Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
VOL. 125, NO. 7

TWO SYMPATRIC CUBAN ANOLES OF THE *CAROLINENSIS* GROUP

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CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
AUGUST, 1961

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INTRODUCTION

The *carolinensis* group of the West Indian iguanid genus *Anolis* consists of forms sufficiently closely related that most or all of them have been considered subspecies of one species. The described forms occur both on the mainland of North America and on the Caribbean islands: *carolinensis* in the southeastern portion of the United States; *lerneri, brunneus, smaragdinus* on the Bahamas; *fairchildi* on Cay Sal; *longiceps* on Navassa; *maynardi* on Little Cayman; *porcatus* on Cuba; and *allisoni* on the Islas de la Bahia off the coast of Honduras and on Half Moon Cay off British Honduras. Only one representative of the group has ever been reported from any one locality. Thus it has always been assumed that *porcatus* was the single Cuban representative of the *carolinensis* group.

Some years ago an examination of the specimens under the name *Anolis porcatus* in the American Museum of Natural History and in the Museum of Comparative Zoology revealed a difference in the shape of the ear opening that initially was presumed to be a dimorphism: the ear opening was in one case circular (Fig. 3), and in the other markedly elongate (Fig. 2). Later, field work in Camaguey, Cuba, indicated that this was not a phenomenon of polymorphism in a single species but instead that two distinct species of the *carolinensis* group existed in central Cuba.

Dr. Richard Etheridge independently discovered the two conditions of the ear opening while studying the *carolinensis* group at the University of Michigan Museum of Zoology. He

called to our attention the apparent identity of the elongate-eared Cuban form with *Anolis allisoni* Barbour (1928) from Roatan Island off the coast of Honduras.

A direct comparison of the types of *A. allisoni* (M.C.Z. 26725, 26727-55) with specimens of both Cuban species in the Museum of Comparative Zoology confirmed Dr. Etheridge's observations. It was thus established that *Anolis allisoni* Barbour was an available name for one of the two Cuban forms. It was necessary, however, to determine the proper allocation of the much older name *Anolis porcatus* Gray 1840. We therefore provided Mr. J. C. Battersby of the British Museum (Natural History) with material to compare with Gray's types. He very kindly informed us that the name *porcatus* Gray applies to a round-eared form.

A. porcatus has been customarily considered as merely one of the subspecies of *carolinensis* (Barbour, 1937; Oliver, 1948). For the purposes of this paper and to facilitate discussion we refer to the Cuban round-eared form as *A. porcatus*. The subspecies of *carolinensis* have been described without any reference to the pronounced geographic variation found within *porcatus* in Cuba. Certainly the level of differentiation of some of the Bahaman subspecies could be duplicated within the Cuban populations of *porcatus*. However, subspeciation within *porcatus* and the relationship of the Cuban populations to the non-Cuban subspecies of *carolinensis* is a taxonomic problem that need not concern us here.

DEFINITION OF THE ANOLIS CAROLINENSIS GROUP

Long-snouted lizards having the nostril median to the canthal ridge and separated from the rostral by three scales (Fig. 1); a rostral that is bordered on the posterior dorsal margin by five scales; loreal rows usually 3-4; the anterior sublabials are wider than long, supradigital scales multicarinate; ventral scales at midbody in transverse and diagonal rows; ventrals and dorsals slightly keeled; dorsals and laterals subequal in size, smaller

than or equal to the ventrals; tail round in cross section. The body color is variable and changeable; it may be yellow, green, grey, blue, brown or variegated. There is pronounced sexual dimorphism. The males are larger, and are characterized by well-marked frontal and/or canthal ridges. The head scales are rugose; there is a reddish or mauve dewlap and enlarged postcloacal scales. In contrast, the females are smaller and lack the enlarged postcloacal scales; they also lack frontal ridges or elevated canthal ridges, the head scales are multicarinate, the dewlap is small.

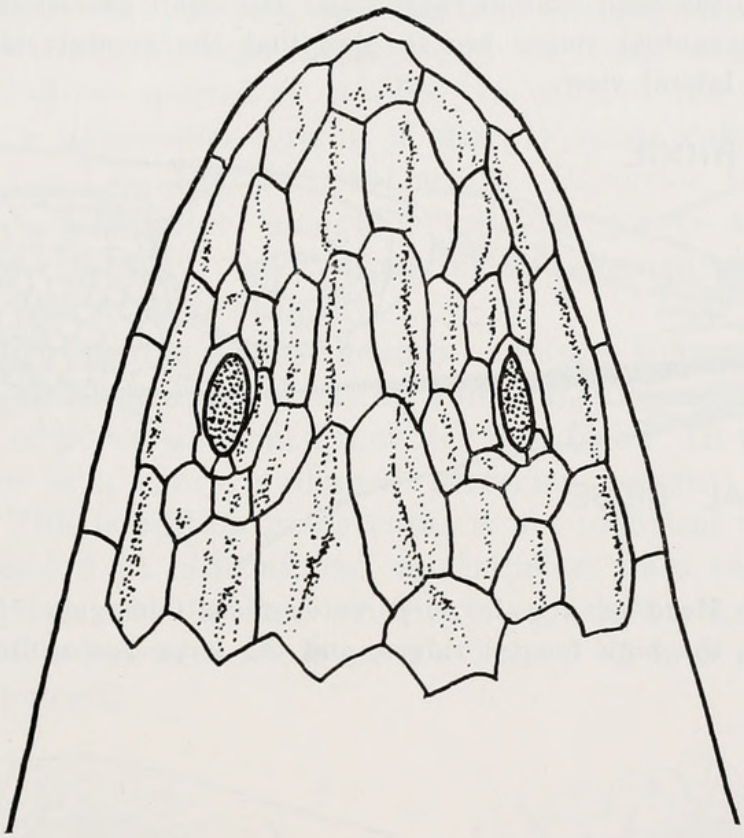


Figure 1. Dorsal view of the tip of the snout of a specimen of *A. porcatus* from Oriente. The *carolinensis* group characters of the rostral are shown: five scales bordering the rostral posteriorly and three scales between the rostral and nostril.

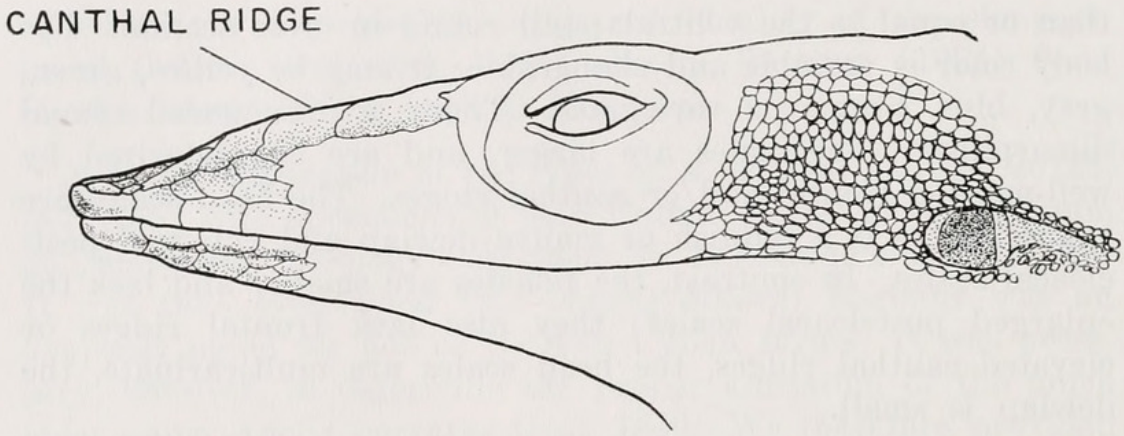


Figure 2. Head of a male *A. allisoni* from Camaguey. The elongate ear opening, the high canthal ridges, and the small postorbital scales are shown. The canthal ridges are so high that the frontal ridges are not visible in a lateral view.

