsal granules. No enlarged supratemporal rows (indistinct supratemporal rows).

Suboculars weakly keeled, in contact with supralabials, grading posteriorly into the supratemporal granules and anteriorly separated from canthals by one scale. Seven supralabials to center of eye.

Mental semidivided, each part almost as wide as deep (wider

than deep), the whole in contact with 3 (4) throat scales between large, smooth sublabials which indent it. Sublabials enlarged, two (3) in contact with infralabials. Gular scales smallest medially, grading laterally toward sublabials.

Trunk: Middorsal scales not differentiated from flank scales (two middorsal rows slightly enlarged), obtusely keeled. Ventrals larger, smooth, quadrate, imbricate, in transverse rows (not imbricate). Lateral chest scales obtusely keeled (smooth).

Dewlap: Large (smaller in ♀, extending only between forelimbs), extending nearly to middle of belly. Scales at the edge much longer than ventrals (in ♀ smaller than or equal to ventrals). Lateral scales narrow, elongate, in well-spaced rows (close packed in ♀), separated by naked skin.

Limbs and digits: Scales on limbs smooth or unicarinate, largest on both arm and hind limb (smaller than ventrals). Supradigital scales multicarinate. Twenty-one (22) scales under phalanges ii and iii of fourth toe.

Tail: Compressed, without verticils or dorsal crest. Two distinctly keeled middorsal rows; the ventralmost two rows even more distinctly keeled. Greatly enlarged postanals (absent in ♀) present. Scales behind vent smooth.

Color (as preserved): ♂ above brown, irregularly punctate with black; below light brown with a few small lateral black spots. Dewlap, both scales and skin, light. ♀ same as above except with a broad middorsal zone light brown, mottled and lined with grey and dewlap with light scales and pigmented skin.

Size: Type (snout–vent length) 72 mm. Paratypes: 60, 56, 55 mm.

Comment. A. nigropunctatus (see Table 1) is extremely close to *A. nigrolineatus* but quite adequately distinct. The two newly discovered specimens of *nigrolineatus* (UMMZ 84114–15) fully confirm the scale and color characters noted in the original description and have the same small size. In the feature of a simple single scale (nasal or circumnasal scale) surrounding the nostril, I regard *nigropunctatus* as more primitive than *nigrolineatus.* The scale called "anterior nasal" in the latter I believe to be a modification of a scale originally anterior to that surrounding the nostril, now become enlarged and triangular, overlapping the anterior margin of the primitive circumnasal scale. The higher number of toe lamellae in *nigropunctatus* accord with its larger size.

Ecological notes are available only for MCZ 136175 for which J. A. Rivero records: "On leaves three feet from the ground at edge of road near a stream."

TABLE I

	nigrolineatus	*nigropunctatus*	*caquetae*	*deltae*	*dissimilis*
	SW Ecuador	NE Colombia and W Venezuela	Amazonian Colombia	Delta of the Orinoco	SE Peru
swollen snout in male	—	+	+	—	—
scales across snout	8–9	7–10	10	8	7
nasal/rostral	anterior nasal scale in contact with rostral, sometimes inferior nasal as well	no differentiated anterior nasal; circumnasal directly in contact with rostral or one rounded scale separating circum-nasal and rostral	anterior and inferior nasal scales in contact with rostral	anterior nasal in contact with rostral	circumnasal scale separated by one rounded scale from rostral
scales between supraorbital semicircles	1–2	0–2	1	0	0
loreal rows	4–7	4–6	5	4	4
interparietal/ear	>	<	>>	>>	>

TABLE I — Continued

	nigrolineatus	*nigropunctatus*	*caquetae*	*deltae*	*dissimilis*
scales between interparietal and semicircles	2–3	1–4	0	0	0
scales around interparietal/dorsals	>	(>)	=	>>	=
scales between suboculars and supralabials	0	0	0	0	0
supralabials to center of eye	7–11	7	7	7	11
lamellae under 4th toe	18–19	21–22	22	24	17
postanals in ♂	+	+	weakly indicated	—	+
middorsal scale rows enlarged	one	two	two	one (tail crest!)	one (tail crest!)
♂ size (snout to vent in mm)	45	72	57	58	56

