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NEW OR PROBLEMATIC *ANOLIS* FROM COLOMBIA. VII. *ANOLIS LAMARI,* A NEW ANOLE FROM THE CORDILLERA ORIENTAL OF COLOMBIA, WITH A DISCUSSION OF *TIGRINUS* AND *PUNCTATUS* SPECIES GROUP BOUNDARIES

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ABSTRACT. A new species, *Anolis lamari,* is described from the eastern slopes of the Cordillera Oriental of Colombia. It is compared with the species previously assigned to the *tigrinus* group. The characters separating the *tigrinus* and *punctatus* species groups are reassessed. A plea is made for the temporary use of informal groupings—recognized as such—whenever sufficient grounds for the recognition of formal taxa do not exist.

INTRODUCTION

A small anole from the eastern slopes of the Cordillera Oriental of Colombia is recognized as another new species apparently allied to the *tigrinus* species group. It is named *Anolis lamari* after its discoverer, W. W. Lamar.

DESCRIPTION

Anolis lamari, new species
Figures 1–4

Holotype. ICN 6762 (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá) (formerly WWL 1576).

Type Locality. Portachuelo, about 2 miles (by air) north of Manzanares, a police inspection station in the Municipio de Aca-

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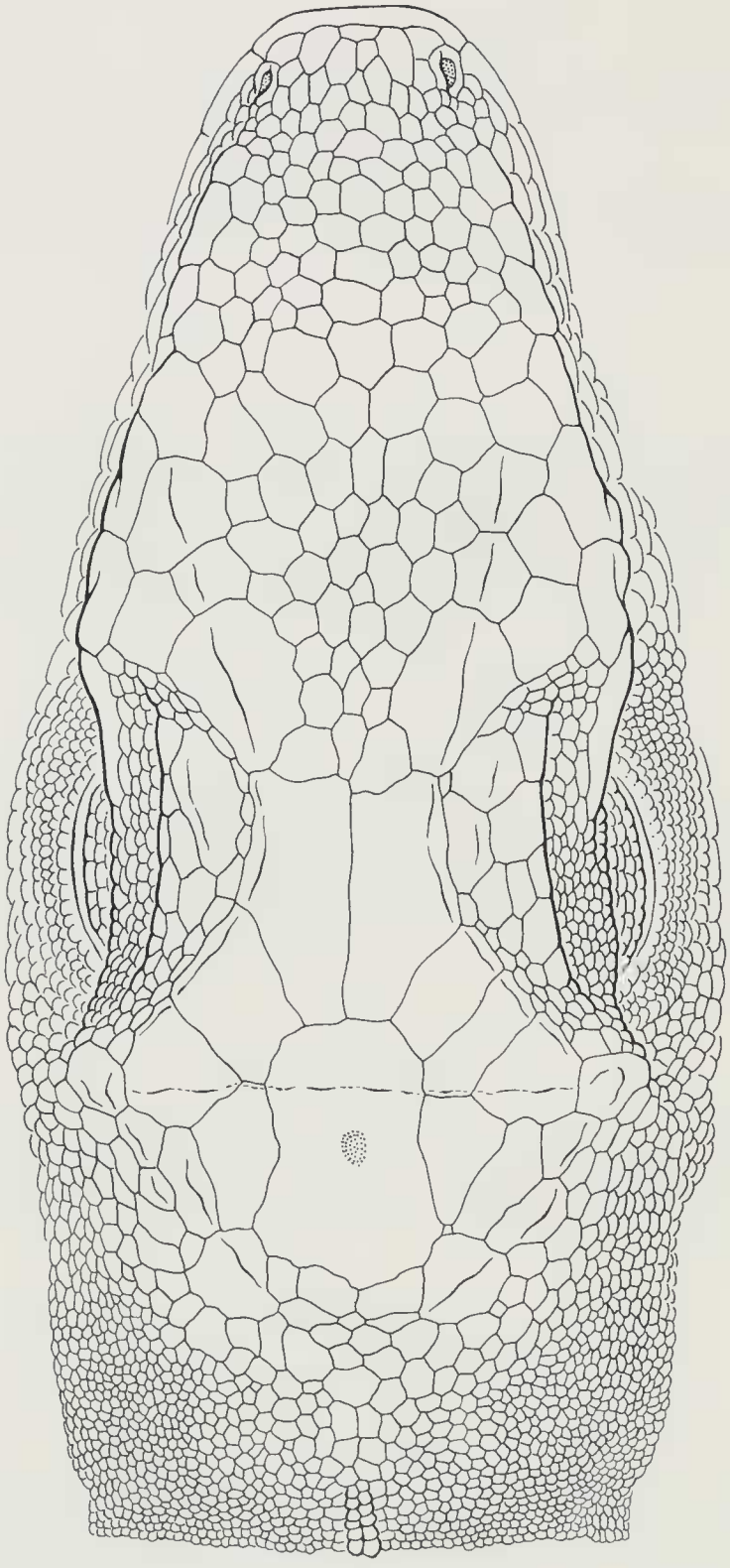

Figure 1. *Anolis lamari,* holotype. Dorsal view of head.

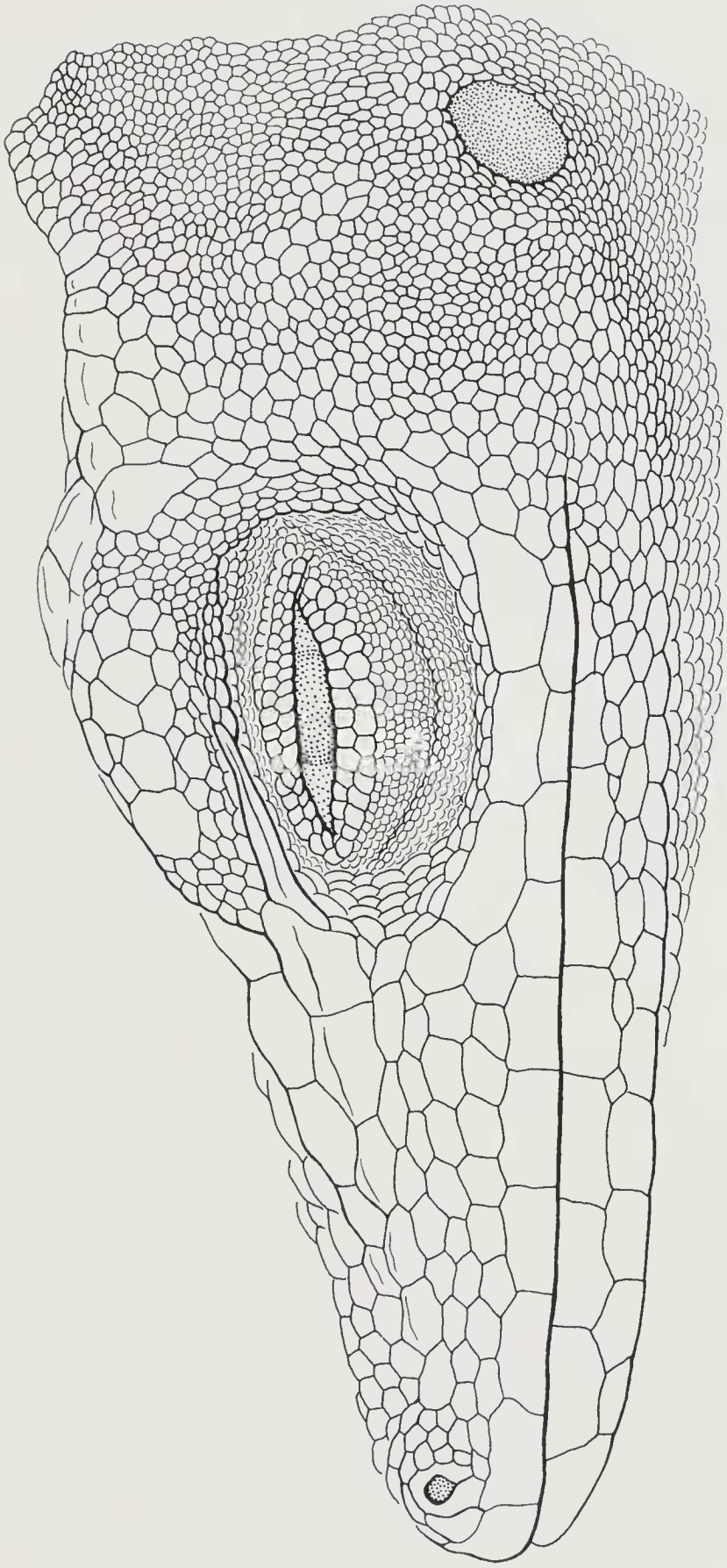

Figure 2. *Anolis lamari*, holotype. Lateral view of head.