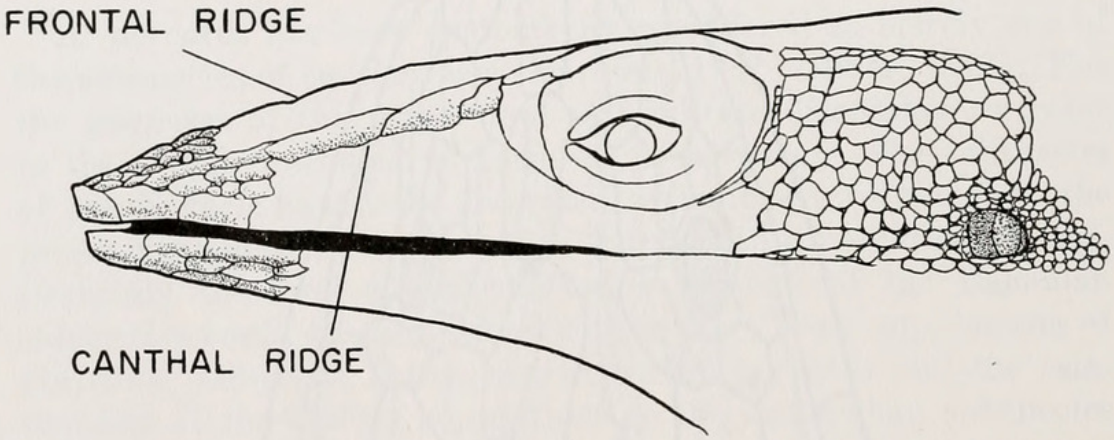


Figure 3. Head of a male *A. porcatus* from Camaguey. The circular ear opening, the high frontal ridges, and the large postorbital scales are shown.

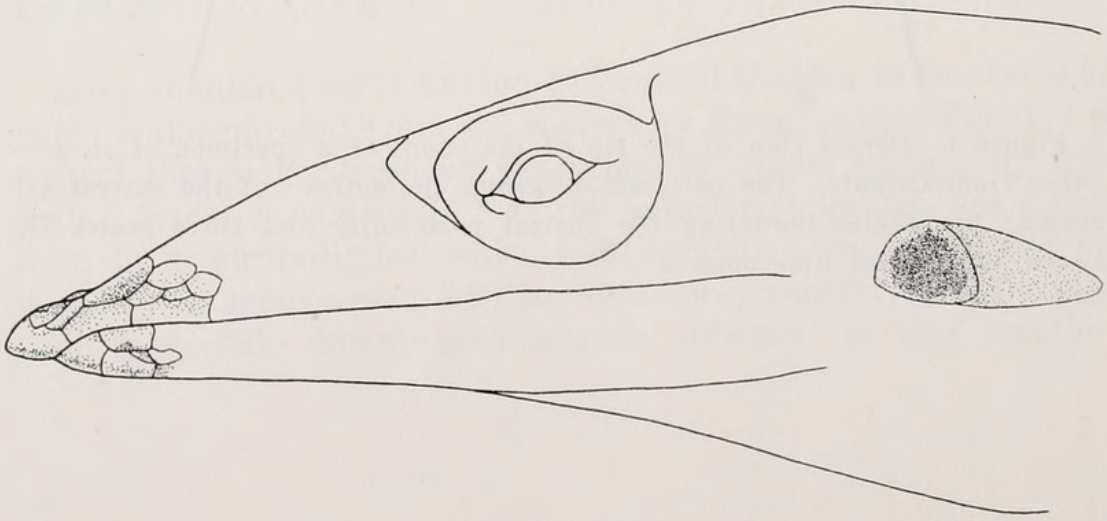


Figure 4. Head of a male *A. allisoni* from Roatan Island. The characteristic overlapping rostral scale of this population is shown.

COMPARISON OF ALLISONI AND PORCATUS

The following characters serve to distinguish *allisoni* from *porcatus*:

A. allisoni (Fig. 2)	*A. porcatus* (Fig. 3)
1. Ear opening is elongate, the posterior margin forming a long longitudinal depression.	1. Ear opening circular, or oval, the posterior margin not forming an elongate depression.
2. Temporal or postocular scales smaller.	2. Temporal or postocular scales larger.
3. Males with canthal ridges higher than the frontal ridges.	3. Males with the frontal ridges higher than the canthal ridges.

The elongate ear opening is a distinctive character of *allisoni* and is very different from the round or vertically oval ear opening of the other species of *Anolis*. In *allisoni* the tympanum resides in a depression having a sharply demarcated anterior margin formed by the temporal scales. Posterior to the tympanum is a triangular, elongate, scaleless groove that tapers posteriorly. Dorsally, the tympanum and groove are bounded by a loose fold of skin (Fig. 5).

In the entire genus *Anolis* the only examples that we have seen of an ear opening approximating this condition occur in some specimens of *porcatus* from Pinar del Rio, Cuba. In these specimens there is a short V-shaped posterior margin to the ear (Fig. 6). This condition in *porcatus* is not identical to the elongate depression in *allisoni*, but nevertheless does represent an approximation. About half of the 65 specimens examined of Pinar del Rio *porcatus* show some evidence of such a V-shaped posterior margin.

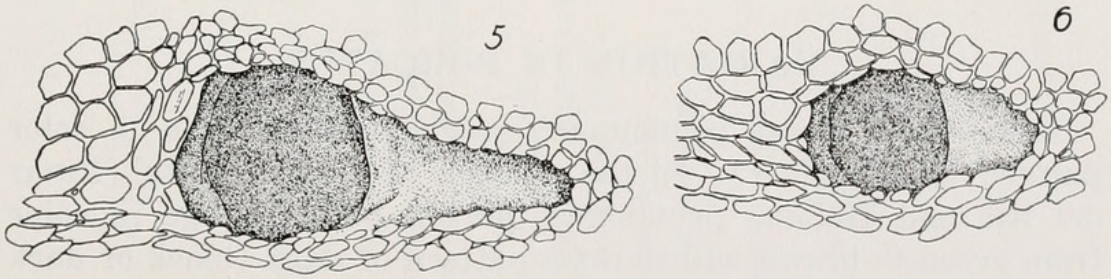


Figure 5. Ear opening of *A. allisoni* from Camaguey.

Figure 6. Ear opening of *A. porcatus* from Pinar del Rio. Some specimens of the allopatric populations of *porcatus* from extreme western Cuba show evidence of convergence toward *allisoni*, in having the posterior margin of the ear V-shaped and resembling the elongated posterior depression of the *allisoni* ear.

In life, the males of the two species are readily distinguishable since *allisoni* males have a brilliant blue head and thorax which is never seen in *porcatus* (Fig. 10). Gundlach (1880) in his discussion of *porcatus* mentions the blue form as a variant of *porcatus*. Similarly, Barbour and Ramsden in the "Herpetology of Cuba" (1919) confused the two species and provided a color description of *porcatus* that is a mingling of the characters of both species. They noted that the species (actually *allisoni*) was very common in the vicinity of Camaguey, and admit to having examined specimens from all six provinces.

The blue and green color of the *allisoni* males can change to an overall brown color. There is another transient color phase in which the green part of the body and limbs assumes a yellow color while the blue portion becomes a light violet color. The throat of the males usually shows some blue pigment, particularly in the area of the folded dewlap. A dark elongate spot is usually evident above the forelimb. The males also have a well-defined stripe from below the eye to the ear. The females of Cuban *allisoni* show no blue color and are solid green, and like the males can change to an overall brown. Living specimens of *allisoni* from the Cuban provinces of Las Villas, Oriente, and Camaguey do not differ in color or pattern. However, after preservation with formalin most of the Las Villas specimens show dark reticular markings over the nape and dorsum. These black reticular markings are present in life only during the brown color phase in the Camaguey specimens and are customarily not seen in the preserved animals.[1]

The blue color so distinctive of *allisoni* males is never present in *porcatus*.