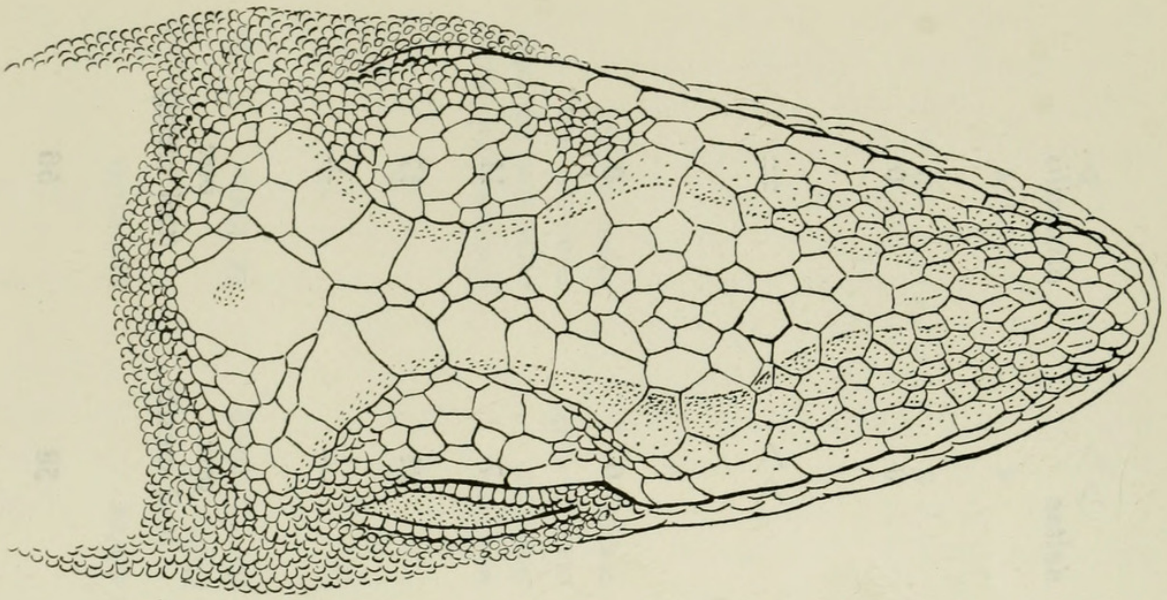

Figure 4. *Anolis caquetae* Holotype. Dorsal view of head.

The two remaining undescribed species appear to be closest to *A. dissimilis,* but the species geographically more remote is more similar than that which is spatially intermediate. The latter is clearly the primitive member of the series and, coming from the upper Rio Apaporis, is within the Amazonian faunal province but in one of the remoter peripheral parts of that region. I name it after the Department of Colombia from which it comes.

Anolis caquetae new species

Holotype: MCZ 131176, an adult male.

Type locality: Camp Soratama, Upper Apaporis, Caqueta, Colombia.

Diagnosis. Close to *A. dissimilis* but without the tail crest characteristic of that species and with a different coloration.

Description. Head: Most head scales smooth, some on the anterior snout unicarinate. Scales in frontal depression distinctly smaller than surrounding scales. Ten flat scales across snout between the second canthals. Eight swollen scales bordering rostral posteriorly. Nasal scale anterior to canthal ridge with one lower and one anterior scale separating it from rostral (see Fig. 5). Seven swollen scales between supranasals. Snout somewhat swollen, protuberant, overhanging lower lip.