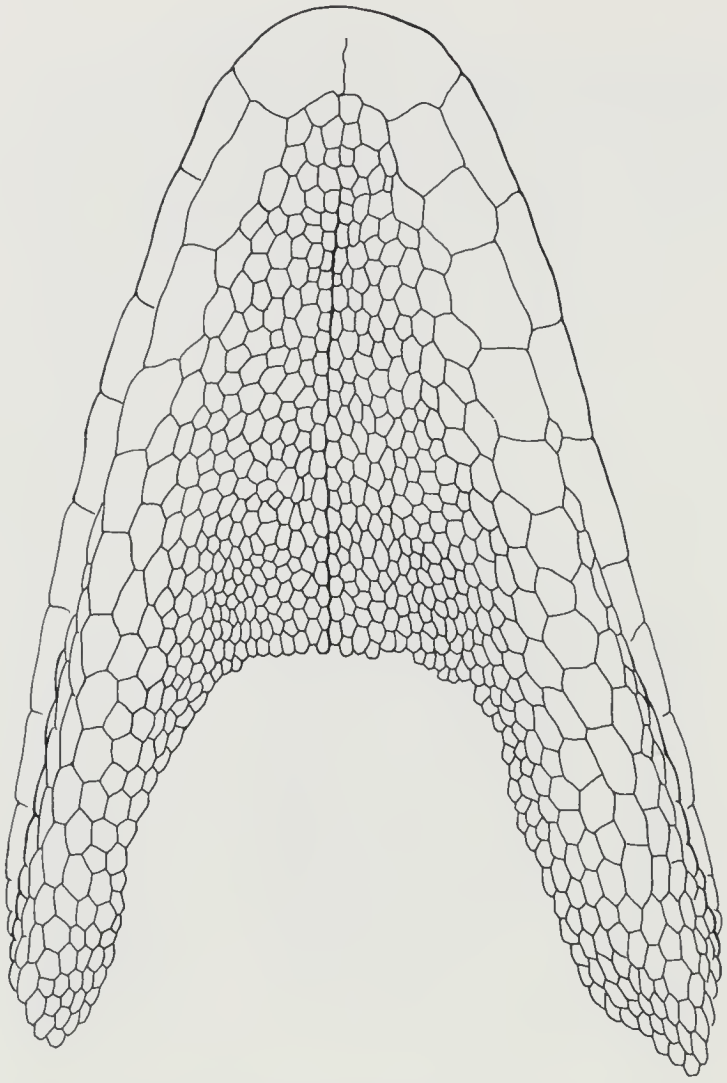

Figure 3. *Anolis lamari,* holotype. Ventral view of head.

cías, Meta, Colombia. W. W. Lamar coll. July 10, 1980. Elevation ca. 1,600 m.

Diagnosis. Close to *Anolis solitarius, tigrinus, menta,* and *ruizi,* apparently differing from all in details of coloration. It differs from *tigrinus* in the absence of minute tubercles on the head scales, from *menta* in that the dewlap is uniform yellow-orange rather than bicolor white and lemon-yellow, from *ruizi* in the possession of a small knob at the posterior edge of the parietal, and from *solitarius* in body pattern and in the presence of a line of enlarged scales continuing back onto the parietal knob. The pattern of the only known specimen, a male, is closest to that of male *ruizi,* but lacks the distinctly reticulate flanks of that species.

Figure 4. *Anolis lamari*, holotype. Lateral view to show pattern.

Description. Head: Dorsal head scales smooth, small anteriorly, much larger from the anterior margin of orbits posteriorly. Eight scales across snout between second canthals. The scales within the moderate frontal depression as large as or larger than those anterior to them. Five postrostrals. Large anterior nasal in contact with the suture between rostral and first supralabial. About eight scales between the circumnasals dorsally.

Scales of supraorbital semicircles very large, broadly in contact with each other and with the supraocular disks. About 16 enlarged scales in each supraocular disk, the largest medial, the disk bordered anteriorly, laterally, and posteriorly by granules. One elongate superciliary on each side, occupying about one half the lateral supraocular margin. The more posterior superciliaries minutely granular.

Canthus blunt, six canthal scales, the first and second largest becoming gradually smaller anteriorly. Three to four loreal rows, subequal; 18–22 total loreals.

Lower temporals finely granular, subequal. Two intertemporal rows on the bony bar that is the lower margin of the upper temporal vacuity. Supratemporals subgranular near the intertemporal rows, becoming abruptly larger near the interparietal. Scales just lateral to the interparietal large, ranging to one third the size of the interparietal, the latter very large, much larger than the ear, in broad contact with the semicircles. Four scale rows posterior to the interparietal relatively large but not as large as those lateral to it, and behind these a further series of four smaller scales leading to a bony boss on the parietal bone, i.e., a total series of eight scales larger than the nape scales behind the interparietal. Nape scales grading rapidly into the granular dorsals.

Suboculars in contact with the supralabials, grading anteriorly into the loreals, posteriorly becoming abruptly smaller, grading into the lower temporals. About seven supralabials to below the center of the eye.

Mental semidivided, in contact with six scales, in a gentle concave arc, between the infralabials: Four medial postmental granules and, lateral to them, a first sublabial on each side at least five times the size of the postmental granules. Behind the first sublabials on each side, three to four additional sublabials in

contact with the infralabials. Medial gulars granular, convex, smooth, becoming larger near the sublabial rows.

Trunk: Dorsals smooth, juxtaposed, the two middorsal rows slightly larger, smooth or very weakly keeled. Flank scales almost as large as dorsals, smooth, juxtaposed. Ventrals much larger, subquadrate, flat, smooth, subimbricate to imbricate, in transverse rows.

Dewlap: Very large, extending posteriorly nearly to middle of belly. Edge scales smooth, imbricate, somewhat smaller than ventrals. Lateral scales narrow, in widely spaced rows separated by naked skin.

Limbs and Digits: Forelimb scales smooth, larger anteriorly, granular posteriorly. Upper thigh scales very weakly keeled, posterior thigh scales granular, lower leg scales smooth. Supradigitals of hand and foot weakly keeled. Nineteen lamellae under phalanges ii and iii of fourth toe.

Tail: Weakly compressed, scales small and smooth at base, becoming larger and keeled distally. A wider row dorsally, sometimes double, keeled. Lateral caudals smaller, weakly keeled. A midventral double row abruptly larger, sharply keeled. Postanals enlarged (male, one hemipenis extruded, bifid at tip).

Measurements. (Before preservation, provided by W. W. Lamar.) SVL 42.8 mm, total length 131 mm, dewlap 19 mm long, 8.5 mm deep.

