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B R E V I O R A

Museum of Comparative Zoology

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NUMBER 239

SOUTH AMERICAN ANOLES:
ANOLIS BIPORCATUS AND *ANOLIS FRASERI*
(SAURIA, IGUANIDAE) COMPARED

By ERNEST E. WILLIAMS

INTRODUCTION

Confusion of the two species *Anolis biporcatus* Wiegmann 1834 and *Anolis fraseri* Günther 1859 first occurred in the original description of *A. fraseri* by Günther. One of the syntypes of *Anolis fraseri* Günther 1859 from western Ecuador was in fact a specimen of *Anolis biporcatus* Wiegmann 1834, a species first described from Mexico. Very unfortunately, it was this syntype which was sent to Paris for examination and which Bocourt (1873, pl. 15, fig. 12) figured as *A. fraseri*. The confusion of these two species which began thus has continued till the present.

Boulenger (1885) did, indeed, correct Günther's error and remove the *biporcatus* specimen from the syntype series, placing it in "*copii*" (= *copei* Bocourt 1873, a synonym of *biporcatus*¹). He was, however, apparently quite convinced that "*copii*" and *fraseri* were closely related; he placed them side by side in his catalogue and a collation of his two descriptions shows only minor differences. This belief in a close relationship continues to the present day: L. C. Stuart (1955) in discussing the affinities of Central American *biporcatus* has suggested that *fraseri* is the South American representative of *biporcatus*.

A contrary view that *A. biporcatus* and *A. fraseri* are not at all close is also currently held. This opinion is implicit in Dunn's 1937 discussion of mainland giant anoles of the *latifrons* group. *A. fraseri* is placed with these, and *biporcatus* or its synonym *copei* goes quite unmentioned. Most recently a more explicit denial of close relationship has been propounded: R. Etheridge,

¹ See Stuart (1948) for discussion of the usage of the name *biporcatus* Wiegmann rather than *copei* Bocourt. The question is one of the identity of the Berlin type of *biporcatus*.

in a doctoral thesis (1960) at the University of Michigan, has placed *A. fraseri* and *A. biporcatus* in separate major sections of the genus *Anolis*, the first in his alpha series, the second in his beta series. (The primary distinction is the presence or absence of transverse processes on certain of the caudal vertebrae, an apparently trivial point which, however, has some very striking zoogeographic and other correlations.)

A. BIPORCATUS IN SOUTH AMERICA

Central to the confusion of *biporcatus* and *fraseri* has been the question of the presence of *biporcatus* itself in South America. This has been so poorly documented in the literature that doubt of the authenticity of the South American records has existed. Thus, while Burt and Burt (1933) list the range of *biporcatus* as "western Ecuador northward into Central America," Smith and Taylor (1950) give, instead, "Chiapas to Panama."

Boulenger, of course, had already listed one of the Günther syntypes from western Ecuador as the *biporcatus* synonym "*copei*," but the absence of further records in the literature has probably progressively diminished for many workers the importance which has been attached to this single specimen. Thus, Barbour (1934), while mentioning the Günther syntype in the synonymy of *copei*, totally ignored it in his discussion of the range, which he regarded as extending only to Panama. Furthermore, the description from the Santa Marta Mountains of Colombia by Ruthven (1916) of *Anolis solifer*, regarded by him as a relative of *copei*, may have seemed to make the occurrence of *biporcatus* itself in South America still more improbable.

It is a measure of our ignorance of the *Anolis* of South America that confusion so extreme could exist regarding one of the larger and more distinct forms occurring there.

It is only because I have been able to see a quite unusual amount of material (some of it only recently collected) that it is possible to bring a measure of clarity into this muddled situation. I have been privileged to examine the material recently collected by James A. Peters (JAP) in Ecuador, as well as material in the American Museum of Natural History (AMNH), the Academy of Natural Sciences, Philadelphia (ANSP), the British Museum (BM), the Chicago Natural History Museum (CNHM), the Instituto La Salle, Bogota, Colombia (ILS), the Institut Royal des Sciences Naturelles, Brussels (IRSN), the Escuela Polytecnica, Quito, Ecuador (Orces), the Universidad Central de Venezuela (UCV), the University of

Michigan Museum of Zoology (UMMZ), the United States National Museum (USNM), the Vienna Museum (VM), and the Berlin Museum (ZMB). To the collectors and curators who have so generously loaned material I am deeply indebted. Dr. Fred Medem graciously donated Colombian material collected by him. National Science Foundation Grant GB 2444 supported this study.

On the basis of this newly examined material — so much more abundant than anything seen before — plus the collections of the Museum of Comparative Zoology, I have been able to come to the following conclusions.

1. *Anolis biporcatus* Wiegmann does occur in both Colombia and Ecuador and also in Venezuela.

2. *Anolis solifer* Ruthven must be considered a synonym of *A. biporcatus* Wiegmann.

3. *A. biporcatus* Wiegmann is at least in a broad sense sympatric with *A. fraseri* but the sympatric populations appear not to belong to the nominate race.

4. *A. biporcatus* belongs to a quite different group from *A. fraseri*, the relationships of which are, as Dunn and Etheridge have suggested, to endemic South American anoles.

COMPARISON OF *A. BIPORCATUS* AND *A. FRASERI*.

The characters of these two species — so often confused — are best compared in tabular fashion (Table 1). In many characters there is wide overlap. If in any numerical character the range

