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HERPETOGEOGRAPHY OF PUERTO RICO. VII. GEOGRAPHIC VARIATION IN THE *ANOLIS CRISTATELLUS* COMPLEX IN PUERTO RICO AND THE VIRGIN ISLANDS.

By
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INTRODUCTION

There are three species-groups of anoles, genus *Anolis,* on the Puerto Rican Bank. These are the *acutus,* primitive alpha, and *cristatellus* groups (Gorman and Atkins, 1969). The last contains three grass- or bush-inhabiting species *(Anolis pulchellus, A. poncensis, A. krugi),* an upland forest species *(A. gundlachi)* and finally an assemblage of forms closely related to *A. cristatellus* that utilize tree trunks, fence posts, and other similar perches. This assemblage will be collectively referred to as the *cristatellus* complex.

Several members of the complex have been described as subspecies of *Anolis cristatellus* by Grant (1931). They are: (1) *A. cristatellus wileyae* from the Virgin Islands and small islands east of Puerto Rico; males are characterized by a red dewlap with a deep green center, the two colors being sharply demarcated, (2) *A. cristatellus cristatellus* from Puerto Rico; males are characterized by an orange dewlap with olive-green center, the two colors gradually blending into each other (Fig. 1), and (3) *A. cristatellus cooki,* from southwestern Puerto Rico; males are characterized by a chocolate-brown to reddish dewlap. The last form seems to be a separate species (Gorman *et al.,* 1968; Gorman and Atkins, 1969) and its status is currently being evaluated by Gorman, Soulé and Yang (in prep.). I have not examined specimens of it and consequently it will not be considered in detail in this paper. In addi-

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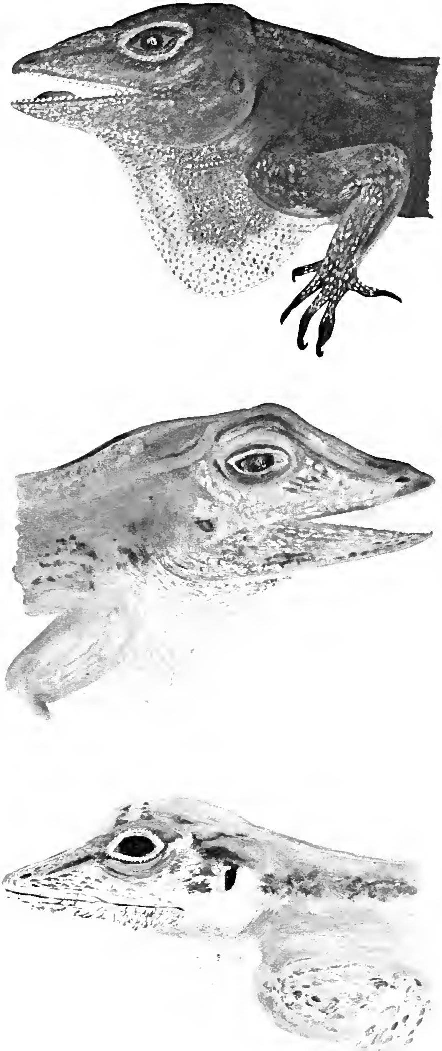
tion, *A. monensis*, a form from Mona Island with a yellow–orange dewlap, has been at times considered a synonym of *A. cristatellus* (Schmidt, 1926). As Schmidt pointed out, the populations in southwestern Puerto Rico have the same color dewlap as do specimens from Mona, and he considered the possibility that these yellow dewlapped lizards constituted one form and the remainder of the Puerto Rican ones another form. However, the southern populations on Puerto Rico have never been officially included with the Mona form as distinct from the typical Puerto Rican, nor have they ever been described as a separate species or subspecies. The anoles on Desecheo Island share dewlap color with the Mona and southern Puerto Rican populations, but previously have not been critically studied. A final member of the complex, *A. scriptus*, occurs outside the Puerto Rican-Virgin Island archipelago (in the Bahamas). Williams (1969) has reviewed its status; it was synonymized in the past with *A. cristatellus* because of the close morphological similarity between the two forms. More recent evidence, including karyotypic data, has clearly established it as a separate, but closely related, species. *A. scriptus* is not included in the present study.