Color. (As preserved.) Purplish to yellow-brown. Occipital area, including interparietal, dark. Snout anteriorly smudged with darker pigment. An irregular hollow triangle behind eye, narrowly bordered by black. Black oblique broken lines on nape in series with similar lines on flanks. A middorsal black line widest and most intense on the nape.

Color in Life. (Adapted from W. W. Lamar's notes.) Overall pattern complex because of scattered speckling.

Snout to eyes weak green. Lips pale creamy-tan. A bold white to gold stripe extending from below eye to ear at the level of the angle of the mouth. Distal portion of head golden tan. Body tan becoming green on posterior third. Beginning just posterior to eyes, four or five bars consisting of pairs of wavy dark green lines slanting backward and downward to venter. Middorsum with six

brown rectangles all poorly defined but increasing in intensity as they approach the tail. Tail boldly banded in maroon brown and green, the brown bands fading to tan posteriorly. Limbs finely barred like sides.

Venter pinkish cream with indistinct specks, but midventer from chest to vent very pale yellow-green. Sides of belly pinkish. Vent and inner thighs and first third of tail pale yellow-green. Limbs brownish beneath, palms and soles maroon brown. Tail below banded brown and tan with some greenish cast.

The very large dewlap pale yellow-orange with pale greenish white raised scales.

Eye iris sooty-bronze, pupil narrowly ringed with gold. Eyelids translucent, tan like body.

Tongue pink.

Habitat. (From Lamar's notes.) Portachuelo is a "cuchilla de la Cordillera Oriental" of the Andes, a ridge that, at its highest point, is about 1,800 m. The area collected by Lamar was in the vicinity of 1,640 m, with the area of collection of the *Anolis* closer to 1,600 m. When collected, the unique type specimen was crawling over the mossy bank of a mountain stream on the property of Señor Chucho Cortez. The air temperature was 17.5°C. The animal was very slow-moving at that temperature but became very active when warmed up.

RELATIONSHIPS

The narrow relationships of *Anolis lamari* seem clear; its wider relationships involve some confusion.

Narrow Relationships

Apparently Corroborated Colombian-Venezuelan Relatives. A. lamari appears, on phenetic grounds, to be a close relative of the one Venezuelan and the three Colombian species with which it has been compared in the diagnosis, so close in all characters that this relationship seems corroborated. All five may then be considered geographically replacing forms within the *tigrinus* species group, as currently understood (Rueda and Williams, 1986): *tigrinus* from various localities in the coastal range of Venezuela, *solitarius* from the northern slopes of the Santa Marta Range in Colombia, *menta* from the southwestern slopes of the same range,

ruizi from the eastern slopes of the Cordillera Oriental in the Departments of Boyaca and Casanare, and *lamari,* also from the eastern slopes of the Cordillera Oriental, but in the Department of Meta. All members of this northwestern South American complex are relatively small species (maximum known size 57 mm SVL in *tigrinus*) in montane forest. All share or tend to share certain features of squamation: (1) a large interparietal, (2) bordered laterally by large scales, and (3) usually in contact with the supraorbital semicircles, which (4) are almost always in contact, (5) relatively few scales across the snout between the second canthals (four–ten), (6) relatively few scales in the supraocular disk (11 or less, except in *lamari* [16]), (7) usually, a series (five or more) of relatively large scales between the interparietal and the nape scales, which are granular like the dorsals, (8) suboculars in contact with the supralabials, (9) large well-differentiated sublabials, except in two of 13 *tigrinus,* (10) dorsal scales uniform in size, (11) smooth ventrals larger than the dorsals, (12) lamellae under phalanges ii and iii of the fourth toe no fewer than 16 nor more than 22.

A further external feature unites *lamari* with *tigrinus, solitarius,* and *menta*: a small parietal knob coincident with the border between post-interparietal scales and the nape scales. A skeleton recently made of *Anolis solitarius* (ICN 6153) shows that the external parietal knob is, as expected, underlain by a bony spur on the parietal bone (Fig. 5). This feature is absent in *A. ruizi.*

Within this complex, differences are not sharp. Color, including dewlap color, is important. The problems within the *tigrinus* group,

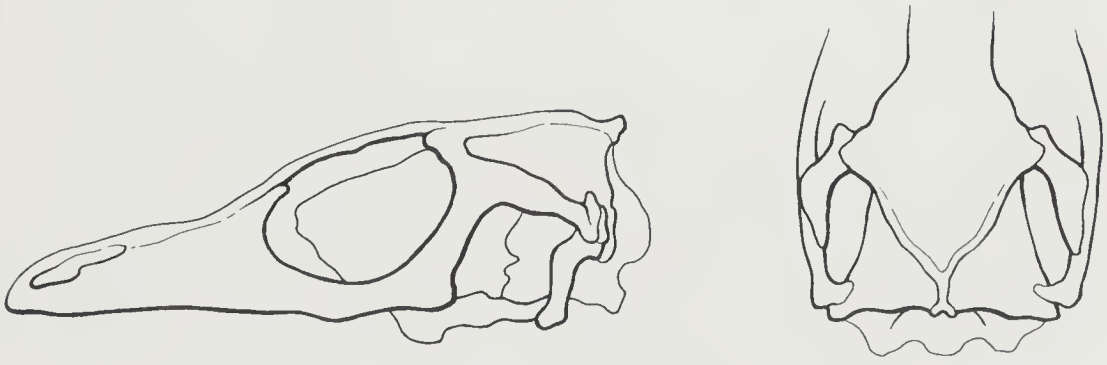

Figure 5. *A. solitarius* (ICN 6153). Left: The skull in profile. Right: The parietal bone to show the "parietal knob" and associated ridging.

as presently understood, are problems of the delimitation of taxa, not of features that unite them. It is, furthermore, not clear that all the populations referable to the group are yet known. Three of the five species, *menta, ruizi,* and *lamari,* have only recently been discovered, and no contact zones are known. The closest approach is that of *menta* and *solitarius,* which are less than 30 km apart in the west and north respectively of the Sierra de Santa Marta. *A. lamari* is the southernmost described Colombian species, but a single unnamed specimen is known from Vista Hermosa in the Sierra de Macarena that is, with high probability, the veritable southernmost Colombian record for the species group.