VARIATION IN PORCATUS

A. porcatus shows pronounced geographic variation in color pattern (see Table 1). In the western portion of Cuba (Pinar del Rio and Habana provinces), *porcatus* can change in color from green to brown and shows a pattern of dark (black or dark green) reticulations over at least part of the body. There is also an elongate dark patch above the forelimb and single scattered white scales on the nape and parts of the body. Figure 7 shows

[1] We have seen two male *allisoni* which lacked the blue on the head and trunk. These animals were observed alive in the field (at the same locality) in Camaguey for a number of days. One of the specimens was collected and preserved (M.C.Z. 60928).

TABLE 1. Variations in the male specimens of *Anolis porcatus* in Cuba

"Eastern" *porcatus* (Oriente)	"Central" *porcatus* (Camaguey)	"Western" *porcatus* (Pinar del Rio)
1. Overall color green or brown. Very few variegations and with scattered white scales on the nape and body.	1. Overall color grey, light green, or brown. Variegated pattern and many white scales over entire body.	1. Overall color green, yellow-green or brown. Variegated dark markings and white scales on the nape.
2. Dark shoulder patch.	2. No shoulder patch.	2. Dark shoulder patch.
3. Males with a light vertebral stripe, bordered by a brown stripe on each side.	3. Males without a vertebral stripe.	3. Males without a vertebral stripe.
4. Round ear opening.	4. Round ear opening.	4. Round or partially elongate ear opening.
5. Low canthal ridges.	5. Low canthal ridges.	5. Very high canthal and frontal ridges.
6. Smaller, maximum size ♂ = 65 mm.	6. Smaller, maximum size, ♂ = 66 mm.	6. Larger, maximum size ♂ = 73 mm.

this type of pattern clearly. In the specimens from Oriente, at the extreme eastern end of the island, the color change ranges from green and grey-green to brown. There is a distinctive mid-dorsal light stripe bordered by darker pigment. The chin and throat area is well marked with longitudinal dark stripes. There is an ocellus (a spherical or elongate dark spot surrounded by white) above the forelimb. There is some evidence of reticular body markings on some specimens and often scattered white scales. Figure 8 is an illustration of an Oriente male of *porcatus*.

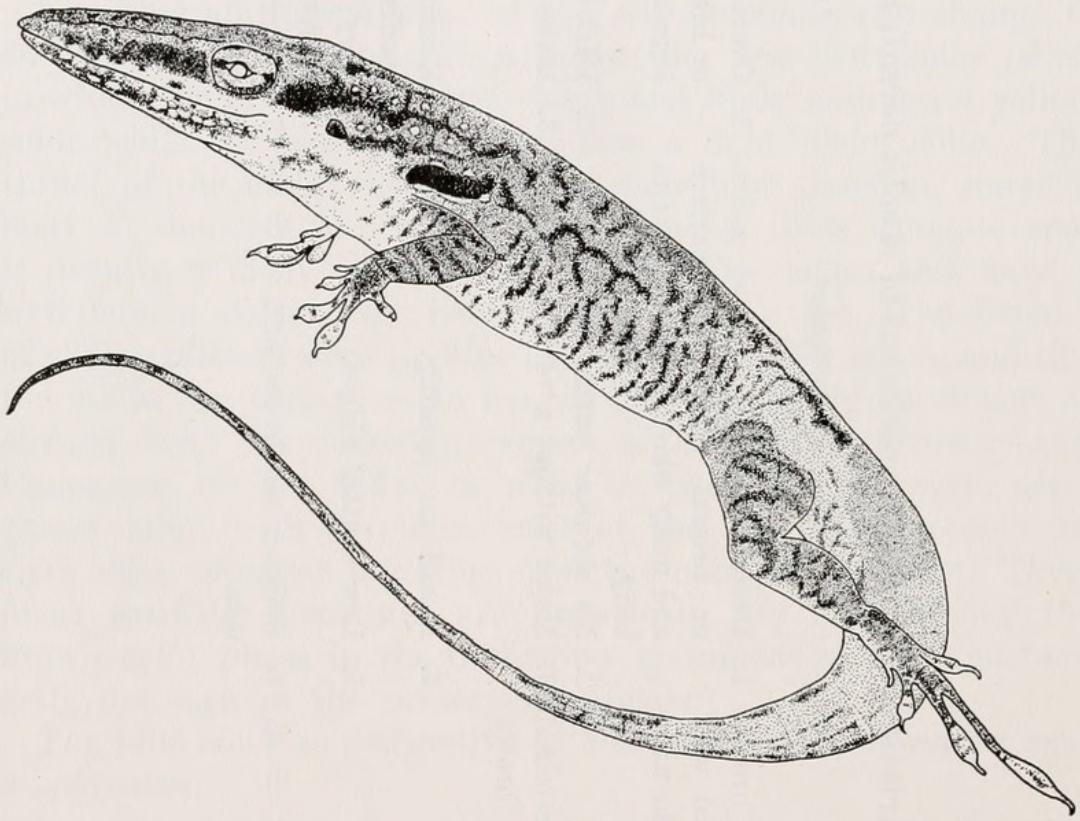


Figure 7. Male *A. porcatus* from Pinar del Rio. An example of a "western" *porcatus*.

In contrast to the eastern and western patterns the Camaguey populations of *porcatus* in the center of the island have an overall color of grey or light green or brown. The larger males are usually grey and some demonstrate no green color; however, females and some males do demonstrate a light green phase. Superimposed upon the grey color is a complicated pattern (Fig. 9) of dark and light reticulations. The body as well as the nape is covered with numerous white scales. The Camaguey

porcatus are thus sharply distinguishable from the sympatric and more abundant blue *allisoni*. The Camaguey specimens of *porcatus* are further distinguished by the absence of a white stripe below the eye which is characteristic and prominent in *allisoni*. However, it is interesting that Pinar del Rio *porcatus*