Distribution of dewlap-color in the *cristatellus* complex in the Puerto Rican area is shown in Fig. 2. Typical *A. c. cristatellus* occurs throughout the northern 2/3 of Puerto Rico, and in this region no altitudinal correlates occur, the same dewlap color being found on the coastal plains as well as at the upper altitudinal limits. However, in parts of the southern coast there is a sharp dividing line between the two dewlap color forms, the location of which corresponds to the topographic division between coastal plain and mountains. North of Villalba (see Fig. 3 for localities on Puerto Rico) typical *A. c. cristatellus* was present at an altitude of 500 m, whereas the yellow dewlapped form was present only 2½ km farther south (altitude 200 m); no intermediates were found. The transition is nearly as sharp in the Coamo area, although intermediates occur at Baños de Coamo (altitude about 60 m). The transition along the coastal plain around the southeastern edge of the island is quite gradual, forms classed to various degrees of intermediacy being found over a large area extending from Yabucoa to Arroyo (a distance of about 25 km; Fig. 2). Insufficient specimens were available for detailed study of the transition zone on the western coast.

FIG. 1.—Male anole heads with extended dewlaps. Upper: *Anolis cristatellus wileyae*. Center: *Anolis cristatellus cristatellus* from northern and central Puerto Rico. The photographic reproduction did not bring out the true intensity of the green color in the center of the dewlap, which was present in the painting and is characteristic of live animals. Lower: *Anolis cristatellus cristatellus* from southern Puerto Rico (*Anolis monensis* and *Anolis desechensis* are both practically identical in dewlap color—and in other gross superficial appearances—with this yellow dewlapped form.



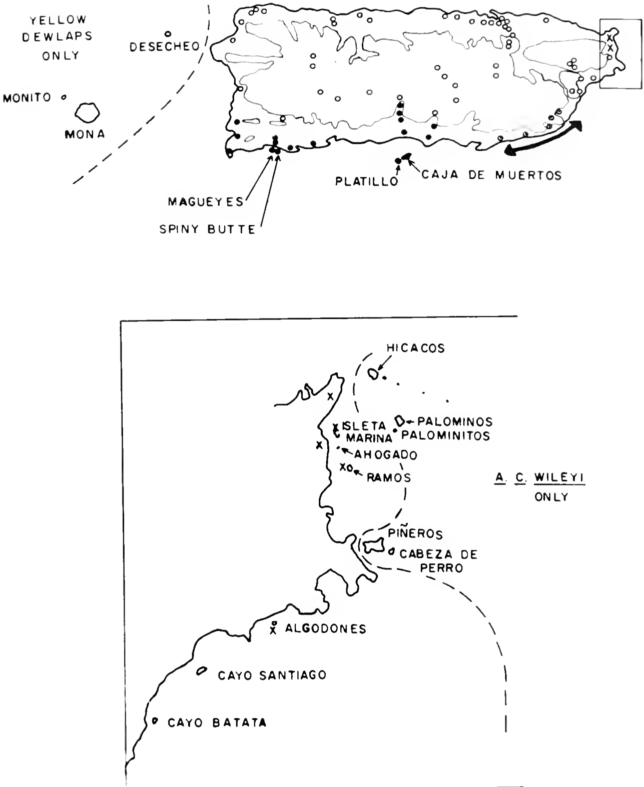


FIG. 2.—Map showing distribution of dewlap color types in the Puerto Rican region. Open circles: records of *Anolis cristatellus cristatellus* with a green center in the dewlap; solid dots: *Anolis cristatellus cristatellus* with yellow dewlaps (based on observation of dewlap color in live specimens). Box on upper map indicates area covered in lower map; areas in which intermediates between *A. c. cristatellus* and *A. c. wileyae* were found indicated by x's. For details of distribution on small eastern islands see text. Coastal area in which intergrades between the two color forms of *A. c. cristatellus* were found is indicated by double-headed arrow and circles with dots in the center. Light line in map of Puerto Rico indicates the 155 m (500 ft) contour line.