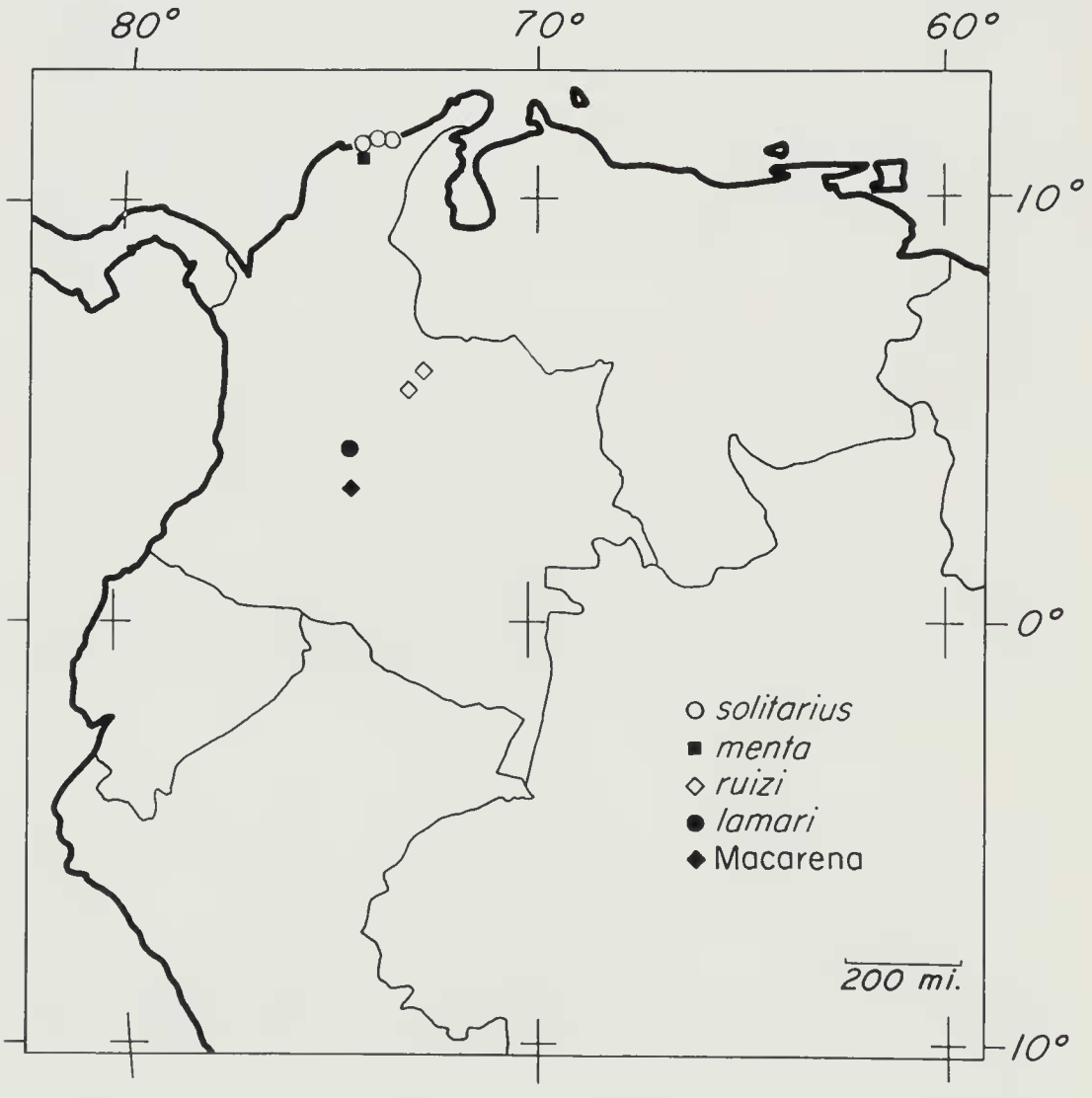

Figure 6. Colombian distribution of the *tigrinus* superspecies. MACARENA marks the presumed locality of an undescribed member of the *tigrinus* superspecies.

The locality has previously been regarded as doubtful, because it was thought to be too distant from the other Colombian species of the *tigrinus* group. No details of collection nor description of colors in life exist. (The distribution of Colombian species of this complex is shown in Fig. 6; *A. tigrinus,* as mentioned, is widely distributed in the coastal range of Venezuela.)

Of this northwestern South American complex *lamari* and *ruizi* are probably closest relatives. They are both on the eastern side of the Cordillera Oriental and show clear similarities in color and pattern (Fig. 7). They differ, however, as mentioned in the diagnosis, in the absence, in *ruizi,* of the parietal knob that is present in *lamari.*

Questionable Relationships with Two Brazilian Species. Two species, *nasofrontalis* and *pseudotigrinus,* in the Atlantic Forest

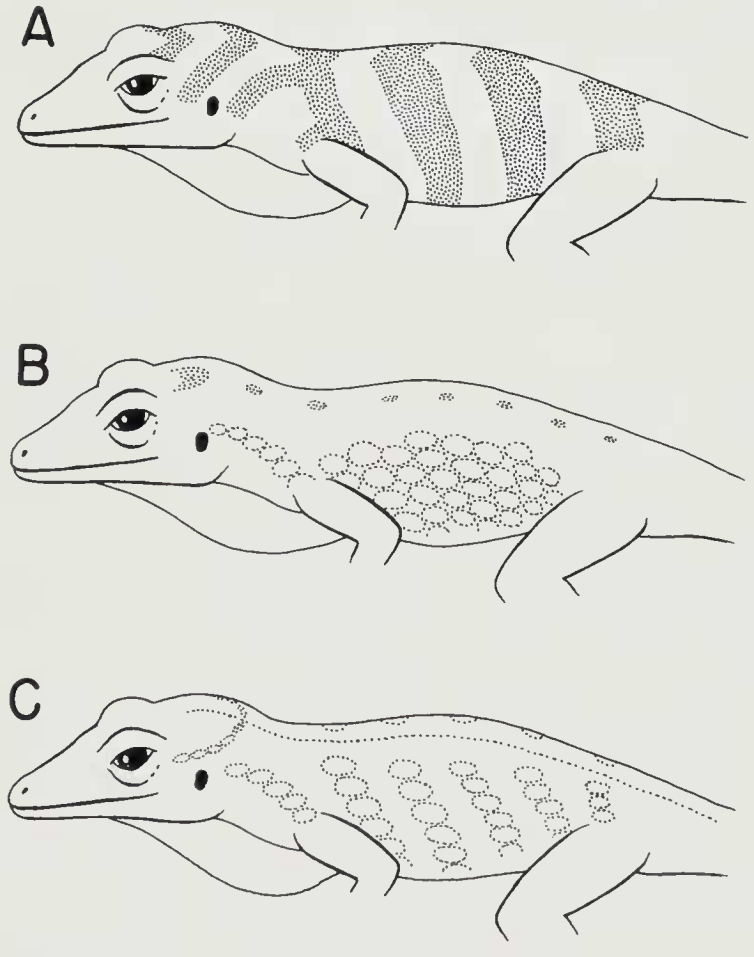

Figure 7. Male dorsal patterns in three species of the *tigrinus* superspecies. A. *A. solitarius.* B. *A. ruizi.* C. *A. lamari.*

in the state of Espirito Santo in Brazil, thus as widely disjunct from the Colombian-Venezuelan complex as the width of the South American continent permits, have been tentatively referred to the *tigrinus* species group. On size (*nasofrontalis* reaches 59 mm SVL, *pseudotigrinus* 54 mm SVL) and all scale characters they do so belong. If these two Brazilian species do belong to the same species group as the Colombian-Venezuelan complex, then, most probably, this is an old group. Relict populations may very possibly exist elsewhere, and the evidence on the present and past distribution of the group must at present be presumed to be very incomplete.

Remoter Relationships

Problems of Distinction of the Tigrinus *Group from the* Punctatus *Species Group.* When *A. lamari* is compared with the *punctatus* species group as presently defined, a problem arises. This is typified by the confusion that occurred even during the discovery of the type specimen.

Because a somewhat atypical adult of *Anolis huilae* (assigned to the *punctatus* species group) was found very close to the locality where the *A. lamari* type specimen was found, the small animal here described was at first thought to be a juvenile of that species. There is, in fact, no similarity in color or in pattern. The new species entirely lacks the bold spotting and nape ocellus of male *huilae.* There is some general similarity in squamation; in particular the interparietal of *huilae* may often be in contact with the supraorbital semicircles. Figure 8A shows the interparietal in *huilae,* but also that there is but one row of enlarged scales behind the interparietal in *huilae,* while in the midline in *lamari* there are eight such enlarged scales in front of the nape scales.