Supraorbital semicircles separated from each other by a single row of small scales, in contact with the supraocular disks, which consist of 24–28 enlarged smooth scales grading into granules

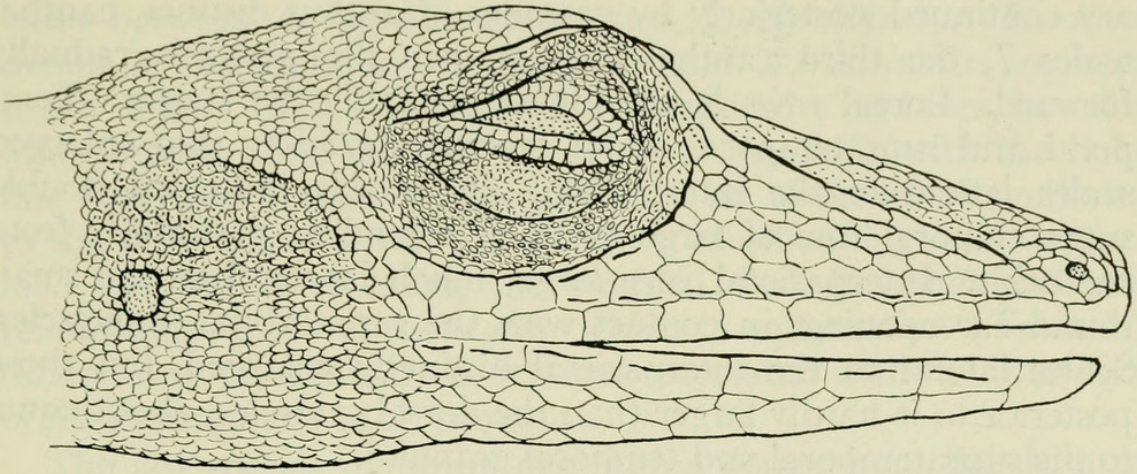

Figure 5. *Anolis caquetae* Holotype. Lateral view of head.

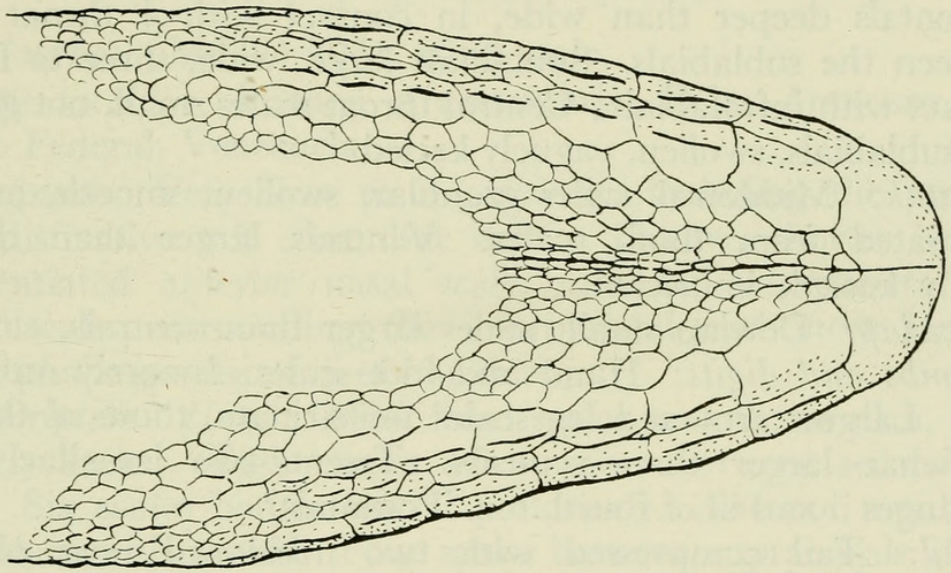

Figure 6. *Anolis caquetae* Holotype. Underside of head.

anteriorly, posteriorly and laterally. A single enlarged supraciliary continued posteriorly by granules. Canthus distinct, canthal scales 7, the third canthal largest, then diminishing gradually forward. Loreal rows 5, the lowest distinctly the largest. Temporal and supratemporal scales granular, grading into enlarged scales lateral to the interparietal. A weakly indicated double supratemporal row of large granules extending posteriorly from the orbit. Interparietal very large, much larger than the small round ear opening, in contact with the supraorbital semicircles. Scales lateral to the interparietal distinctly enlarged, but those posterior to it hardly larger than the dorsal granules, about equal to the supratemporal and temporal granules.