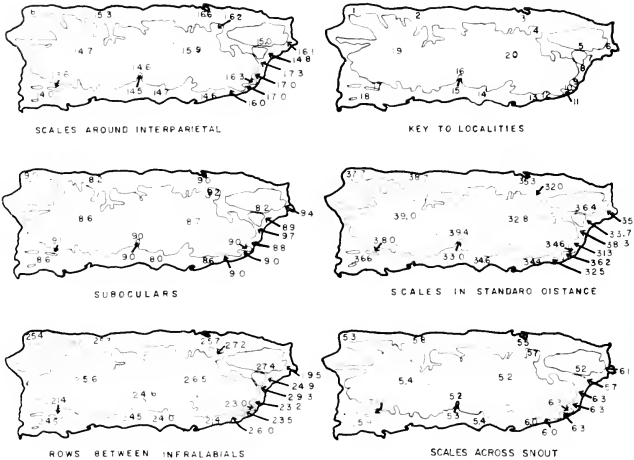


Fig. 3.—Mean values of various scale characters at Puerto Rican localities. Maps include only characters that show significant interlocality differences. Key to localities (upper right): 1, Northwestern Puerto Rico; 2, Arecibo; 3, San Juan; 4, Trujillo Alto; 5, El Yunque; 6, Ceiba; 7, Rio Blanco; 8, Humacao; 9, Yabucoa; 10, Cerro La Pandura; 11, Maunabo; 12, Hacienda San Isidro; 13, Arroyo; 14, Coamo region; 15, Villalba; 16, Jayuya region; 17, San German; 18, Southwestern Puerto Rico; 19, Western Central Highlands; 20, Eastern Central Highlands. Light line indicates the 155 m (500 ft) contour line.

Several individuals were found on the northeastern coast of Puerto Rico which were intermediate in dewlap color between *A. c cristatellus* and *A. c. wileyae* (Fig. 2). The small off-shore cays east of Puerto Rico contain typical *A. c. wileyae* except for (a) Ramos, Isleta Marina and Algodones which had *A. c. wileyae* and intermediates between this form and *A. c. cristatellus,* and (b) Cayo Santiago and Cayo Batata, upon which only *A. c. cristatellus* occurs. Also *A. c. cristatellus* seems to have drifted out to Cayo Ahogado on occasions (Heatwole and Levins, 1973). Thus, the greatest distance east of Puerto Rico to which the effect of *A. c. cristatellus* was detectable in dewlap color was less than 2 km; some islands even closer to Puerto Rico, e.g. Piñeros, have only *A. c. wileyae* recorded.

Materials and Methods

In addition to the study of dewlap color mentioned above, the present investigation consisted of an analysis of geographic variation in 9 scale characters of *Anolis c. cristatellus* and its nearest relatives. The characters were as follows: (1) number of lamellae under the 4th toe on the left front foot, (2) number of rows of loreal scales on the left side of the head, (3) number of forearm scales, (4) number of scales surrounding (touching) the interparietal scale (circumparietal plates), (5) number of suboculars, (6) number of scales across snout between second canthals as defined by Williams (1963), (7) number of longitudinal scale rows across throat on a line connecting the 3rd infralabials, (8) number of scales touching rostral (post-rostrals), and (9) number of dorsal scales in standard distance (as defined by Lazell, 1964). Dorsal color pattern also would be worthy of analysis. However, we identified at least 13 distinctly different ones, many of which occurred in a given locality. Our sample sizes were too small to identify possible changes in ratio of color types with locality. Inter-island or inter-locality scutellation differences were tested by the Dice-Leraas graphic method (Dice and Leraas, 1936). Both sexes were grouped as they were not significantly different in localities from which there was a large enough sample for such tests to be made.