The source of the initial confusion between *A. lamari* and *A. huilae* was, in fact, the conspicuous very large interparietal scale in contact with the supraorbital semicircles. This condition is relatively unusual in *Anolis,* perhaps never invariable, but in certain groups or species characteristic to the point of being almost or quite diagnostic. It is one of the features apparently primitive for the *Anolis roquet* series of the southern Lesser Antilles, lost only, and then only sometimes, in the two giant species, *A. griseus* and *A. richardi.* In continental South America I count 18 described

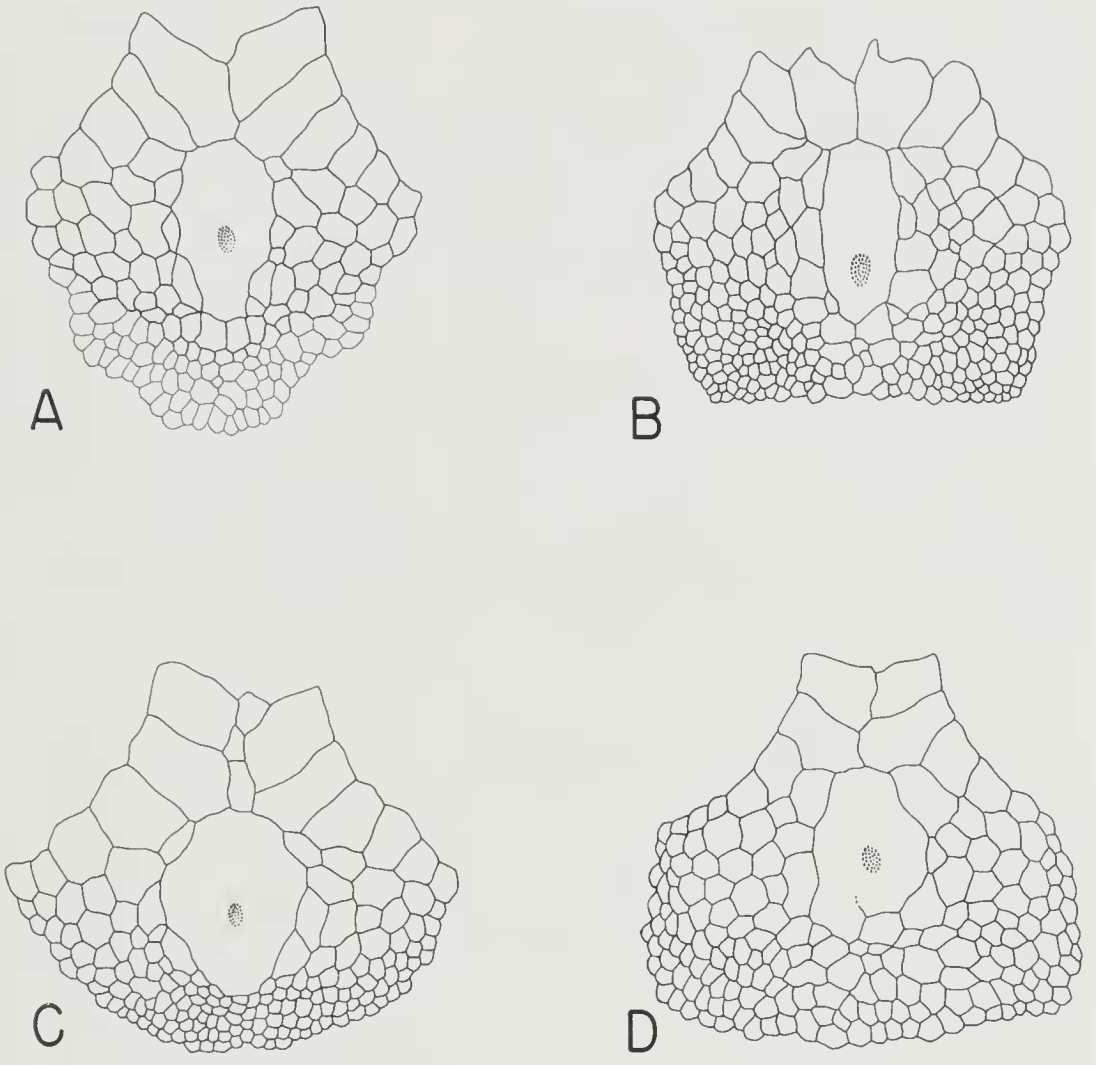

Figure 8. Scales of the parietal area in some members of the "*punctatus* species group." A. *A. huilae,* paratype: MCZ 159122. B. *A. caquetae,* holotype: MCZ 131176. C. *A. boettgeri*: MCZ 173111. D. *A. deltae,* holotype: MCNC 2031.

species of *Anolis* and three described species of *Phenacosaurus* that are known to have the interparietal in contact with the semicircles in at least some specimens. The three species of *Phenacosaurus* and five species belonging to the beta section of *Anolis, ibague, lineatus, macrolepis, rivalis,* and *meridionalis,* require no comparison with *lamari.* They and the groups to which they belong show abundant differences from the present species. Of the remainder, one, *laevis,* is known from a poorly preserved single specimen; there are not many characters to check, but *laevis* is a proboscis anole and *lamari* is clearly not.

The other species in which a large interparietal in contact with the semicircles is known are currently allocated to two species

groups, the *punctatus* group and the *tigrinus* group (Williams, 1976).

In the paper just cited I provided a key in which the *punctatus* group and the *tigrinus* group were separated by couplets 5 and 6:

5. Ventrals smooth and/or dorsal squamation quite uniform 6
   Ventrals keeled, middorsals noticeably larger than flank scales 11
6. Small anoles (ca. 50 mm snout–vent length) with large flat head scales ..... *tigrinus* group
   Anoles large or small but not with large head scales ..... *punctatus* group

The confusion, however momentary, of *lamari,* presumed on the basis of general similarity to be a member of the *tigrinus* group, with *huilae,* assigned to the *punctatus* group anoles, demonstrates that the distinction provided by the key is inadequate. Clearly the reality of the distinction between the *punctatus* group and the *tigrinus* group needs to be better demonstrated.

The type species of the two species groups, *A. punctatus* and *A. tigrinus,* do seem to differ impressively. Three characteristics only need be mentioned: *A. punctatus* is primarily green in color, *A. tigrinus* primarily lichenate; *A. punctatus* reaches a maximum size of 89 mm SVL, *A. tigrinus* only 57 mm SVL; and in *A. punctatus* the parietal area of the head is devoid of any median prominence, in *A. tigrinus* there is posteriorly a distinct parietal knob (Ayala *et al.,* 1984). Differences of the first two sorts, color and size, however, are ecomorphic (Williams, 1972, 1983) and imply neither relationship nor lack of it. In the West Indies *A. punctatus* would fit the classic definition of a trunk-crown ecomorph, and *A. tigrinus* that of a classic twig dwarf (Williams, 1983). The character of the parietal knob is equivocal both in the South American complex that has been assigned to the *A. tigrinus* group and in the West Indies twig dwarfs: three of the West Indian twig dwarf species, *insolitus, sheplani,* and *placidus,* have such a knob; *occultus* does not; four of the South American species that are inferentially twig dwarfs have an analogous knob—*tigrinus, solitarius, menta,* and *lamari*; *ruizi* does not, and such a knob is not obvious in the two Brazilian species that have been referred to the *tigrinus* group.