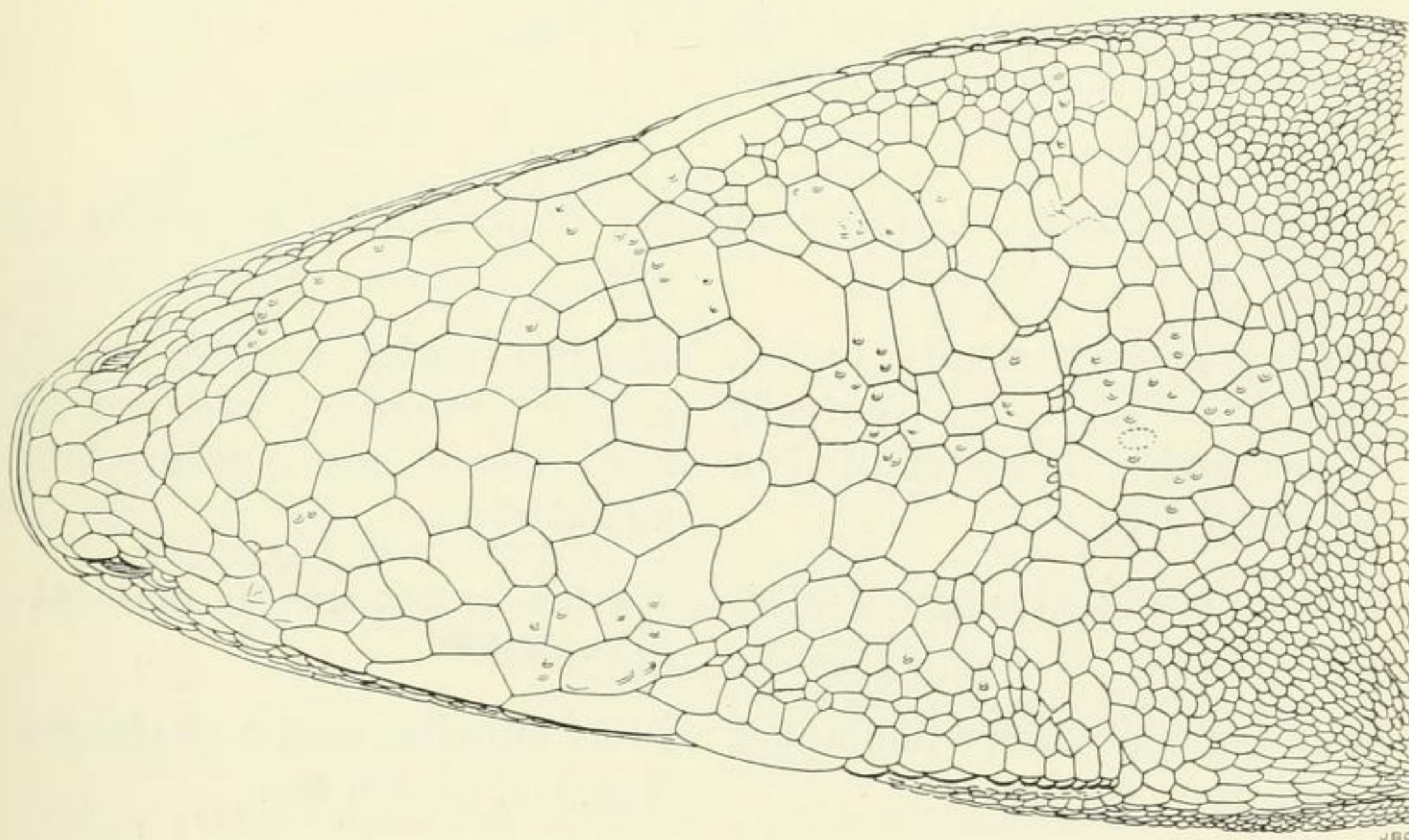


Fig. 1. *Anolis fraseri*, MCZ 70227. Dorsal view of head.

TABLE 1

<i>South American biporcatus</i>	<i>fraseri</i>
Head scales, at least anteriorly, keeled.	<i>Head scales never keeled, usually flat, pavementose, but sometimes swollen or wrinkled.</i>
2-3 scales between circumnasal and rostral.	1-2 scales between circumnasal and rostral.
Supraorbital semicircles separated by 0-3 scales.	<i>Supraorbital semicircles separated by 2-4 scales.</i>
Supraocular scales keeled.	<i>Supraocular scales smooth.</i>
2-3 more or less elongate supraciliary scales followed by a double series of scales which become smaller posteriorly and merge into granules like those medial to the series.	<i>Usually no elongate supraciliary scales; instead, the whole supraciliary margin of round or squarish scales distinctly larger than the granules medial to them.</i>
6-9 loreal rows.	4-9 loreal rows.
Interparietal small (but sometimes larger than the ear which is usually very small).	Interparietal larger (larger than the ear which is moderate in size).
Subocular scales usually completely and always at least partially separated from the supralabials by a row of intervening scales.	<i>Subocular scales broadly in contact with supralabials.</i>
7-12 supralabials to center of eye.	6-9 supralabials to center of eye.
Dewlap scales strongly keeled, almost as large as ventrals, rather uniformly distributed on the small fan.	<i>Dewlap scales smooth, small, almost granular, grouped in rows which are separated by naked skin.</i>
Ventral scales strongly keeled, mucronate.	<i>Ventral scales smooth or weakly keeled.</i>
22-26 lamellae under phalanges ii and iii of 4th toe.	20-24 lamellae under phalanges ii and iii of 4th toe.

in one species *completely* overlaps the known range of the other, I have omitted this character. The most striking differences are emphasized by italicizing the pertinent characters for *fraseri*. Both are large, short-legged, stout-bodied, relatively short-headed forms. The similarities are indeed amazing since the two species are, according to Etheridge, osteologically in totally different sections of the genus. The similarities would be even greater if Mexican and other northern *biporcatus* were compared with *fraseri* since the northern animals tend to have 3-4 scales between the supraorbital semicircles (*cf.* Stuart, 1955).

Overlapping variation in many features, as shown in Table 1, is characteristic of many sympatric species in *Anolis* and is one of the several reasons why this genus is described as "difficult." As in all such cases, the recognition of the valid species depends upon recognition of the constant (or almost constant) association of characters, however trivial. Smooth or keeled scales, suboculars in contact with or separated from supralabials, interparietal large or small are none of them characters universally useful in *Anolis*. The distinctive supraciliaries of *fraseri* are more useful because a substantial morphological gap between this condition and that shown by *biporcatus* will always distinguish these two species. (The *fraseri* supraciliaries occur, however, also and in a more exaggerated degree in *latifrons*; the condition is not unique to *fraseri*.)