Suboculars smooth, broadly in contact with supralabials, grading into large granules behind the eye; anteriorly grading into loreals. Seven supralabials to the center of the eye.

Mentals deeper than wide, in contact with 4 throat scales between the sublabials. Sublabials large, wide, three to four in contact with infralabials. Central throat scales small, not grading into sublabials, swollen, vaguely keeled.

Trunk: Middorsal scales granular, swollen, smooth, not differentiated from flank scales. Ventrals larger than dorsals, weakly keeled, imbricate.

Dewlap: Dewlap small, scales larger than ventrals, close set.

Limbs and digits: Hand and foot scales obscurely multicarinate. Largest arm and leg scales unicarinate, those of the arm somewhat larger than ventrals. Twenty-two lamellae under phalanges ii and iii of fourth toe. Postanals?

Tail: Tail compressed with two middorsal rows obtusely keeled and the two midventral rows larger, sharply keeled. Verticils not evident. Lateral caudal scales increasing in size toward ventrals.

Color (as preserved): Dorsum brown with a narrow black vertebral line bifurcating on nape. Broad oblique transverse banding of obscure dark blotches, limbs obscurely banded. Belly and throat light brown, sparsely punctate with darker. Tail very obscurely banded.

Size (snout–vent length): 57 mm.

Comment. Like a number of South American anoles that do not seem closely related (*e.g., A. jacare, A. nigropunctatus*), *A. caquetae* has a double row of scales surmounting the tail rather than the more usual one. This is very different from the tail crest of a single row of enlarged triangular scales characteristic of *A. dissimilis*. This difference does not seem, however, a

bar to the close relationship. A similar if less extreme difference exists between *A. nigropunctatus* and *A. nigrolineatus.* In other details of squamation *A. caquetae* and *A. dissimilis* are very much alike (Table 1). They differ strikingly, however, in color and pattern. The dark dorsal color of *dissimilis* with the light line from supralabials to shoulder has no elements of similarity to the middorsal dark line and broken crossbanding of *A. caquetae.* On the other hand, the vestigial dark line may indicate relationship to *A. nigrolineatus,* which in squamation (Table 1) differs most prominently in features associated with the huge size of the interparietal in *A. caquetae.*

The last species requiring description comes from the delta of the Orinoco. I have therefore named it:

Anolis deltae new species

Holotype: (MCN) 2031, adult male.

Type locality: Mission Araquaimujo, Delta Amacuro, Territorio Federal, Venezuela.

Diagnosis. Very close to *A. dissimilis* including the presence of a distinctive tail crest, but with a blunter, shorter head, a differentiated anterior nasal scale, a larger interparietal with larger scales surrounding the interparietal and more lamellae under phalanges ii and iii of fourth toe.

Description. Head: Most head scales smooth, swollen, a few obtusely keeled. Eight scales across snout between second canthals. Six scales border rostral posteriorly. Anterior nasal scale in contact with rostral. Four scales between supranasals. Scales in frontal depression smaller than surrounding scales.

Supraorbital semicircles in contact, separated from the supraocular disks on each side by one row of scales. Supraocular disks of 12–14 strongly enlarged scales. Supraciliaries one on each side, continued by granules. Canthus distinct. Canthal scales 6, the second and third largest. Loreal rows 4, the lowermost largest.