Is it possible that the "*tigrinus* species group" is at best an ecomorphic (*sensu* Williams, 1972, 1983) subgroup of the *punctatus* assemblage? Even in squamation there is overlap between

the two species typical for the supposed species groups. Counts across the snout between the second canthals are eight to 14 in *A. punctatus,* five to eight in *A. tigrinus.* This is confirmation that head scales tend to be smaller in *punctatus* than in *tigrinus,* but there is also overlap. Despite the difference in maximum size there is overlap in fourth toe lamellae, 22–32 under phalanges ii and iii in *A. punctatus,* 18–22 in *A. tigrinus.* While in the 11 specimens of *A. tigrinus* there is no example in which the supraorbital semicircles are not in contact medially, there are 14 examples of separation in 110 specimens examined of *A. punctatus.* In the nine specimens of *A. tigrinus* in which the interparietal can be seen, eight have the interparietal in broad contact with the semicircles; only the type of the inferred *tigrinus* synonym, *impetigosus,* has it separated by two scales. However, in none of the 110 specimens of *punctatus* is the interparietal even in point contact with the supraorbital semicircles.

And, while these two type species of the two "species groups" are on balance rather sharply distinct, the additions made to our knowledge of old species placed in the two groups and the recent referral of new species to one or the other of the two assemblages have greatly reduced the distinctiveness of one assemblage as compared with the other.

In the case of the *tigrinus* group, *solitarius* and *menta* are green rather than lichenate. A parietal knob is not visible externally in *ruizi,* nor in Brazilian *nasofrontalis* and *pseudotigrinus.* Some species currently referred to the *punctatus* group are nearly as small as members of the *tigrinus* set, and some of these are species that have or frequently have a large interparietal broadly in contact with the supraorbital semicircles: *caquetae* (maximum SVL 58 mm), *deltae* (maximum SVL 58 mm), *dissimilis* (maximum SVL 56 mm).

The one character that, on inspection of all species belonging to both species groups, appears to separate all members of the *tigrinus* grouping from all species—*except one, Anolis santamartae*—referred to the *punctatus* grouping is the enlarged scales lateral to the very large interparietal (Fig. 9). Such enlarged scales are not seen in even those species (with the exception of *santamartae*) now referred to the *punctatus* group that have a large interparietal and are similar in size to members of the *tigrinus*

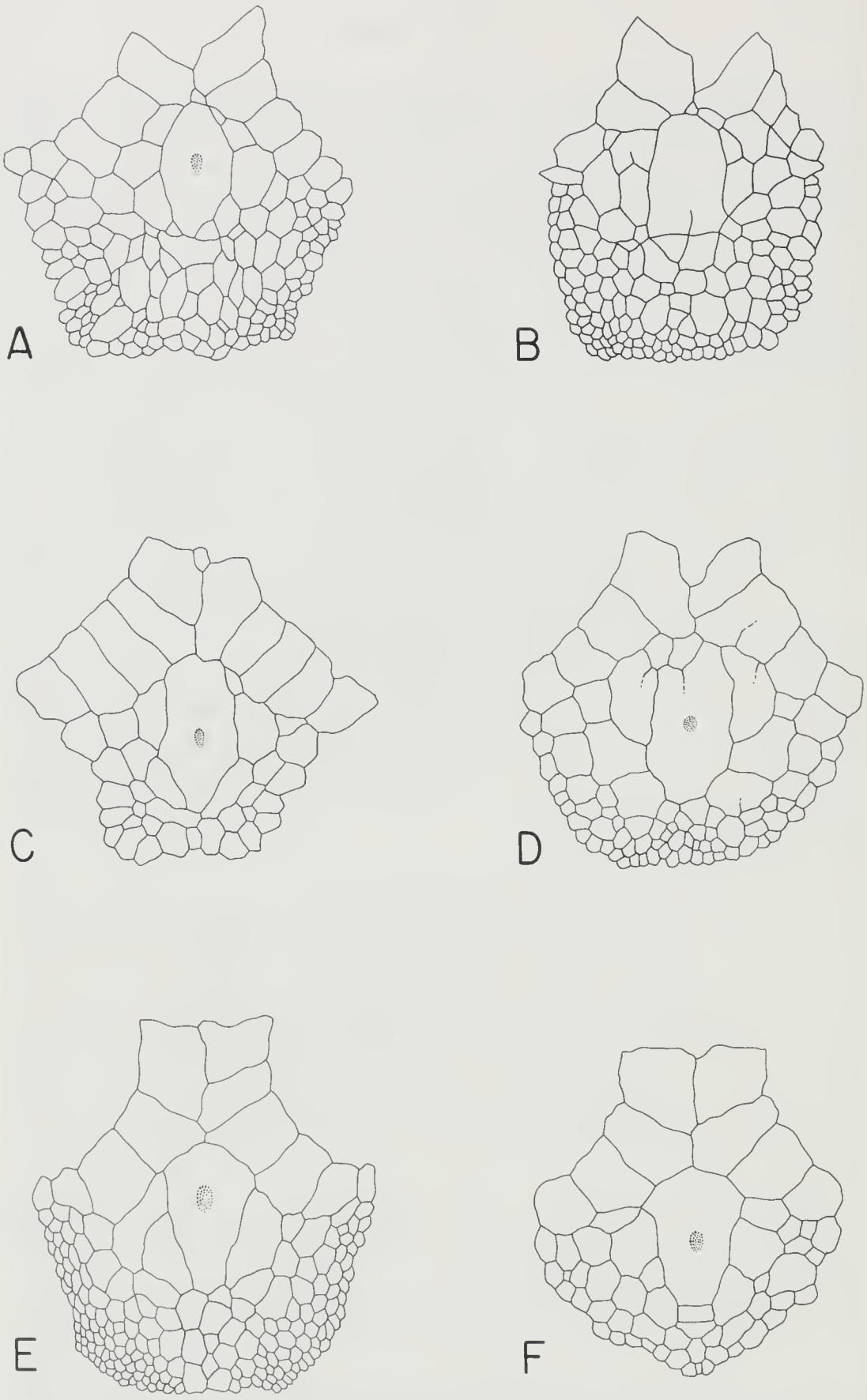

Figure 9. Scales of the parietal area in members of the "*tigrinus* species group." A. *A. nasofrontalis.* B. *A. pseudotigrinus.* C. *A. tigrinus.* D. *A. solitarius.* E. *A. menta.* F. *A. ruizi.*

group (Figs. 8, 10). (It is noteworthy that the members of the *roquet* series, which primitively show the interparietal in contact with the supraorbital semicircles, also lack these large scales lateral to the interparietal.)

A. santamartae: An Anomalous Species. The one exception within what I have called the *punctatus* species group, *Anolis santamartae* Williams, 1982 (the significant parietal area is shown in Fig. 11), is the only species of alpha anoles known to occupy the southeast corner of the Sierra de Santa Marta, the north end of which is occupied by *A. solitarius* and the southwest by *A. menta.* It might be plausible to consider *A. santamartae* on geographic grounds alone as a possible member of the *tigrinus* group.