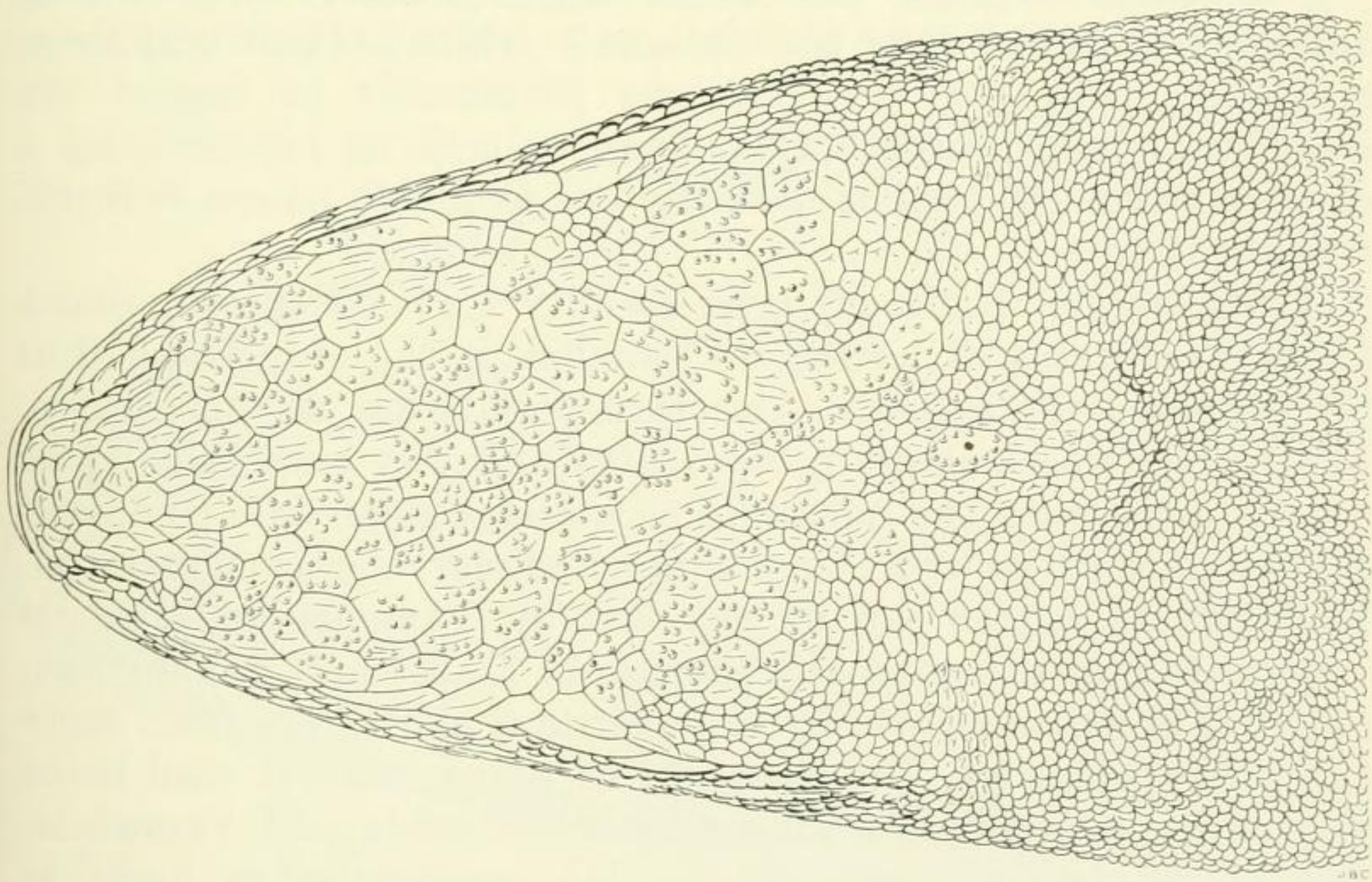


Fig. 2. *Anolis biporcatus parvaauritus*, new subspecies, MCZ 78935. Dorsal view of head of type.

INTRASPECIES VARIATION: *A. BIPORCATUS*

While I have not endeavored to examine all specimens of *A. biporcatus* from all parts of its range, I have sampled the northern populations (Panama, Costa Rica, Guatemala, Mexico), and I have had the especial advantage of examining the series of 122 specimens taken by Slevin near Boquete, Panama (Slevin, 1942).¹

Having seen this series I am impressed by the similarities of the various populations. There is indeed considerable variation within *A. biporcatus*, as I understand it. Thus, the number of scales between the semicircles, the number of scales between interparietal and semicircles, the number of loreal rows, the amount of keeling of the head scales, the contact or separation of suboculars and supralabials, and the length of the hind limbs all appear to be quite variable from individual to individual. Yet the species has a strong habitus character and is quite recognizable in spite of very striking variation.

A very few characters appear to sort out geographically. The supraocular scales and those surrounding the interparietal are extraordinarily small in Ecuadorian and southern Colombian specimens. In these same populations the ear opening is circular and very small in contrast to the rather oval opening of northern specimens.

Since there seem also to be some color differences of both body and dewlap in these same populations — which are precisely those sympatric with *fraseri* — it seems permissible to regard the Ecuadorian and southern Colombian animals as representing a distinct subspecies. Some discussion of available names is therefore required.

Anolis solifer Ruthven, type locality La Concepción, Santa Marta Mountains of northern Colombia, is the only name thus far proposed for a South American population of this species. That *solifer* does belong in *biporcatus* and may provisionally be synonymized with the nominate race seems clear from the comparison of the type with Panamanian and more northern material. The type of *solifer* can be matched by Panamanian material (except for the exceptionally short hind limbs) and Panamanian material is not separable by any constant characters from more northern specimens. The character of the very short hind limbs may define a population in northeast Colombia and Venezuela. One of the two available Venezuelan specimens has limbs as

¹ I am indebted to Dr. Allan Leviton of the California Academy of Sciences for this opportunity.

short as those of the *solifer* type but the other does not. In any event, the name *solifer* is clearly not available for the distinctive Ecuadorian and south Colombian populations. In the critical characters *solifer* resembles northern *biporcatus*.

The other names referable to the species *biporcatus* are equally unavailable. None of them refer to South American material. The nominate race *biporcatus* Wiegmann 1834 has the type locality "Mexico," now restricted to Piedra Parada, Chiapas. *A. copei* Bocourt 1873 has the type locality Santa Rosa de Pansas, Guatemala. *Anolis brevirostris* Peters 1873, next in date, has the type locality Chiriquí Prov., Panama. *Anolis brevipes* Boettger 1893 came from Cairo Plantation, La Junta near Limón, Costa Rica. Every one of these seems at present best grouped under the name *biporcatus*.

The southern race is thus without a name. In reference to the small ear it may be called:

ANOLIS BIPORCATUS PARVAURITUS new subspecies

Holotype: MCZ 78935, an adult ♂, "banana plantation, woods and penal colony camp, northern Gorgona Island, Cauca, Colombia, 5-45 meters altitude," collected by F. Medem and L. Salazar G., 1 to 23 February 1961.

Paratypes: **Colombia**. *Cauca*: MCZ 78933-34, 78936-41, same data as type. *Nariño*: MCZ 79142, Rio Mataje. **Ecuador**. *Esmeraldas*: USNM 157105, Cachavi; BM 1901.6.27.1, Carondolet;