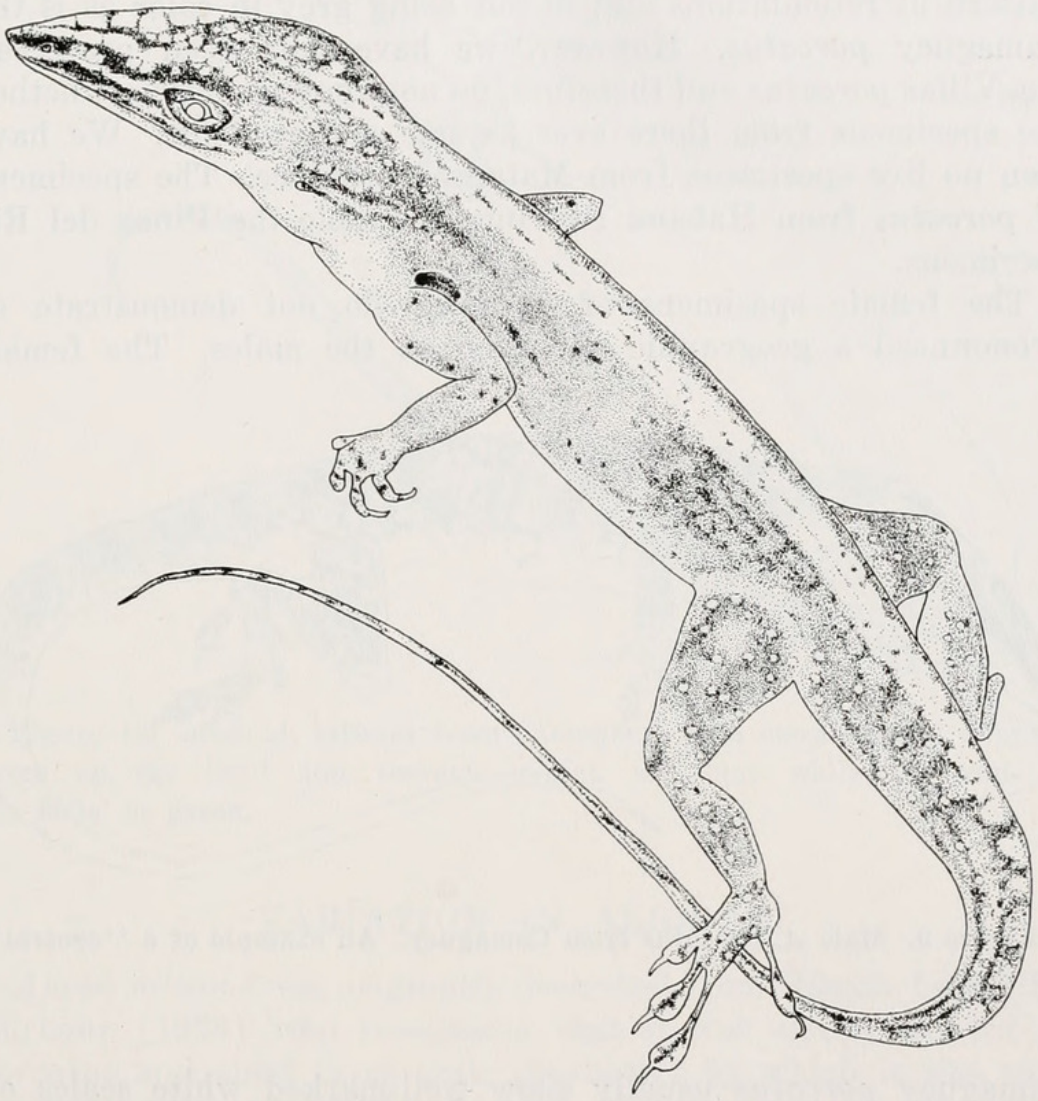


Figure 8. Dorsolateral view of a male *A. porcatus* from Guantanamo, Oriente. An example of an "eastern" *porcatus*.

show convergence to *allisoni* in having a white stripe below the eye similar to that of *allisoni*. Some of the other characters that readily distinguish the sympatric Camaguey *porcatus* from *allisoni* are not found outside the range of *allisoni*. The large flat temporals of Camaguey *porcatus*, which differ markedly from the small temporals of *allisoni*, are not so characteristic of the

Oriente *porcatus* where only the postoculars appear to be enlarged. Similarly some of the large males of *porcatus* from Pinar del Rio have canthal crests that are higher than the frontal crests and thus further resemble *allisoni* in this character. The specimens of *porcatus* from Las Villas (where *allisoni* is also found) seem to resemble the Pinar del Rio *porcatus* in the pattern of reticulations and in not being grey in color as is the Camaguey *porcatus*. However, we have only seen preserved Las Villas *porcatus* and therefore, do not know definitely whether the specimens from there ever assume a grey color. We have seen no live specimens from Matanzas province. The specimens of *porcatus* from Habana Province resemble the Pinar del Rio specimens.

The female specimens of *porcatus* do not demonstrate as pronounced a geographic variation as the males. The female

Figure 9. Male *A. porcatus* from Camaguey. An example of a "central" *porcatus*.

Camaguey *porcatus* usually show well-marked white scales on the lateral surfaces of the body and are thus readily distinguished from the eastern and western forms. The eastern females, like the males, show a middorsal light stripe bordered by a darker pigment. The females from western Cuba often show a brownish middorsal stripe similar, but not identical, to that of the eastern form. (Actually the middorsal stripe is a common characteristic of the female of many species of *Anolis*.) Even some female specimens of *allisoni* will at times have a narrow middorsal brown stripe that contrasts with the overall green.

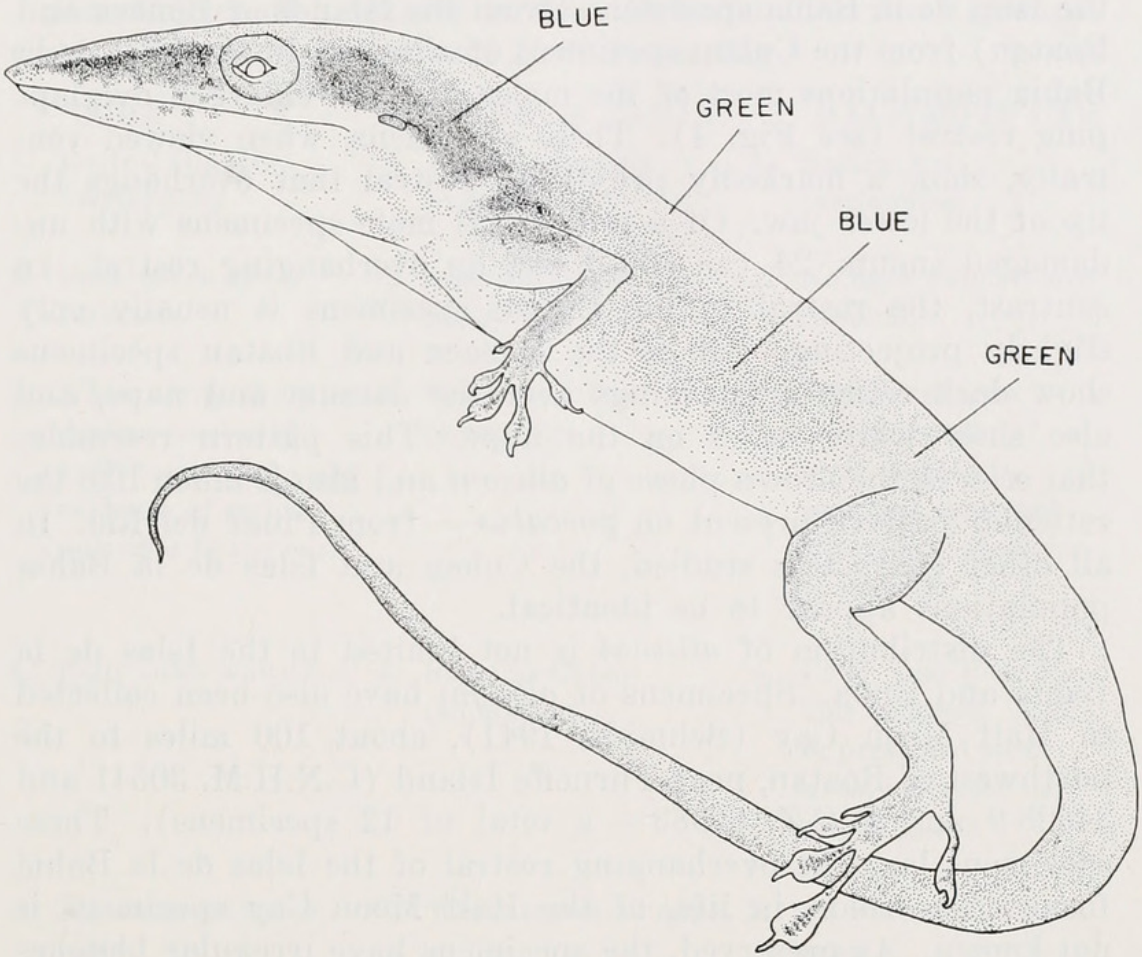


Figure 10. Male *A. allisoni* from Camaguey. The more heavily stippled areas on the head and thoracic region are blue while the rest of the body is green.