Temporals and supratemporals subgranular, grading into enlarged scales surrounding interparietal. Interparietal very large, larger than ear, in contact with supraorbital semicircles. Scales behind interparietal grading gradually into dorsal granules. Suboculars in contact with supralabials, grading posteriorly into supratemporal granules, anteriorly separated from the canthals by one to two scales. Seven supralabials to the center of the eye.

Mental wider than deep, in contact with four throat scales,

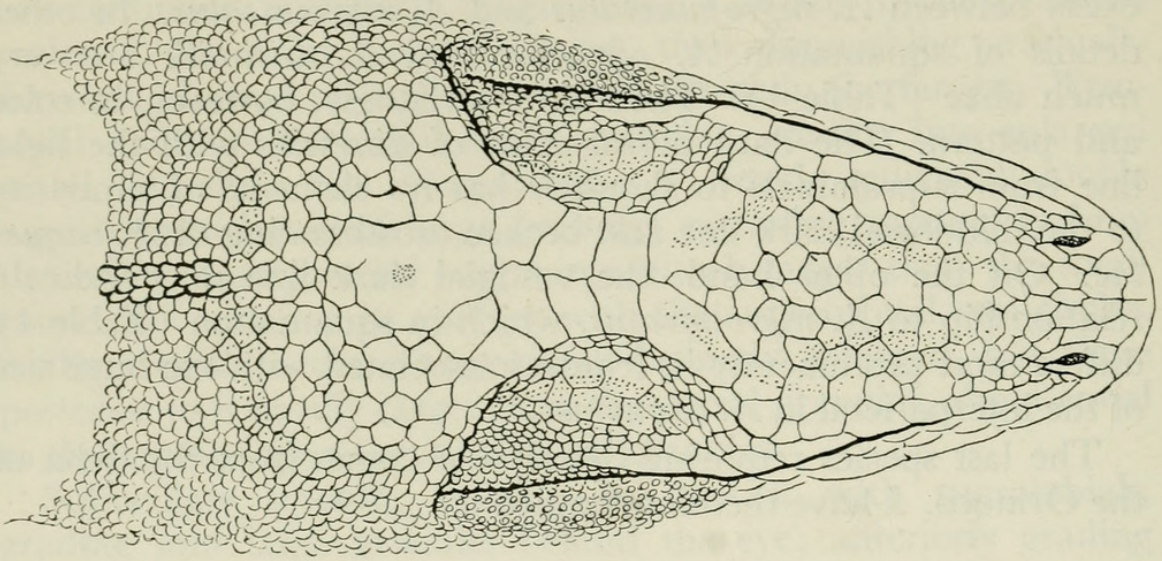

Figure 7. *Anolis deltae* Holotype. Dorsal view of head.