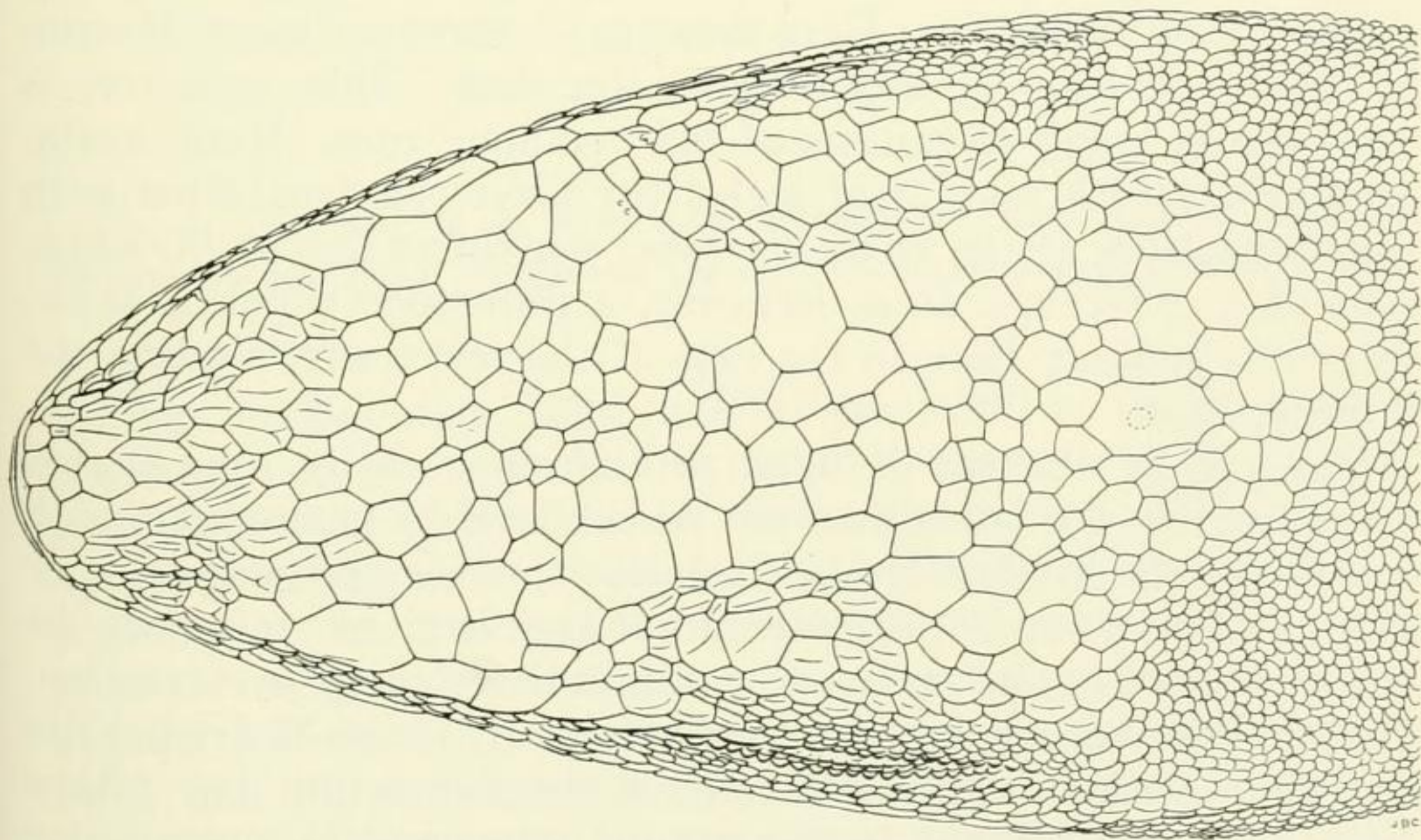


Fig. 3. *Anolis biporcatus biporcatus*, MCZ 56243, from Los Diamantes, Costa Rica. Dorsal view of head.

AMNH 6967, Rio Capayas; BM 1907.7.29.10-11, ZMB 18213, VM 12755, Rio Sapayo; BM 1901.8.3.1, Salidero; BM 1901.6.27.1, San Javier; Orces 3898, San Lorenzo. *Imbabura*: BM 98.4.28.13, Paramba. *Pichincha*: Orces 4596, Santo Domingo de los Colorados. "West Ecuador": BM 1946.8.13.21 (*fraseri* syntype). "Ecuador": USNM 20610, ANSP 7910.

Diagnosis. A subspecies of *Anolis biporcatus* distinguished by the small size of the scales surrounding the interparietal which are smaller than or only equal to middorsal scales (instead of distinctly larger than middorsal scales), by the small round ear rather ventrally placed (instead of a large oval ear extending well dorsally), and by a black-edged dewlap.

Comment. None of the conventional numerical counts in *Anolis* (e.g. scales across snout, scales between semicircles, scales between interparietal and semicircles, etc.) reveal the distinctness of *parvauritus*, though it is visually apparent immediately on inspection of the specimens (Figs. 2 and 3). The number of scales between interparietal and semicircles might be expected to correspond neatly to the very striking difference in the size of scales surrounding the interparietal in the nominate race and in *parvauritus*. In fact, however, there is wide overlap, and no discrimination could be based on the numerical character. However, comparison of the scales around the interparietal and the scales on the midline of midbody of the same animal gives instant conviction of the difference between the two races.

The character of the small size of supraocular scales is equally apparent on inspection. Here there is in *parvauritus* an absence of clear definition of any supraocular disk. This, however, is true also in many specimens of the nominate race. Here, again, comparison with middorsal scales (or direct confrontation with representatives of the northern race) convinces one of the existence of a difference. It is, however, a difference which is somewhat less striking than in the case of the scales surrounding the interparietal.

The size of the ear is again a character easily appreciated visually (Fig. 4), but it does not reveal itself by comparison with the size of the interparietal, which itself varies and may be very small. Comparison with the temporal area is more useful but the size and shape of the ear are sometimes distorted by preservation. Certain specimens seem intermediate: MCZ 79656-57 from Villa Arteaga, Antioquia, Colombia, have the ear round but rather large. In other regards (scales around interparietal, supraocular scales) these are northern in type. MCZ 79842 from Sincelejo,

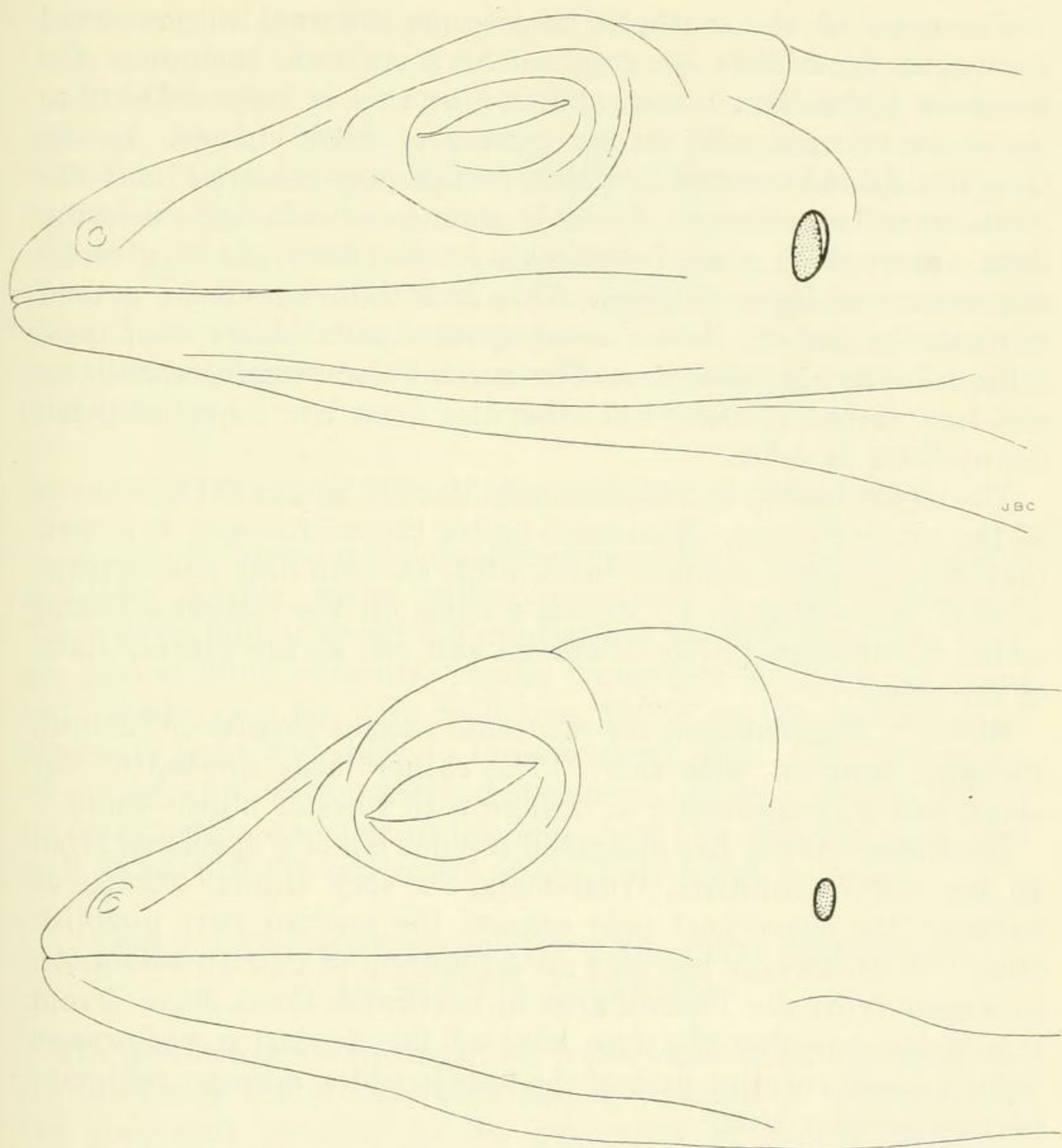


Fig. 4. Ear size in *A. biporcatus biporcatus* (top) and *A. biporcatus parvauritus* (bottom). Specimens are of the same snout-vent length.