A total of 735 specimens was examined, 185 from Puerto Rico proper and 550 from the various other islands in the archipelago (including 34 from Mona, 7 from Monito and 11 from Desecheo).

Results

Various of the localities close to each other on Puerto Rico were grouped together and treated as a single locality for the study of variation within the island (Fig. 3). There were four characters (loreal scales, post-rostrals, lamellae of 4th toe, and forearm scales) in which there were no significant differences among any of the Puerto Rican localities. Consequently, for these characters all data for Puerto Rico were pooled according to dewlap color type for comparison with other islands. These characters will be discussed first.

Loreal rows.—No significant differences exist among the larger islands, with the exceptions that the St. John population had significantly lower values than the Mona one, and Tortola significantly lower ones than Culebra (Fig. 4). Many of the smaller cays and islands are not represented by a sufficiently large number of specimens for statistical analysis. Of those that are, many showed little or no divergence from the conditions found on neighboring larger islands. Several had small, though significant, differences with respect to one or more nearby cays but not with respect to most, e.g. Cayo Santiago, Isleta Marina and Palominitos tend toward higher values than most of the islands, and Lobos toward lower ones; some of the differences were significant with respect to Puerto Rico or to other cays. Of more importance are the values for Tobago, Little

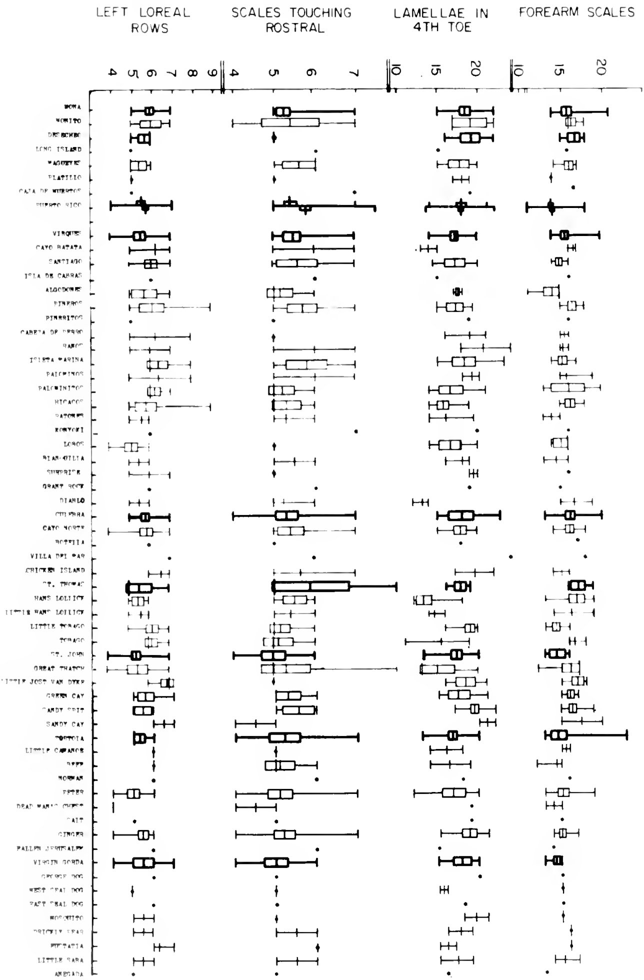


FIG. 4.—Variation in four characters of members of the *Anolis cristatellus* complex among various islands of the Puerto Rican-Virgin Island Archipelago. Figures in heavy lines indicate the larger islands, those in light lines smaller islands or cays. Horizontal lines represent ranges, and rectangles two standard errors on either side of the enclosed mean (vertical line). Failure of rectangles to overlap suggests significant differences between means at the 5% level. Fig-

Tobago and Little Jost van Dyke, which are significantly higher than those of most nearby islands, and in the case of the last, significantly higher than most of the other islands studied (Fig. 4).