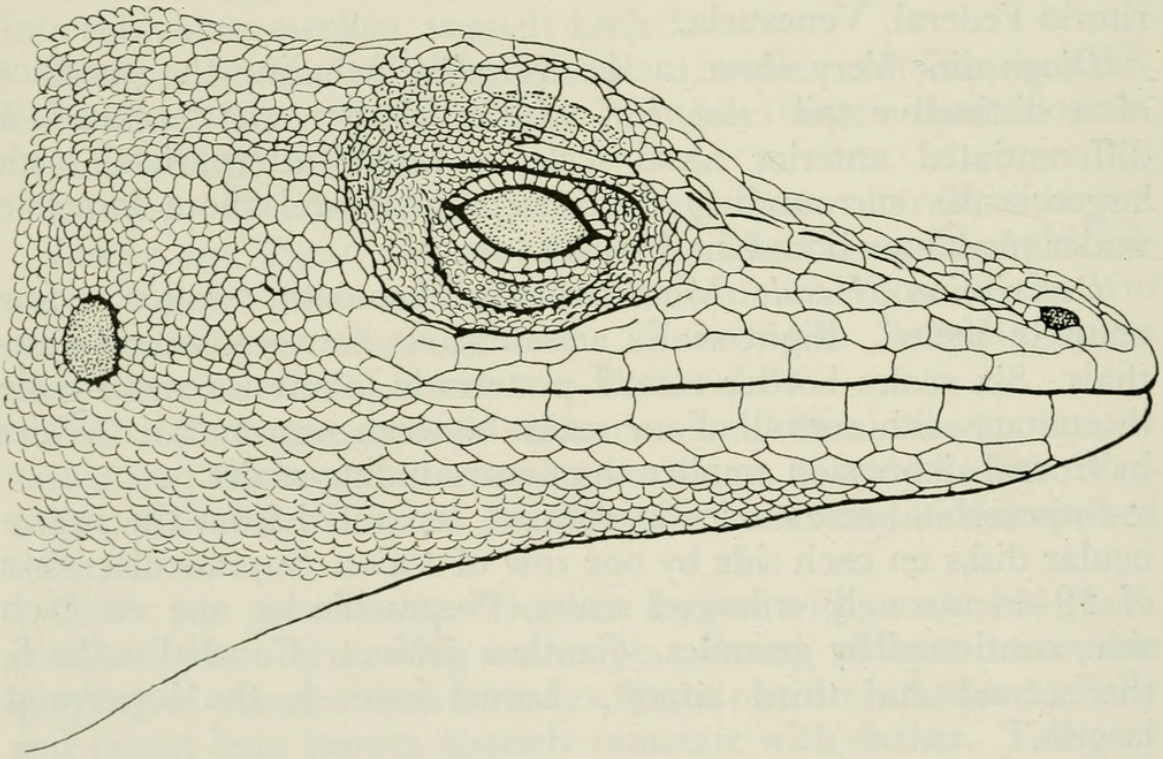

Figure 8. *Anolis deltae* Holotype. Lateral view of head.

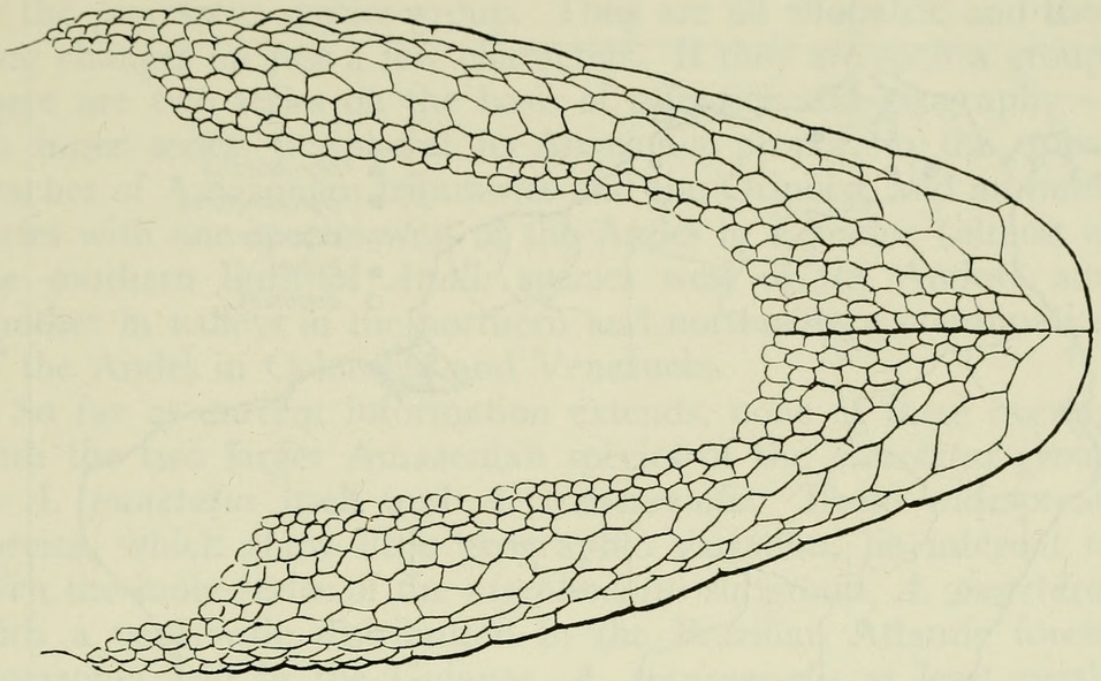

Figure 9. *Anolis deltae* Holotype. Underside of head.