Bolivar, on the other hand, has the ear small as in the southern race and the supraocular scales definitely large as in the northern race. A juvenile from Pizarro, Choco, Colombia (CNHM 43778), appears, in agreement with expectations from its geographic position, to be intermediate in size of ear and size of scales around interparietal and, like the nominate race, in size of supraocular scales. From this small sample one may perhaps infer that the ear character and the other characters that distinguish the races vary erratically and not in any correlated fashion in northern Colombia.

The color of the southern race seems different in preserved specimens from that of any northern animals including the northern Colombian intermediates, but this is very difficult to define in animals with strong powers of color change. In the Gorgona Island material, which is the largest series and the most recently collected, there is strong reticulation enclosing light areas which may, in animals in the dark phase, give an appearance of light spotting. This reticulation tends to extend to the belly, but the throat is not spotted with darker as it typically is in the northern race. The north Colombian intermediates also lack throat spotting but otherwise seem like other northern populations in color.

The small dewlap is conspicuously black in preserved specimens of the southern race. Examined under the microscope, it is seen that the scales are intensely black while the skin may have a trace of red. According to F. Medem's notes on the Gorgona Island series, the dewlap in life is orange and red at the center, black at the edge.

Slevin's 1942 notes on the nominate race at Boquete, Chiriquí, Panama, contrast with this: "The rather large dewlap of the males had a ground color of orange with rows of bluish scales."

Duellman (1963) has described the dewlap of a specimen from 20 km NNW Chimapa, Guatemala, in very similar terms, as having "the outer part pale orange, the median part purplish blue." J. M. Savage has sent me a diagram of dewlap coloration in a male from the Tilaran area in northwest Costa Rica. From this it appears that the free edge of the dewlap is red-orange while a small anterior part of the base is white, a larger posterior portion powder blue.¹

These three descriptions, all in essential agreement, are from specimens which bracket much of the range of the typical race and indicate a dewlap color consistently and sharply different from that of the southern race. Unfortunately, the dewlap color in Venezuelan specimens, for which "*solifer*" is an available name, is unknown.

Behavioral notes. F. Medem (field notes) remarks on the Gorgona Island topotypic series of *parvauritus* that the gular sac is "extended *laterally*" and that this species is here found

¹ The description by Taylor (1956, p. 136) of the dewlap of Costa Rican specimens as "white or slightly greenish" appears on careful reading to result from a complex confusion of notes for *A. capito* with the text for *A. biporcatus*, and apparent resulting omission of some of the pertinent data for *biporcatus*. See the reference to *A. capito*, top of page 137.

on trees up to 5 meters or more in height, rarely on the ground. It is seen most often early in the morning (7:30-9:30 AM).

A. biporcatus is everywhere known as a strongly arboreal species. Slevin (1942) reports on it at Boquete, Panama, as follows: "It was generally found in the larger and higher trees, but occasionally on fence posts and once or twice on the ground. While most frequently seen on the tree trunks, it was often discovered on fairly high limbs, crouching down as if to avoid detection." This compares very well with Medem's notes on *parvauritus*, and the two races are probably very similar ecologically.

INTRASPECIES VARIATION: *A. FRASERI*

A. fraseri, with a much smaller geographic range and a smaller available sample, seems rather consistent in scale characters.¹ There is no hint of racial differentiation. In color, however, there are two striking variants: strong transverse banding extending onto flanks (see fig. 3 in Williams, 1963), or the restriction of alternate light and dark to the vertebral zone. This statement, of course, applies to preserved specimens; there is unfortunately no information on color in life and these two patterns may very well be part of the repertoire of one individual.

THE DISTRIBUTION OF THE TWO SPECIES IN SOUTH AMERICA

The number of specimens of *A. fraseri* and of South American *A. biporcatus* that I have been able to examine is large only by the standards peculiar to the generality of South American anoles: for *A. fraseri*, 14 specimens; for *A. biporcatus*, 32. *A. biporcatus*, as may often be true for an invader from Central America, extends not only down through the Chocoan area of Colombia into Ecuador west of the Andes but also along the northern edge of Colombia in the Santa Marta Mountains into Zulia and Táchira in Venezuela. *A. fraseri* — a South American endemic — is apparently restricted to Colombia and Ecuador west of the Andes, and is mainly Ecuadorian. I list below the

¹ *Anolis devillei* Boulenger 1880 (type examined) is an unequivocal synonym of *A. fraseri* Günther 1859, and Boulenger (1885) himself synonymized it. The juvenile specimen referred to *devillei* by Boulenger (1880) is very poorly preserved and indeterminable; Boulenger utilized it with great hesitation.

South American *A. biporcatus* examined (except for the paratypes of *parvauritus*, which have been listed previously) and also all specimens of *A. fraseri*.

Anolis biporcatus. **Colombia**. *Antioquia*. Villa Arteaga, MCZ 79656-57. *Magdalena*. La Concepción, Santa Marta Mtns., MCZ 6549 (type of *solifer* Ruthven). *Bolivar*. Sincelejo, MCZ 78942. Turbaco (?), Leiden 2807. *Norte de Santander*. Near Rio Zulia, 32 km N Cúcuta, ILS 19. *Choco*. Pizarro, CNHM 43778. **Venezuela**. *Táchira*. La Fría, UMMZ 55994. *Zulia*. La Kasmera, Parija 300 m, UCV 8023. ? **Brasil**. "Silva, See Saraca," VM 5904.¹

Anolis fraseri. **Colombia**. *Cauca*. Buenaventura, CNHM 43771; El Tambo, ANSP 25563; Jamundí, CNHM 43772. **Ecuador**. *Esmeraldas*. San Mateo, CNHM 27681. *Imbabura*. Apuela, JAP 4331. *Pichincha*. Mindo, UMMZ 55525; Nanegal, BM 83.2.23.11, JAP 925; Quito, BM 72.2.26.16. *Guayas*. Rio Pescado, nr. Naranjal, AMNH 23432; Bucay, AMNH 23030. *El Oro*. 7 km SE Buenavista, JAP 2485. "West Ecuador": BM 60.6.16.36 (1946.8.8.47) (lectotype of *fraseri*). "Equateur": IRSN 2006 (type of *devillei* Boulenger).