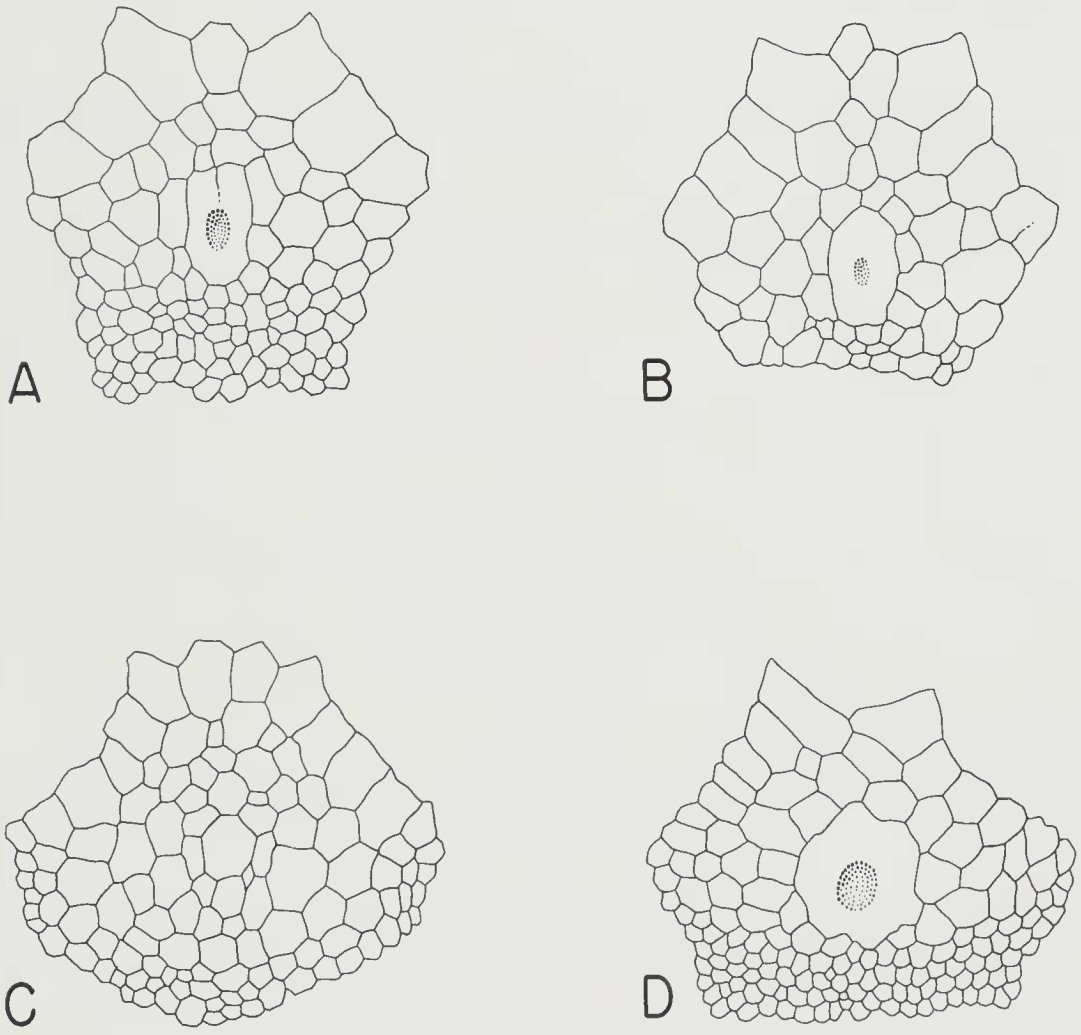

Figure 10. Scales of the parietal area in some members of the "*punctatus* species group." A. *A.* sp. ? near *transversalis*: MHNJP 1192. B. *A. jacare*: AMNH. C. *A. calimae,* holotype: MCZ 158392. D. *A. dissimilis*: FMNH 81369.

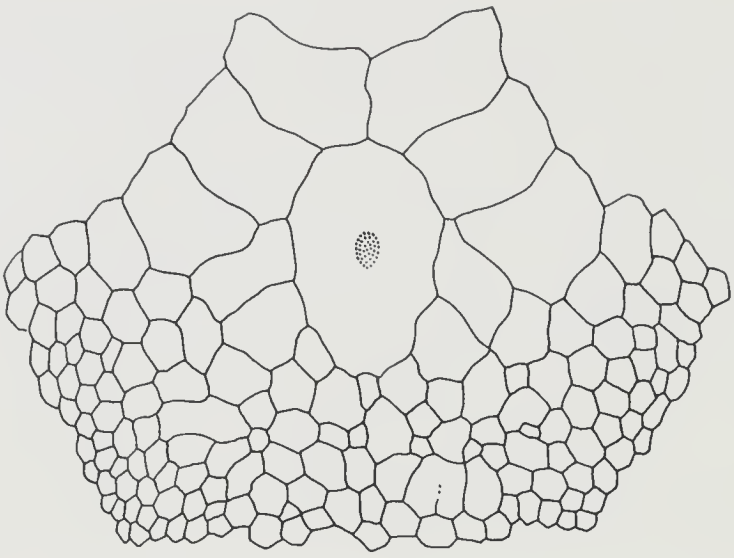

Figure 11. Scales of parietal area in *A. santamartae,* holotype: CAS 113922.

I did consider this possibility when I described it: it is the right size, approximately the right habitus. Its habits and habitat are undescribed.

Why did I reject this hypothesis? On the basis, first, of the distinctive pattern, in particular the light line from the lower jaw onto the upper arm (not emphasized in the rather muted figure of the type in the original description, but stressed in the text and very evident in one of the paratypes, MCZ 156311, the pattern of which is diagrammed in Fig. 12). This is a singular and distinctive pattern for any anole. I was much more comfortable in assigning *santamartae* to the *punctatus* species group, which I knew to be quite varied in pattern, rather than to the *tigrinus* species group, which I then believed to be rather uniform in pattern, its members differing among themselves primarily in dewlap color.

When *santamartae* was described in 1982, *menta* Ayala, Harris, and Williams, 1984, and *ruizi* Rueda and Williams, 1986, were not yet recognized. I had not yet seen the large new series of *solitarius,* collected by Pedro Ruíz and John Lynch, and I was not aware that the ground color of that species in life was green. I was confident that the *tigrinus* series was ecologically the equivalent of the twig dwarf species of the West Indies. The West Indian twig dwarf anoles are basically cryptic in pattern, lichenate, as *tigrinus* was known to be. I did not expect a relative of *tigrinus* to have the pattern of *santamartae,* even if *santamartae* did have

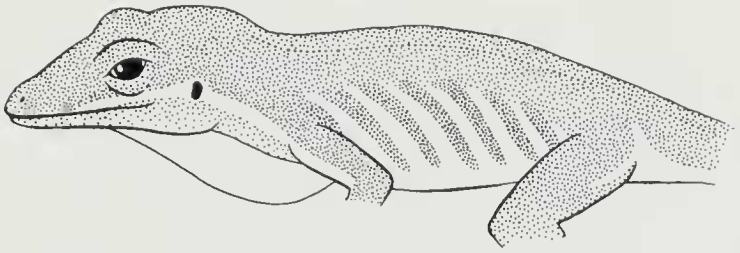

Figure 12. Male dorsal pattern in *A. santamartae,* after MCZ 156311, a paratype.

much of the size and habitus of *tigrinus.* Unhappily, the extrapolations as regards pattern from the West Indian twig dwarf ecomorphs have proved quite wrong. Additionally, the distinctly, although rather weakly keeled, dorsals and ventrals influenced me. Keeled ventrals are unusual even in the *punctatus* species group, but they are known in *punctatus* itself. The *boulengeri* morph of that species, characteristic in western populations, has keeled ventrals. There was no indication of comparable conditions in the known species of the *tigrinus* species group. There is also no evident parietal knob in *santamartae.* If *santamartae* belongs to the *tigrinus* species group, it is the most distinctive of the included species.

Remaining Problems in the Recognition of the Tigrinus *Group.* Even if the *tigrinus* group is phenetically recognizable, is it phylogenetically a unit? There are several difficulties here. One is the possibility, mentioned above, that the *tigrinus* group is an ecomorphic grouping: The *tigrinus* group may be the South American twig dwarfs. On the limited present evidence they seem likely to be so in an ecological sense. However, the scale character, the enlarged scales lateral to the parietal, by which the group may possibly be recognized morphologically, is not an attribute of twig dwarfs as an ecomorphic category. It is not present in any of the classic West Indian twig dwarfs. This possibility may provisionally be dismissed.