set in a gentle forward arc between sublabials. Sublabials enlarged, two in contact with infralabials on each side. Gular scales subequal centrally but grading laterally into sublabials.

Trunk: A few middorsal rows slightly enlarged, obtusely keeled, grading into flank granules. Ventrals larger, smooth, quadrate, imbricate, in transverse rows.

Dewlap: Large, extending nearly to midbelly. Scales at edge as large as ventrals. Lateral scales narrow, elongate, in rows separated by naked skin.

Limbs and digits: Largest limb scales unicarinate, almost equal ventrals. Supradigital scales obscurely uni- or bicarinate. Twenty-four lamellae under phalanges ii and iii of fourth toe.

Tail: Most of tail missing but a distinct crest on the portion present. Enlarged postanals absent. Scales behind vent smooth.

Color (as preserved): Straw. A series of broad but vague darker blotches middorsally. Obscurer and quite irregular spots and mottling on flanks. Belly with vague markings. Above and below head and limbs very obscurely mottled. Dewlap skin and scales light.

Size (snout–vent length): 58 mm.

Comment. The tail crest of *A. deltae* and *A. dissimilis* in particular is a highly distinctive common feature. It is entirely a crest of slightly raised keeled scales that gives the appearance of a serrate upper border to the tail, not at all like the huge tail