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¹ I assume that this is Lago Saracá, Amazonas, but this locality is very remote from any other record. There are no other specimens of *biporcatus* from Brasil. Locality records in the Vienna Museum are so often erroneous that I cannot accept this without confirmation.

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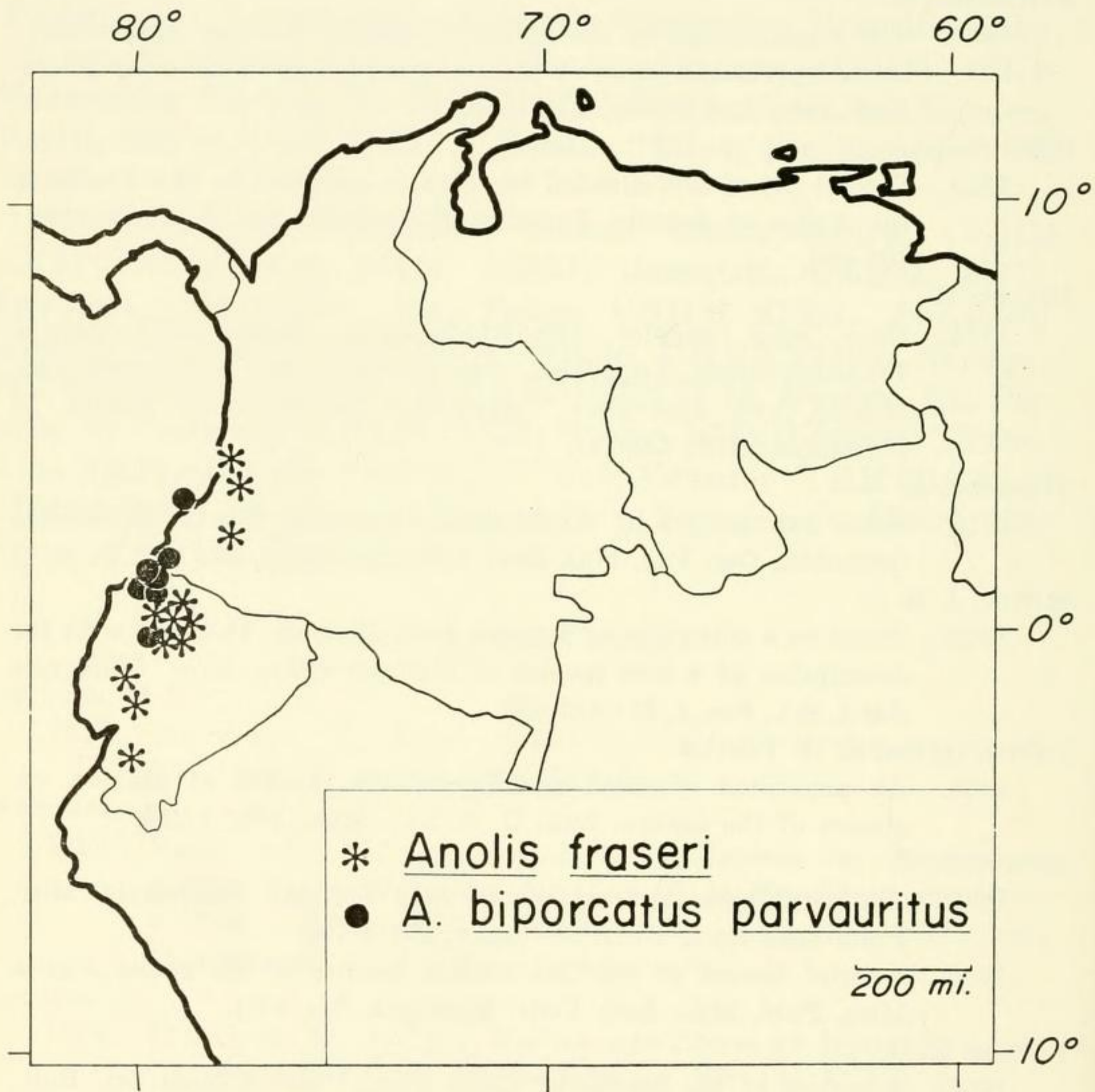


Fig. 5. Map of distributions of *A. fraseri* and *A. b. parvauritus*. Intermediates and representatives of the typical race of *biporcatus* in northern Colombia and Venezuela omitted.

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1966 ANOLIS BIPORCATUS AND ANOLIS FRASERI 3

Michigan Museum of Zoology (UMMZ), the United States National Museum (USNM), the Vienna Museum (VM), and the Berlin Museum (ZMB). To the collectors and curators who have so generously loaned material I am deeply indebted. Dr. Fred Medem graciously donated Colombian material collected by him. National Science Foundation Grant GB 2444 supported this study.

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1. *Anolis hiporcatus* Wiegmann does occur in both Colombia and Ecuador and also in Venezuela.
2. *Anolis solifer* Ruthven must be considered a synonym of *A. hiporcatus* Wiegmann.
3. *A. hiporcatus* Wiegmann is at least in a broad sense sympatric with *A. fraseri* but the sympatric populations appear not to belong to the nominate race.

4. *A. hiporcatu*s belongs to a quite different group from *A. fraseri*, the relationships of which are, as Dunn and Etheridge have suggested, to endemic South American anoles.

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The characters of these two species — so often confused — are best compared in tabular fashion (Table 1). In many characters there is wide overlap. If in any numerical character the range

Fig. 1. *Anolis fraseri*, MCZ 70227. Dorsal view of head.

[Begin Page: Page 2]

BREVIORA

No. 239

Table 1

South American biporcatns

Flead scales, at least anteriorly,
keeled.

2-3 scales between clrcnmnasal
and rostral.

Supraorbital semicircles separated by 0-3 scales.

Supraocular scales keeled.

2-3 more or less elongate supra-ciliary scales followed by a double series of scales which become smaller posteriorly and merge into granules like those medial to the series.

6-9 loreal rows.

Interparietal small (but sometimes larger than the ear which is usually very small).

Subocular scales usually completely and always at least partially separated from the supralabials by a row of intervening scales.

fraseri

Head scales never keeled, usu-

ally flat, pavementose, but sometimes swollen or wrinkled.

1-2 scales between circumnasal and rostral.

Supraorbital semicircles separated by 2-4 scales.

Supraocular scales smooth.

Usually no elongate supraciliary scales; instead, the whole supraciliary margin of round or squarish scales distinctly larger than the granules medial to them.

4-9 loreal scales.

Interparietal larger (larger than the ear which is moderate in size).

Subocular scales broadly in contact with supralabials.

7-12 supralabials to center of 6-9 supralabials to center of

eye. eye.

Dorsal scales strongly keeled, Dorsal scales smooth, small,

almost as large as ventrals, almost granular, grouped in

rather uniformly distributed on rows which are separated by

the small fan.

Ventral scales strongly keeled,

mucronate.

22-26 lamellae under phalanges

ii and iii of 4th toe.

naked skin.

Ventral scales smooth or weak-

ly keeled.

20-24 lamellae under phalanges

ii and iii of 4th toe.

[Begin Page: Figure 1, Page 3]

in one species completely overlaps the known range of the other.

I have omitted this character. The most striking differences are emphasized by italicizing the pertinent characters for *fraseri*.