VARIATION IN ALLISONI

Anolis allisoni was originally described from Roatan Island by Barbour (1928) who recognized that it was closely related to *porcatus* and cited three scale characters by which it was supposed to differ from that species. Not one of these characters appears to be valid. His description of the male color pattern agrees with that given above for the Cuban *allisoni*. However, Barbour did not notice the peculiarity of the ear opening nor did he recognize that the Roatan *allisoni* was the same species that he had undoubtedly observed many times in Las Villas (at Soledad) and Camaguey. We have examined the types and paratypes in the Museum of Comparative Zoology, and a large series of specimens of *allisoni* from the Chicago Natural History Museum, and we can find only two characters that distinguish

the Islas de la Bahia specimens (from the Islands of Bonaca and Roatan) from the Cuban specimens of *allisoni*. In the Islas de la Bahia populations most of the males have an enlarged overlapping rostral (see Fig. 4). These specimens, when viewed ventrally, show a markedly projecting rostral that overhangs the tip of the lower jaw. Of a total of 34 male specimens with undamaged snouts, 24 (or 70%) had an overhanging rostral. In contrast, the rostral in the Cuban specimens is usually only slightly projecting. All of the Bonaca and Roatan specimens show dark reticular markings over the dorsum and nape, and also show white scales on the nape. This pattern resembles that seen in the brown phase of *allisoni* and also is much like the reticular pattern present on *porcatus* — from Pinar del Rio. In all other characters studied, the Cuban and Islas de la Bahia populations appear to be identical.

The distribution of *allisoni* is not limited to the Islas de la Bahia and Cuba. Specimens of *allisoni* have also been collected in Half Moon Cay (Schmidt, 1941), about 100 miles to the northwest of Roatan, near Turneffe Island (C.N.H.M. 30541 and 34628-9 and M.C.Z. 60983 — a total of 12 specimens). These specimens lack the overhanging rostral of the Islas de la Bahia forms. The color, in life, of the Half Moon Cay specimens is not known. As preserved, the specimens have irregular blotches of blue and purple and would thus appear to possess the blue pigment characteristic of the Cuban and Islas de la Bahia populations. The absence or presence of blue after preservation is, of course, not a definite indication of the true color in life. Unfortunately, the color of anoles is subject to unpredictable variation following death and preservation. Thus, the C.N.H.M. specimens from Bonaca and Roatan are all brown with dark reticulations and a single specimen from Half Moon Cay has the same pattern. However, Barbour's description of the Roatan populations does not mention such a pattern except as appearing after preservation. It is therefore possible that the reticulated pattern is made evident after preservation, and in life is only evident when the animal is in the brown color phase. The Half Moon Cay specimens, besides lacking an enlarged rostral, are also distinctive in that no dark shoulder patch is evident on any of the twelve specimens, that blue pigment is present on the ventral surface of the body, and that the white head stripe while evident below the orbit fades in the temporal area and is not visible posterior to the ear opening.

Morphologically, *allisoni* is thus divisible into three groups: Cuba, Islas de la Bahia, and Half Moon Cay.

CUBA	ISLAS DE LA BAHIA	HALF MOON CAY
1. Rostral slightly overlapping	1. Rostral strongly overlapping	1. Rostral not overlapping
2. Dark patch above forelimb	2. Same as Cuban population	2. No dark patch above forelimb
3. White stripe from ventral border of orbit to ear and some evidence of stripe posterior to the ear	3. Same as Cuban population	3. White stripe on ventral border of orbit, fading in temporal area, and not evident posterior to the ear
4. Belly color whitish	4. Same as Cuban population	4. Belly color possibly blue or green. Blue in preserved specimens, but color in life unknown
5. No white scales on nape	5. White scales on nape	5. No white scales on nape

It is immediately evident from the above that the Cuban and Islas de la Bahia populations are very similar while the Half Moon Cay population stands out as distinct from the other two. We believe that the morphological differentiation that has occurred in the Half Moon Cay and Islas de Bahia populations is evidence for assuming that these Central American populations of *allisoni* are old in these islands and not recent introductions by man. These three populations should probably be given subspecific designation to emphasize this fact. However, we have refrained from this step in the hope that we may be able to observe and compare living specimens of all three populations and thus confirm the color differences.

The differentiation of the Half Moon Cay and Islas de la Bahia populations is also evidence for assuming that the two populations represent separate invasions from Cuba. Thus, the Half Moon Cay population being the most differentiated can be considered to be the oldest or first invaders, while the Islas de la Bahia forms represent a more recent dispersal to the Central

American shore and thus more resemble the Cuban population. Certainly the differentiation of the two offshore populations precludes our considering them as derived one from the other.

DISTRIBUTION

The round-eared form (or forms) which we are calling *A. porcatus* is found throughout the island of Cuba and on Isla de Pinos. At the western end of the island (Pinar del Rio and Habana) and at the eastern end (Oriente) it is the very common arboreal lizard found in well lighted areas around houses, in gardens, in pastures, in the edges of the forests, and probably in the forests in the higher sunnier portions of the trees. Next to *A. sagrei* it is the most common lizard on the island. However, in the provinces of Camaguey and Las Villas, *porcatus* is a rarer lizard. In this area *allisoni* is the common species, found in the identical habitats that *porcatus* occupies in the eastern and western portions of the island.

The abundance of *allisoni* in central Cuba, of *porcatus* in the eastern and western portions of the island, and of *sagrei* throughout the island is probably a recent phenomenon associated with the destruction of the forest and the introduction of agriculture. In a recent article (Ruibal, 1961) it was shown that *allisoni* and *sagrei* are ecologically restricted to open areas of high insolation. Both these species (and presumably *porcatus* as well) demonstrate a high temperature preference and bask in open exposed habitats. Previous to the destruction of the forests these species were probably restricted to the savannas, the open coastal vegetation (thickets), and similar sparsely covered areas. Using Waibel's (1943) estimates about the former plant life of Cuba, it appears reasonable to assume that probably 80 per cent of pre-Columbian Cuba was covered with broadleaf or hardwood forest. Currently only 11 per cent of the surface area of Cuba remains covered with broadleaf forests (Smith, 1954). *Allisoni, porcatus,* and *sagrei* thus represent species that originally were restricted in their distribution in Cuba, but with the destruction of the natural vegetation have spread and become the predominant anoles of the island.

Figure 11 shows that the range of *allisoni* is completely included within the range of *porcatus*. In Camaguey and Las