Unfortunately another possibility cannot be so readily dismissed. The polarity of the diagnostic scale character is in doubt. One of the two possibilities in the analysis of head scale characters in the Squamata is that small undifferentiated head scales are primitive, and that they have repeatedly united in larger units. The other is that large scales like parietals, frontals, postparietals, etc., are primitive. In the first hypothesis the larger scales lateral

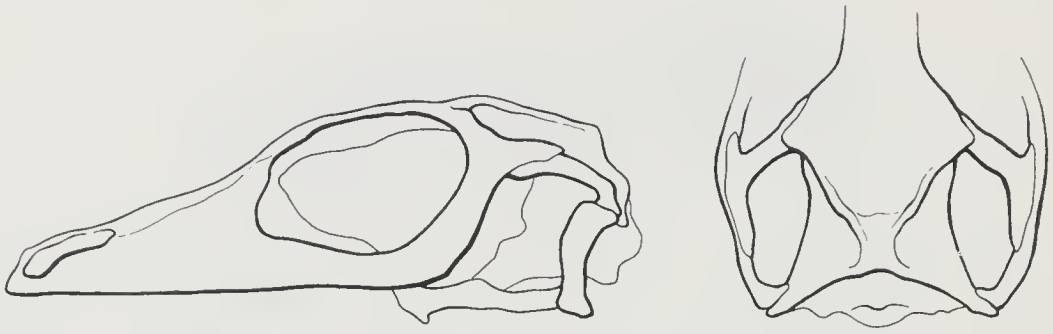

Figure 13. *A. punctatus* (MCZ 155994). Left: The skull in profile. Right: The parietal bone to show absence of the parietal knob.

to the interparietal are genuinely synapomorphic, and the *tigrinus* group is a genuinely monophyletic unit that includes the two widely disjunct Brazilian species. In the second hypothesis, which I favor on general grounds rather than the specifics of this case, the larger scales lateral to the interparietal are remnants of primitively present parietal scales in this area. Then, the *tigrinus* group may not be monophyletic, but merely an assemblage of possibly only remotely related species that happen to remain plesiomorphic in the size of the scales lateral to the interparietal. The Colombian set of species might be genuinely a superspecies, but the Brazilian members of the assemblage would be only species that by a combination of ecomorphology and symplesiomorphy have come to resemble their relatively distant relatives on the other side of the continent.

The parietal knob seen in *tigrinus, solitarius, menta,* and now in *lamari* seems certainly a derived character. Figure 5 shows the bony structure underlying the external parietal knob in *A. solitarius.* Figure 13 shows the complete absence of such a structure in *A. punctatus.* An approach to the *solitarius* condition is seen in *A. jacare* (Fig. 14), and in no other of the South American alpha anoles examined (*punctatus, agassizi, chloris, peraccae, gemmosus, ventrimaculatus, aequatorialis, princeps, squamulatus, latifrons,* and *frenatus*).

Etheridge in his thesis (1960) discussed the ontogenetic and phylogenetic history of parietal crests in *Anolis.* He was able to show that in the ontogeny of *Anolis carolinensis* (well illustrated in his fig. 9) the parietal crests first delimit a distinctly trapezoidal area, then a triangular area, and finally have a Y shape with the

Figure 14. *A. jacare* (MCZ 112096). Left: The skull in profile. Right: The parietal bone to show similarity to *A. solitarius* in the incipient or convergent crest structure of the parietal in this species.

arms bounding the triangular area continued backward as a median ridge. He asserted that this ontogenetic sequence was precisely parallel to the sequence seen in phylogeny: *A. carolinensis,* a relatively derived species on other characters, had the Y crests in adults, whereas the South and Central American alpha anoles and the southern Lesser Antilles anoles, which are primitive in a number of other osteological characters, retain a trapezoidal crest pattern. My own observations confirm Etheridge's statements with minor revisions. Derived anoles definitely have Y-shaped parietal crests with a relatively long and narrow median posterior ridge. However, in relatively basal anoles the crests bound a trapezoidal area consistently only in the *roquet* series of the southern Lesser Antilles. In this set of species the lateral ridges do turn inward posteriorly to provide a raised transverse boundary to the parietal roof (called the occipital crest by Etheridge). However, in the primitive mainland alphas (e.g., *A. punctatus,* Fig. 13) the Y stem frequently is broad and short, a condition transitional to the fully derived Y shape. The parietal roof anterior to this posterior ridge is still trapezoidal, but lacks the distinct posterior boundary of an occipital crest that is present in the ontogenetically and phylogenetically primitive condition. *A. jacare* (Fig. 14) is still more derived. The stem of the Y is narrow—a single ridge, differing from the more advanced condition only in being short. *A. solitarius* (Fig. 5) retains the short narrow single ridge of *A. jacare,* but adds a small bony knob at the end of it, the skeletal underpinning of the external parietal knob.

The similar bony parietal knob according to this analysis occurs in some of the dwarf West Indian species (Williams, *in* Ayala *et*

Figure 15. *A. insolitus* (MCZ 107018). Left: The skull in profile. Right: The parietal bone to show a parietal knob convergent with that of *A. solitarius.*

al., 1984; Fig. 15 in this paper). (In *A. sheplani* and *A. placidus* the skull is not known.) In *A. insolitus,* at least, the skeletal knob is at the end of a triangular parietal; there is not even a short-stemmed Y. Clearly this condition is convergent and not relevant to the issue of the monophyly of the *tigrinus* species group.

The parietal knob, defined as the condition seen in *solitarius,* might then be a synapomorphy of the *tigrinus* species group, *but* only *if* this feature has been lost in *ruizi, nasofrontalis,* and *pseudotigrinus,* as well as *santamartae, if* the latter belongs in the group. The similarity of pattern in *ruizi* and *lamari* and their geographic proximity suggest that this hypothesis of loss may be true for *ruizi.* The widely disjunct range of the two Brazilian species does not rule out this possibility for those two species, but it is clearly not as well supported. The Brazilian species were always problematic members of the *tigrinus* species group. They remain so.

CONCLUSION

I see no means to resolve the tangle presented here. I am content to speak of a *tigrinus* species group, *provided* it is recognized as a convenient means to call attention to phenetic resemblances that may or may not be phylogenetically meaningful.

As currently used, the *punctatus* group is clearly the residue of those South American alpha *Anolis* believed or known to have arrow-shaped interclavicles (Williams, 1989) that are not placed in the presumed *tigrinus* lineage. It might be a rescue of the *punctatus* group concept if the *tigrinus* lineage were placed within

it. It would then consist of all South American alpha *Anolis* known or believed to have arrow-shaped interclavicles and known to have non-autotomic caudal vertebrae as adults. Even this would be a dubious rescue, again because of a question of polarity. I see no objective grounds for deciding whether arrow- or T-interclavicles, *sensu* Etheridge (1960), are primitive. This leaves me again with the *punctatus* group as a cluster of convenience, intended not to formally decide a phylogenetic question but to informally raise that question.

The problem of which the present case is an example is a pervasive and difficult one, and very clearly not limited to the genus *Anolis*. A useful recent discussion, with a summary of the pertinent literature, is that of Bauer *et al.* (1988). *I very much concur with their point that "species groups" are not formal taxa, but often, perhaps usually, operational clusters, phenetic groupings of convenience, intended at best to suggest possible affinities but not pretending at all to their demonstration.* I disagree with Bauer *et al.* in being less optimistic than they that data sufficient for the analysis that they hope for will soon be available.

I plead for extensive periods of use of informal groupings in cases in which taxonomic decisions must be based on evidence that is less than conclusive. The levels of confidence for every taxon erected or changed need not be quantified—there may be no plausible means of doing so—but the grounds for these levels of confidence should always be spelled out in detail, as I have attempted to do in this paper.

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