Both are large, short-legged, stout-bodied, relatively short-headed forms. The similarities are indeed amazing since the two species are, according to Etheridge, osteologically in totally different sections of the genus. The similarities would be even greater if Mexican and other northern *biporcatus* were compared with *fraseri* since the northern animals tend to have 3-4 scales between the supraorbital semicircles (c/. Stuart, 1955).

Overlapping variation in many features, as shown in Table 1, is characteristic of many sympatric species in *Anolis* and is one of the several reasons why this genus is described as "difficult."

As in all such cases, the recognition of the valid species depends upon recognition of the constant (or almost constant) association of characters, however trivial. Smooth or keeled scales, *sul*-oculars in contact with or separated from supralabials, interparietal large or small are none of them characters universally useful in *Anolis*. The distinctive supraciliaries of *fraseri* are more useful because a substantial morphological gap between this condition and that shown by *biporcatus* will always distinguish these two species. (The *fraseri* supraciliaries occur, however, also and in a more exaggerated degree in *latifrons*; the condition is not unique to *fraseri*.)

Fig. '2. *Anolis biporcatus* parrauril its, iiuw subspecies, MCZ 78935. Dorsal view of head of type.

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6 BREVIORA No. 239

INTRASPECIES VARIATION: A. BIPORCATUS

While I have not endeavored to examine all specimens of *A. biporcatus* from all parts of its range, I have sampled the northern populations (Panama, Costa Rica, Guatemala, Mexico), and I have had the especial advantage of examining the series of 122 specimens taken by Slevin near Boquete, Panama (Slevin, 1942).!

Having seen this series I am impressed by the similarities of the various populations. There is indeed considerable variation within *A. biporcatus*, as I understand it. Thus, the number of scales between the semicircles, the number of scales between interparietal and semicircles, the number of loreal rows, the amount of keeling of the head scales, the contact or separation of suboculars and supralabials, and the length of the hind limbs all appear to be quite variable from individual to individual. Yet the species has a strong habitus character and is quite recognizable in spite of very striking variation.

A very few characters appear to sort out geographically. The supraocular scales and those surrounding the interparietal

are extraordinarily small in Ecuadorian and southern Colombian specimens. In these same populations the ear opening is circular and very small in contrast to the rather oval opening of northern specimens.

Since there seem also to be some color differences of both body and dewlap in these same populations — which are precisely those sympatric with *fraseri* — it seems permissible to regard the Ecuadorian and southern Colombian animals as representing a distinct subspecies. Some discussion of available names is therefore required.

Anolis solifer Ruthven, type locality La Conepcion, Santa Marta Mountains of northern Colombia, is the only name thus far proposed for a South American population of this species. That *solifer* does belong in *biporcatus* and may provisionally be synonymized with the nominate race seems clear from the comparison of the type with Panamanian and more northern material. The type of *solifer* can be matched by Panamanian material (except for the exceptionally short hind limbs) and Panamanian material is not separable by any constant characters from more northern specimens. The character of the very short hind limbs may define a population in northeast Colombia and Venezuela. One of the two available Venezuelan specimens has limbs as

I am indebted to Dr. Allan Leviton of the California Academy of Sciences for this opportunity.

[Begin Page: Figure 2, Page 5]

19GG ANOLIS BIPORCATUS AND ANOLIS FRASERI 7

short as those of the solifer type but the other does not. In any event, the name solifer is clearly not available for the distinctive Ecuadorian and south Colombian populations. In the critical characters solifer resembles northern hiporcatatus.

The other names referable to the species hiporcatatus are equally unavailable. None of them refer to South American material.

The nominate race hiporcatatus Wiegmann 1834 has the type locality "Mexico," now restricted to Piedra Parada, Chiapas.

A. copei Bocourt 1873 has the type locality Santa Rosa de Pansas, Guatemala. *Anolis hrcvirostris* Peters 1873, next in date, has the type locality Chiriqui Prov., Panama. *Anolis hrevipes* Boettger 1893 came from Cairo Plantation, La Junta near Limon, Costa Rica. Every one of these seems at present best grouped under the name hiporcatatus.

The southern race is thus without a name. In reference to the small ear it may be called :

Anolis biporcatatus parvauritus new subspecies

Holotype: MCZ 78935, an adult i , "banana plantation, woods and penal colony camp, northern Gorgona Island, Cauca,

Colombia, 5-45 meters altitude," collected by F. Medem and L. Salazar G., 1 to 23 February 1961.

Paratypes: Colombia. Cauca: MCZ 78933-34, 78936-41, same data as type. Narifio: MCZ 79142, Rio Mataje. Ecuador. Esmeraldas: USNM 157105, Cachavi; BM 1901.6.27.1, Carondolet ;

Fig. 3. *Anolis biporcatus biporcatus*, MCZ 56243, from Los Diamantes, Costa Rica. Dorsal view of head.

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8 BREVIORA No. 239

AMNH 9967, Rio Capayas ; BM 1907.7.29.10-11, ZMB 18213, VM 12755, Rio Sapayo; BM 1901.8.3.1, Salidero; BM 1901.6.27.1, San Javier; Orces 3898, San Lorenzo. Imhahura: BJ[^].I 98.4.28.13, Paramba. Pichincha: Orces 4596, Santo Domingo de los Colorados. "West Ecuador": BM 1946.8.13.21 (/Vrt.srn sy ntype) . "Ecuador": USNM 20610, ANSP 7910.

Diagnosis. A subspecies of *Anolis hiporcatus* distinjj;-uislied by the small size of the scales surrounding the interparietal which are smaller than or only equal to middorsal scales (instead of distinctly larger than middorsal scales), by the small round ear rather ventrally placed (instead of a large oval ear extending well dorsally), and hy a black-edged dewlap.

Commetit. None of the conventional numerical counts in Anolis (e.g. scales across snout, scales between semicircles, scales between interparietal and semicircles, etc.) reveal the distinctness of parvauriins, though it is visually apparent immediately on inspection of the sjjecimeus (Figs. 2 and 3). The number of scales between interparietal and semicircles might be expected to correspond neatly to the very striking difference in the size of scales surrounding the interparietal in the nominate race and in parvauritits. In fact, however, there is wide overlap, and no discrimination could be based on the numerical character. However, comparison of the scales around the interparietal and the scales on the midline of midbod}' of the same animal gives instant conviction of the difference between the two races.

The character of the small size of supraocular scales is equally apparent on inspection. Here there is in parvauritns an absence of clear definition of any supraocular disk. This, however, is true also in many specimens of the nominate race. Here, again, comparison with middorsal scales (or direct confrontation with representatives of the northern race) convinces one of the existence of a difference. It is, however, a difference which is somewhat less striking than in the case of the scales surrounding the interparietal.

The size of the ear is again a character easily appreciated visually (Fig. 4), but it does not reveal itself by comparison with the size of the interparietal, which itself varies and may be very small. Comparison with the temporal area is more useful but the

size and shape of the ear are sometimes distorted by preservation.