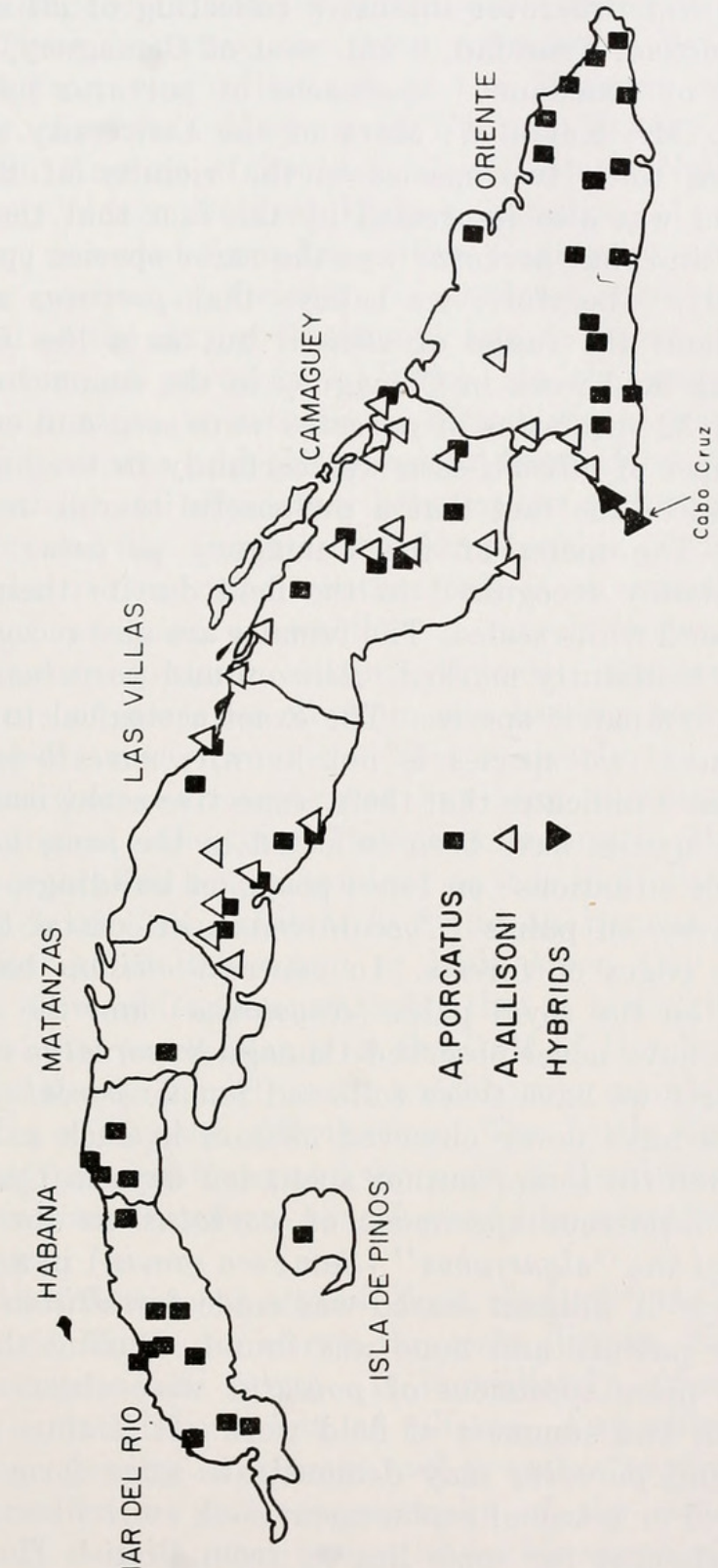


Figure 11. Map of the distribution of *A. allisoni* and *A. porcatus* in Cuba.

Villas the two species have not been collected together at all localities; however, wherever intensive collecting of *allisoni* has been done (Soledad, Trinidad, 9 km. west of Camaguey, and 15 km. southwest of Camaguey) specimens of *porcatus* have also been collected. Mr. Kevin W. Marx of the University of Minnesota observed these two species in the vicinity of Soledad, Las Villas, and was also impressed by the fact that the forms are sympatric and that *porcatus* was the rarer species (personal communication). Therefore, we believe that *porcatus* may be found throughout the range of *allisoni* but as a less common species. During field work in Camaguey in the summer of 1957 and 1959, only 12 specimens of *porcatus* were seen and collected while the number of *allisoni* seen was certainly in the hundreds — this, in spite of the fact that a purposeful search was made for *porcatus*. The males of the Camaguey *porcatus* are, of course, immediately recognized in the field due to their variegated pattern and white scales. The females are also recognizable but are not as brilliantly marked. *Allisoni* and *porcatus* in central Cuba are sympatric species. The exact ecological interrelationship of these two species is not known; nevertheless, the available evidence indicates that their respective ecological niches overlap. Both species have been collected in the same localities and in the same situations: on fence posts, on buildings, corrals, in banana groves, on palms (*Coccothrinax*) in coastal thickets, and along the edges of forests. In contrast *allisoni* has often been observed on the royal palm (*Roystonea*) and the coconut palm while we have never observed Camaguey *porcatus* on these palms. Similarly we have twice collected female *porcatus* inside the forest, and have never observed *allisoni* in such a habitat. In April of 1960 the senior author spent ten days in Camaguey and observed numerous specimens of *porcatus* on the trunks and branches of the "*algarrobas*" (*Samanea saman*) in a pasture near Camaguey. A diligent search was made for *allisoni* in this portion of the pasture and none was found. During these ten days in April more specimens of *porcatus* were observed than in the previous two summers of field work. It is thus possible that *allisoni* and *porcatus* may demonstrate some form of ecological temporal or seasonal replacement such as Neill and Allen (1959) have claimed for some lizards from British Honduras. However, the ecological data that we have obtained for *porcatus* in Camaguey has been of a fortuitous nature and thus prevents us from reaching any definite conclusions at this time.

The distribution of the two species has been plotted on the map in Figure 11 and the localities are listed at the end of the text. These localities are those represented by specimens examined from the collections of the Museum of Comparative Zoology, American Museum of Natural History, University of Michigan Museum of Zoology, United States National Museum, and the Chicago Natural History Museum. *A. allisoni* has so far been recorded from Las Villas, Camaguey, and the lowland western portion of Oriente. In contrast, *porcatus* is recorded from all of the six provinces and Isla de Pinos. In Oriente the distribution of *porcatus* is limited to the more mountainous areas and there is actually a distributional gap between the Oriente *porcatus* and the *porcatus* from Camaguey. This is a gap of about 150 kilometers between the easternmost Camaguey localities and the Oriente sites for *porcatus*. It is impossible at this time to determine whether this is an actual break in the range of *porcatus* or whether it merely reflects the lack of collecting in lowland western Oriente. Similarly only three specimens of *porcatus* all from one locality have been seen by us from Matanzas province. This is clearly the consequence of Matanzas being an area that has been singularly ignored by herpetological collectors. Future collecting in Matanzas should show *porcatus* to be as abundant as it is in Habana province.

Outside of Cuba, *allisoni* is found on Bonaca and Roatan in the Islas de la Bahia and at Half Moon Cay near Turneffe Island. It would appear probable that it is distributed throughout the other small islands in the Gulf of Honduras and it may possibly also be found in the neighboring mainland. *A. allisoni* thus has a disjunct distribution. The Little Caymans located part way between Cuba and the coast of Honduras are populated by *A. maynardi*, a form round-eared like *porcatus* and not close to *allisoni*.

The distribution of *allisoni* from central Cuba to the offshore islands of Honduras shows the most distant dispersal of any of the *carolinensis* group. It immediately raises the question of the evolutionary origin of *allisoni*. Any attempt to explain the zoogeography of *allisoni* and *porcatus* requires an analysis of the evolution and zoogeography of the entire *carolinensis* group. It would appear best to leave this aspect of the discussion to a later paper.

DISCUSSION

In all of the preceding discussion, the assumption has been that we are dealing with two species, one of which (*allisoni*) has a central distribution in Cuba while the second (*porcatus*) is represented by three geographic races spread along the entire length of the island. We made this assumption to facilitate the presentation of the data, and it is now necessary to critically examine the distribution and morphology of the Cuban forms and determine what other interpretations may be made of the data.