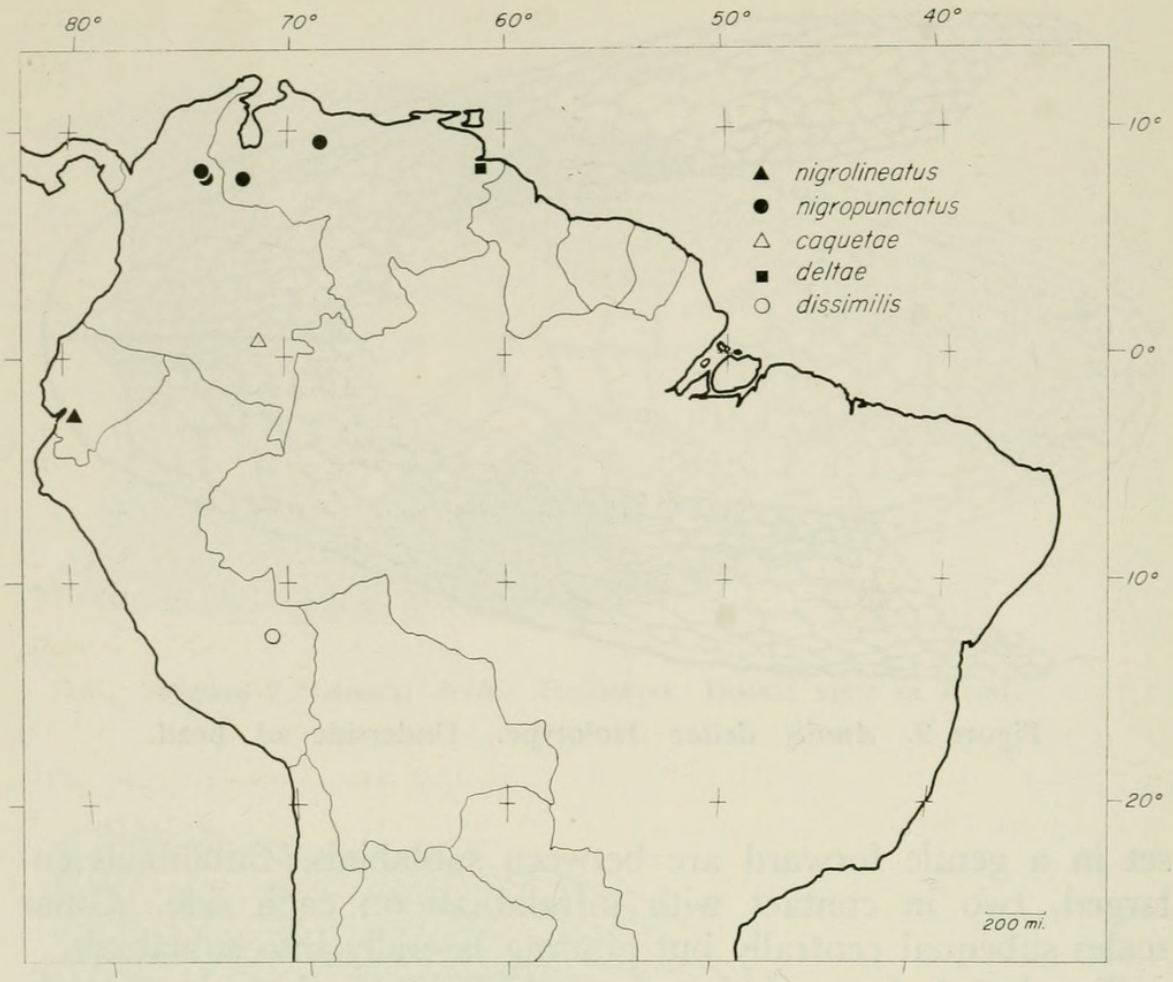

Figure 10. Distribution of the *Anolis* of the *A. nigrolineatus* subgroup.

fins supported by vertebral spines of the considerable number of West Indian species that have compressed crested tails — not therefore impressive except that it is very unusual in South America. Even the South American giants (the *latifrons* group *sensu stricto*), though they have compressed tails, lack any sort of crest. The closest resemblance in tail type is perhaps provided by the anoles of the *pentaprion* group (Myers, 1971) in which the serrate crest, however, is surely convergent, since these are beta anoles belonging to quite a distinct section within the genus *Anolis*.

A. deltae is quite different from *dissimilis* in color and pattern, closer in this to *A. caquetae* which it resembles also in the strongly enlarged interparietal. It differs, however, from both species in the enlarged scales behind the interparietal, markedly larger than the dorsals.

Discussion. The five species that have been discussed here are perhaps a natural subgroup — the *A. nigrolineatus* subgroup —

of the *punctatus* species group. They are all allopatric and they ring changes on just a few characters. If they are such a group, there are two series on the basis of affinities and geography — an inner series, peripheral to Amazonia proper, in the upper reaches of Amazonian tributaries and the Orinoco, and an outer series with one species west of the Andes in Ecuador (almost at the southern limit of *Anolis* species west of the Andes) and another in valleys in the northern and northeastern continuation of the Andes in Colombia and Venezuela.

So far as current information extends, none of these overlap with the two larger Amazonian species of the *punctatus* group — *A. punctatus* itself and *A. transversalis*. These widespread species, which show little geographic variation, lie internal to even the inner series of the *nigrolineatus* subgroup, *A. punctatus* with a very wide distribution in the Brazilian Atlantic forest, Amazonia and in the Guianas, *A. transversalis* at least partly sympatric with *punctatus* in western Amazonia. With South American anoles so little known, this apparent geographic pattern could well be factitious. However, *A. punctatus* and *A. transversalis* are among the first collected of anole species wherever they occur. Their absence from the collections that record the *dissimilis-caquetae-deltae* series may therefore be real.

Acknowledgments

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