Certain specimens seem intermediate : MCZ 79656-57 from Villa Arteaga, Antioquia, Colombia, have the ear round but rather large. In other regards (scales around interparietal, supraocular scales) these are northern in type. MCZ 79842 from Sincelejo,

[Begin Page: Figure 3, Page 7]

19GG

AXOLIS BIPORCATUS AND ANOLIS FRASERI

Fig. 4. Ear size in *A. biporcatus* (top) and *A. biporcatus* (bottom). Specimens are of the same snout-vent length.

Bolivar, on the other hand, has the ear small as in the southern race and the supraocular scales definitely large as in the northern race. A juvenile from Pizarro, Choco, Colombia (CXHM 43778), appears, in agreement with expectations from its geographic position, to be intermediate in size of ear and size of scales around interparietal and, like the nominate race, in size of supraocular scales. From this small sample one may perhaps infer that the ear character and the other characters that distinguish the races vary erratically and not in any correlated fashion in northern Colombia.

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The color of the southern race seems different in preserved specimens from that of any northern animals including the northern Colombian intermediates, but this is very difficult to define in animals with strong powers of color change. In the Gorgona Island material, which is the largest series and the most recently collected, there is strong reticulation enclosing light areas which may, in animals in the dark phase, give an appearance of light spotting. This reticulation tends to extend to the belly, but the throat is not spotted with darker as it typically is in the northern race. The north Colombian intermediates also lack throat spotting but otherwise seem like other northern populations in color.

The small dewlap is conspicuously black in preserved specimens of the southern race. Examined under the microscope[^] it is seen that the scales are intensely black while the skin may have a trace of red. According to F. Medem's notes on the Gorgona Island series, the dewlap in life is orange and red at the center, black at the edge.

Slevin's 1942 notes on the nominate race at Boquete, Chiriqui, Panama, contrast with this : ' * The rather large dewlap of the males had a ground color of orange with rows of bluish scales."

Duellman (1963) has described the dewlap of a specimen from 20 km NNW Chimapa, Guatemala, in very similar terms, as having "the outer part pale orange, the median part purplish blue." J. M. Savage has sent me a diagram of dewlap coloration in a male from the Tilaran area in northwest Costa Rica. From this it appears that the free edge of the dewlap is red-orange while a small anterior part of the base is white, a larger posterior portion powder blue.^

These three descriptions, all in essential agreement, are from specimens which bracket much of the range of the typical race and indicate a dewlap color consistently and sharply different from that of the southern race. Unfortunately, the dewlap color in Venezuelan specimens, for which "solifer" is an available name, is unknown.

Behavioral notes. F. Meclen (field notes) remarks on the Gorgona Island topotypic series of *parvauritus* that the gular sac is "extended laterally" and that this species is here found

1 The description by Taylor (1956, p. 136) of the dewlap of Costa Rican specimens as "white or slightly greenish" appears on careful reading to result from a complex confusion of notes for *A. capita* with the text for *A. biporcatus*, and apparent resulting omission of some of the pertinent data for *hipocatus*. See the reference to *A. capita*, top of page 137.

[Begin Page: Figure 4, Page 9]

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on trees up to 5 meters or more in height, rarely on the ground.

It is seen most often early in the morning (7:30-9:30 am).

A. hiporcatus is everywhere known as a strongly arboreal species. Slevin (1942) reports on it at Boquete, Panama, as follows : "It was generally found in the larger and higher trees, but occasionally on fence posts and once or twice on the ground. While most frequently seen on the tree trunks, it was often discovered on fairly high limbs, crouching down as if to avoid detection." This compares very well with Medem's notes on parvauritus, and the two races are probably very similar ecologically.

IXTRASPECIES VARIATION: .4. FRA8EBI

A. fraseri, with a much smaller geographic range and a smaller available sample, seems rather consistent in scale characters.^ There is no hint of racial differentiation. In color, however, there are two striking variants: strong transverse banding extending onto flanks (see fig. 3 in Williams, 1963), or the restriction of alternate light and dark to the vertebral zone. This statement, of course, applies to preserved specimens ; there is unfortunately no information on color in life and these two patterns may very well be part of the repertoire of one individual.

THE DISTRIBUTION OF THE TWO SPECIES

IN SOUTH AMERICA

The number of specimens of *A. fraseri* and of South American *A. hiporcafus* that I have been able to examine is large only by the standards peculiar to the generality of South American anoles: for *A. fraseri*, 14 specimens; for *A. hiporcatus*, 32. *A. hiporcatus*, as may often be true for an invader from Central America, extends not only down through the Chocoan area of Colombia into Ecuador west of the Andes but also along the northern edge of Colombia in the Santa Marta Mountains into Zulia and Tachira in Venezuela. *A. fraseri* — a South American endemic — is apparently restricted to Colombia and Ecuador west of the Andes, and is mainly Ecuadorian. I list below the

'>- *Anolis deii* Uci Boulenger 1880 (type examined) is an unequivocal synonym of *A. fraseri* Günther 1880. and Boulenger (1880) himself synonymized it. The juvenile specimen referred to *deii* Uci by Boulenger (1880) is very poorly preserved and indeterminate: Boulenger utilized it with great hesitation.

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South American *A. hiporcatus* examined (except for the paratypes of *parvmitus*, which have been listed previously) and also

all specimens of *A. fraseri*.

Anolis hiporcatatus. Colombia. Antioquia. Villa Arteaga, MCZ
79656-57. Magdalena. La Concepcion, Santa Marta Mtns., MCZ
6549 (type of *solifer* Ruthven). Bolivar. Sincelejo, MCZ 78942.
Turbaco (?), Leiden 2807. Norie de Santander. Near Rio Zulia,
82 km N Cucuta, ILS 19. Cjioco. Pizarro, CNHM 43778.
Venezuela. Tachira. La Fria, LTMMZ 55994. Zulia. La Kasmera,
Parija 300 m, UCV 8023. ? BrasU. "Silva, See Saraca," VM
5904.1

Anolis fraseri. Colombia. Cauca. Buenaventura, CNHM
43771; El Tambo, ANSP 25563; Jamundi, CNHM 43772.
Ecuador. Esmeraldas. San Mateo, CNHM 27681. Imhahura.
Apuela, JAP 4331. PichincJw. Mindo, UMMZ 55525; Nanegal,
BM 83.2.23.11, JAP 925; Quito, BM 72.2.26.16. Guayas. Rio Pes-
cado, nr. Naranjal, AMNH 23432 ; Bucay, AMNH 23030. El Oro.
7 km SE Buenavista, JAP 2485. "West Ecuador" : BM 60.6.16.36
(1946.8.8.47) (lectotype of *fraseri*). "Equateur": IRSN 2n0(
(type of *devillei* Boulenger) .

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1 1 assume that this is Lago SaracA, Amazonas, luit tliis hicality is very remote
from any other roconl. Tliere are no other specimens of hiporcatus from Brasil.

l.ocality'n cords in tie Vienna Museum are so often erroneous thiat I cannot accept
cliis without confirmation.

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(Received 15 September 1965.)

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14

BREVIORA

No. 239

Anolis fraseri

A. bi porcQtus parvauritus

200 mi.

10

-O'

10'

Fig. 5. Map of distributions of *A. fraseri* and *A. h. parvauritus*. Intermediates and representatives of the typical race of *hiporcatus* in northern Colombia and Venezuela omitted.

[Begin Page: Page 13]

[Begin Page: Figure 5 (map), Page 14]