The variations described above for *allisoni* and *porcatus* permit us to distinguish, in Cuba, four morphological forms of the *carolinensis* group: *allisoni,* "western" *porcatus,* "central" *porcatus,* and "eastern" *porcatus.* Using these names now as simple labels without any taxonomic implications will allow us to analyze the distributional patterns. From the field observations in Camaguey and the morphology of *allisoni* and "central" *porcatus* it is obvious that these two sympatric forms are separate species. No morphological intermediates between *allisoni* and *porcatus* are known from Camaguey and Las Villas provinces. However, the relationship of these two central species to the eastern and western forms is not immediately apparent. At least the following four alternative interpretations (see Table 2) are possible:

Hypothesis 1. The "western" *porcatus* and *allisoni* are geographic races of one species, and the "central" and "eastern" *porcatus* are geographic races of another species. The main evidence in support of this hypothesis is that only in the "western" *porcatus* do we find an elongate ear opening approximating the external ear opening of *allisoni.* Furthermore, some of the large "western" *porcatus* males resemble *allisoni* in having a large canthal ridge. However, this hypothesis must assume a zone of morphological intergradation between the Pinar del Rio "western" *porcatus* and the *allisoni* from Las Villas and Camaguey. This hypothesis is untenable since the specimens from Habana and the few from Matanzas show no evidence of being morphologically intermediate between *allisoni* and *porcatus.* In addition, the "central" *porcatus* show a color pattern that closely resembles the variegated pattern of "western" *porcatus.* The hypothesis further assumes that the "central" and "eastern" *porcatus* are geographic races and should therefore

demonstrate morphological intermediates between the two races in Oriente. As mentioned previously, there is a distributional gap between the "central" *porcatus* in Camaguey and the "eastern" *porcatus* in Oriente (see Fig. 11). This gap may be more apparent than real; nevertheless, on present evidence it is a distributional hiatus.

Hypothesis 2. This is the reverse of the preceding hypothesis. In this instance, *allisoni* is considered to be a geographic race of "eastern" *porcatus* while the "central" and "western" *porcatus* would be geographic races of a second species. The similarity in ear and canthal ridges between *allisoni* and "western" *porcatus*, previously mentioned, would be interpreted as the result of convergence. Thus in central Cuba where the two species overlap they demonstrate pronounced divergence (*allisoni* as contrasted to "central" *porcatus*) while in the zones where a single species is to be found there appears to be morphological convergence ("eastern" and "western" *porcatus*). This interpretation would consider the *carolinensis* group in Cuba as an example of "character displacement" similar to previously cited cases of this type (Brown and Wilson, 1956). In support of this hypothesis it can be said that the patterns of the "central" and "western" *porcatus* are similar and can be easily imagined to be derived one from the other. The specimens of *porcatus* from Habana and Matanzas are variegated and do not present an obstacle to this interpretation as they do to the first hypothesis.

A further corollary of this hypothesis is that intermediate populations between *allisoni* and "eastern" *porcatus* should be found in Oriente. There is support for this from four male specimens (U.S.N.M. 138117, 138126-28) collected by Mr. Jerry D. Hardy, Jr., about 10 miles north of Cabo Cruz and at nearby Jucural. All specimens resemble *allisoni* but have the following *porcatus*-like characters:

1. A round ear opening in one specimen and the others with only a shallow groove posterior to the ear opening.
2. Two of the specimens show white spots on the nuchal area.
3. Three of the specimens demonstrate postoculars and temporals that appear to be intermediate in size between *allisoni* and *porcatus*.

However, a single female from the same area (U.S.N.M. 138125 from Jucural) shows no evidence of *porcatus* characters.

A series of 18 specimens from Cabo Cruz collected by Albert Schwartz also show evidence of hybridization between *allisoni* and "eastern" *porcatus*. Of the 11 males in the series only one shows a well developed ear depression while the others have poorly developed shallow areas posterior to the ear opening. These ears are morphologically very similar to some of the Pinar del Rio *porcatus* (Fig. 6). One male also has white spots on the nape. Four of the females have well developed *allisoni*-like ear openings. A single male (with an *allisoni* ear) shows a light middorsal stripe bordered by darker pigment like that of "eastern" *porcatus*.

The area of the hybrids (Fig. 11) lies where one would assume a zone of contact between *allisoni* and *porcatus; allisoni* is in the lowland western portions of Oriente while *porcatus* is in the more mountainous southern and eastern portions. *Porcatus* is found throughout the Sierra Maestra and would be expected to contact *allisoni* on the northern slopes and along the coastal area near Cabo Cruz. Collecting in this area indicates that the intermediate zone between *allisoni* and "eastern" *porcatus* must in any case be narrow — at San Ramon, 20 ml. northeast of this area "typical" *allisoni* have been collected.

Hypothesis 3. *Allisoni* is a species limited to the central portion of the island while *porcatus* is islandwide in its distribution. (The "eastern," "central" and "western" *porcatus* represent geographic races of the same species.) This, of course, is the way in which the data were presented preceding this section. We may now consider the evidence for and against this theory:

a) "Central" *porcatus* and *allisoni* are sympatric and do not interbreed. This fact at least establishes the distinctness of the two forms in Las Villas and Camaguey.

b) "Central" *porcatus,* though different from "eastern" and "western" *porcatus* in color pattern, shows many similarities to these two forms (structure of the ear opening, temporals, reticular markings, white scales, and low canthal ridges).

c) "Eastern" and "western" *porcatus* morphologically resemble each other more than either of them does *allisoni.*

Therefore, on morphological grounds alone it would be possible to consider "central" *porcatus* conspecific with the "eastern" and "western" forms. The "central" *porcatus* would still represent an example of character displacement where the

species is sympatric with *allisoni*. The "eastern" and "western" populations would in this case be considered to be connected across the length of Cuba by the rarer "central" *porcatus*.

This interpretation is weakened by the apparent distribution gap mentioned previously between "central" and "eastern" *porcatus*. The gap may or may not be real and all that we can do is hope that intensive collecting can be done in this area in the near future. It should be pointed out that a similar distributional gap exists in this area for *Anolis allogus* and *A. homolechis* (Ruibal and Williams, 1961). Furthermore, a comparable situation exists at the western end of the distribution of *allisoni*, in the province of Matanzas where very few records are available for any of the Cuban species of *Anolis*. Both the eastern and western distributional gaps may merely reflect the lack of herpetological collecting that has been done in these areas.

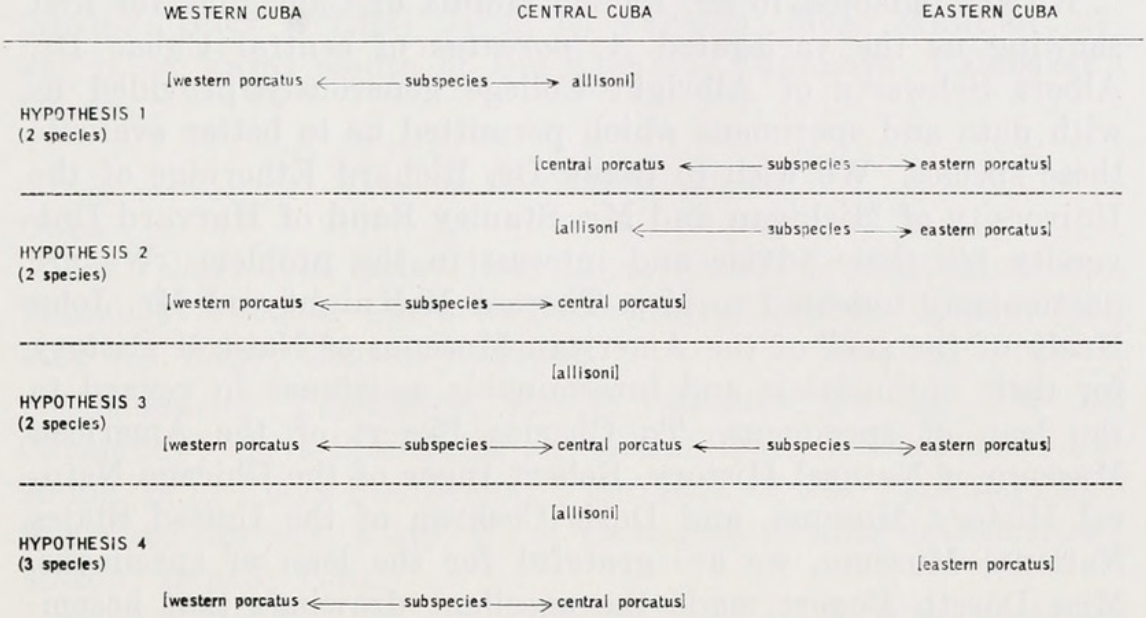
Also weakening this interpretation is the presence of hybrids in the area of Cabo Cruz, Oriente, between "eastern" *porcatus* and *allisoni*. However, the hybrids do not necessarily commit us to discarding this hypothesis. Sufficient cases are known in various animal species (Blair, 1941; Volpe, 1959; Gilliard, 1959) where hybrids occur when the ecological isolation between species has been disturbed. The evidence for intermediates between *allisoni* and "eastern" *porcatus* indicates that the zone of contact between the two morphological types must be narrow and that it corresponds to the border between the lowland agricultural areas and the less modified mountains. The Cabo Cruz area may represent a situation where the isolating mechanisms between the two species have broken down in an ecologically disturbed zone (i.e., where agriculture is actively encroaching into a forested area). It is of course also possible that a narrow zone of hybridization between *allisoni* and *porcatus* may exist throughout the periphery of the distribution of *allisoni*. In central Cuba the two species are presumed to have evolved mechanisms to reduce interspecific competition. The existence of character displacement and the fact that in the area of sympatry *porcatus* is less common and occupies a more restricted habitat than where it is allopatric to *allisoni* suggest that isolating mechanisms (behavioral, ecological, etc.) have evolved. However, at the periphery of the distribution of *allisoni* this species would be adjacent to populations of *porcatus* that have not been subjected to competition with *allisoni*. These populations of *porcatus* would be occupying the habitats

in which *allisoni* has proved superior (such as the arboreal habitat around houses and gardens). If these populations are brought into contact, by let us say a human disturbance of the habitat or by an expansion of one of the populations, an initial hybridization between the species is not unreasonable. With time, selection would operate so that each species would be segregated in the ecological niche to which it was best adapted and the hybrids would be eliminated. This of course presupposes that the hybrids are not as successful or well adapted as the parental species. Unfortunately, we have no data concerning the viability of the hybrids from Cabo Cruz or the precise ecology of this area.

Hypothesis 4. The final hypothesis to be considered is a three-species one (see Table 2). In this case *allisoni* and the "eastern" *porcatus* would be two separate species while the "western" and "central" *porcatus* would constitute a third species. This assumes that the distributional gap in Oriente between "central" *porcatus* and "eastern" *porcatus* is a real one or at least not occupied by populations morphologically intermediate between "central" and "eastern" *porcatus*. It would also assume that the hybrids between *allisoni* and "eastern" *porcatus* are explainable in the same manner as for the previous hypothesis.

Three of these hypotheses can be discarded if collecting in the distributional gap between "central" and "eastern" *porcatus* yields specimens that are morphological intermediates between these two forms. The only hypothesis that would be retained would then be the third case presented — *allisoni* as a centrally distributed species with *porcatus* represented by three geographical races, "eastern," "central" and "western." If no intermediates are found in this zone then a more detailed analysis of the zone of contact between *allisoni* and *porcatus* in Oriente will be mandatory.

TABLE 2. Diagram of the four hypotheses that are considered applicable to the data presented on A. allisoni and A. porcatus.



SUMMARY

1. The *carolinensis* group of *Anolis* is defined and two closely related Cuban representatives of the group, *porcatus* and *allisoni* are described.

2. *A. allisoni* is found in central Cuba (Las Villas, Camaguey, and western Oriente) and is sympatric with *porcatus* in this area. *A. porcatus* is apparently island-wide in its distribution and is a common species in eastern and westernmost Cuba, but it is rare in central Cuba.

3. *A. allisoni* is also found on a number of islands off the Central American mainland. Evidence is presented that indicates that *allisoni* is not a recent introduction by man into these offshore islands.

4. On Cuba, *allisoni* and *porcatus* show evidence of character displacement and convergence.

5. Both species on Cuba are considered examples of species that were preadapted to occupy the areas cleared of forest and modified by man's activities.

6. Three morphological forms of *porcatus* are described in Cuba, "western" *porcatus*, a "central" *porcatus*, and an "eastern" *porcatus*.

7. Evidence of hybridization between *allisoni* and "eastern" *porcatus* is presented.

8. Four hypotheses are presented to explain the distribution and biology of the three forms of *porcatus* and of *allisoni*.

ACKNOWLEDGMENTS

We are indebted to Sr. Ramon Molina of Camaguey for first showing us the variegated *A. porcatus* of central Cuba. Dr. Albert Schwartz of Albright College generously provided us with data and specimens which permitted us to better evaluate these species. We wish to thank Dr. Richard Etheridge of the University of Michigan and Mr. Stanley Rand of Harvard University for their advice and interest in the problem. We are particularly indebted to Mrs. Theresa McKnight and Mr. John Healy of the staff of the American Museum of Natural History for their enthusiastic and interminable assistance in regard to the loan of specimens. To Charles Bogert of the American Museum of Natural History, Robert Inger of the Chicago Natural History Museum, and Doris Cochran of the United States National Museum, we are grateful for the loan of specimens. Miss Dereth Bogert made the excellent drawings that accompany the text.

This investigation is part of a study of Cuban anoles financed by National Science Foundation Grant No. G-5634.

LOCALITY LIST

Hybrids

CUBA

Oriente: Cabo Cruz; 10 ml. N. of Cabo Cruz; Jucural (between Cabo Cruz and Niquero).

A. porcatus

CUBA

Pinar del Rio: San Diego de los Baños; Viñales; Guane; Pinar del Rio; San Vicente; just N. of San Vicente; near Isabel Rubio; Cayo la Reina near Puerto Esperanza; nr. Herradura; Guanajay; Dimas.

Habana: Habana; Regla; San Antonio de los Baños; San Jose de las Lajas; Isla de Pinos.

Matanzas: Alacranes (Alfonso XII).

Las Villas: Rodas; Baños de Ciego Montero; Soledad; Central Purio; Caibarien; Sierra de Trinidad; Trinidad; Cienfuegos.

Camaguey: Marti; 9 km. W. of Camaguey; 15 km. S.W. of Camaguey; Playa Sta. Lucia (E. of the Bahia de Nuevitas); Sierra de Cubitas; Sierra de Najasa; Loma de Cunagua.

Oriente: Santiago; Jiguani; Upper Rio Ovando; Coast S. of Pico Turquino; Pico Turquino: Imias; Banes; Baracoa; Guantanamo: Buey Arriba; Sagua de Tanamo; Moa; Miranda; 27 km. S. of Yara; mouth of Rio Yumuri; Cananova; Calabazar; Bayate.

A. allisoni

CUBA

Las Villas: San Isabel de la Lajas; Baños de Ciego Montero; Trinidad; Soledad; Caibarien; Central Covadonga; Rodas; San Jose del Lago; Central Caracas.

Camaguey: Camaguey; Marti; Cascorro; 15 km. S.W. of Camaguey; Playa Sta. Lucia (E. of the Bahia de Nuevitas); 13-20 km. S. of Playa Sta. Lucia; 7 km. N.E. of Sta. Cruz del Sur; Sta. Cruz del Sur; 9 km. W. of Camaguey; Bahia de Nuevitas; Moron; Banao; Tana.

Oriente: Birama; Omaja; San Ramon; 5 ml. S.W. of Manzanillo.

HONDURAS

Islas de la Bahia: Roatan; Bonaca.

BRITISH HONDURAS

Half Moon Cay

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