Scales touching rostral (postrostrals).—No significant differences were noted among any of the islands, large or small, with one exception. Range in values over the entire archipelago was 4–8, range of island means was 4.5–6.0, the extremes of which occurred in very small samples. Of those samples with an *N* of 6 or more the range in means was 4.9–5.0. The single island significantly different from the condition shared by most of the others was Desecheo. All 11 individuals from Desecheo had 5 postrostrals, a value outside the range of significance for either Mona or the Puerto Rican populations with yellow dewlaps. Although on Puerto Rico no single population differed significantly from any other, when all individuals with yellow-orange dewlaps were pooled and compared with the pooled average of all *A. c. cristatellus* with olive-centered dewlaps, the former had a significantly lower number of postrostrals than the latter (Fig. 4).

Lamellae of 4th toe.—Among the larger islands, none of those east of Puerto Rico show significant differences among themselves (Fig. 4). Furthermore, they do not differ significantly from those west of Puerto Rico except for Vieques and Tortola, both of which had significantly lower counts than Mona and Desecheo. No consistent geographic trend was found in the pattern of variation among the cays between Puerto Rico and Culebra, several of which were significantly different from each other; Hicacos differed significantly from both Culebra and Vieques (Fig. 4). In the Virgin Islands, various of the northern cays had significantly higher values than the nearest larger islands to their south (St. Thomas, St. John, Tortola). An exception was Hans Lollick, which had significantly lower values than any of the principal islands, and, in fact, than any other island or cay except Great Thatch (Fig. 4).

Forearm scales.—Mona and Desecheo are not significantly different from each other or from the other large islands as far east as St. Thomas. The latter has particularly high values (significantly higher than those of Vieques and those of all the large islands to its east). Except for this difference the pattern of geographic variation could be interpreted as a cline with values decreasing on the aver-

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ures with rectangles are derived from samples of 6 or more animals; those with only means and ranges are derived from samples of 2-5 individuals. Dots indicate single individuals and dots with a horizontal line indicate multiple individuals with identical values. Figures for Puerto Rico differ in that the left half of the figure refers to all specimens (pooled) with uniformly yellow-orange dewlaps, the right half of those with green centers in an orange dewlap; localities containing intermediates between these two forms are excluded.

age toward the east, and with the two ends significantly different from each other, but connected by intermediate populations.

The cays between eastern Puerto Rico and Culebra vary among themselves and from nearby large islands, sometimes significantly so, but without any consistent geographic trends. The smaller islands of the Virgin Islands resemble nearby larger ones (Hans Lollick agrees with St. Thomas in having unusually high values) except that some of the islands north of Tortola and St. John have significantly higher values than either of these larger islands.

The remaining characters showed considerable variation within Puerto Rico (Fig. 2), significant differences occurring among some of the localities according to Dice-Leraas (1936) graphic tests. Hence, localities cannot be lumped for these characters for inter–island comparisons.

Scales surrounding interparietals (circumparietal plates).—When various islands are compared, a west-east trend is noted (Fig. 5); Mona has values significantly higher than any of the other large islands. All of the islands to the east of Culebra and Vieques have significantly lower values than these two, except St. John, which is just at the 5% border of significance with Vieques. Few significant differences were demonstrated among small cays or between cays and nearby larger islands. Exceptions were that Cayo Norte had significantly lower values than Culebra, and Lobos significantly lower ones than Hicacos.

Within Puerto Rico this character showed high values along the eastern coastal plain. One exceptional locality, the Humacao region, had lower values than expected from its geographic position. There was a trend toward decreasing values from north to south throughout the rest of the island and an especially strong decrease in values from east to west on the southern coast. The lowest values occurred in specimens from southwestern Puerto Rico. Thus, these populations differ more from the Mona and Desecheo ones (even though sharing the same dewlap color) than does the different dewlap–color form from the central mountains and northern coastal region.

Suboculars.—Mona had significantly lower values than Desecheo and was much lower than Puerto Rico; Desecheo and Puerto Rico were similar. Of the larger islands east of Puerto Rico only Vieques and Culebra differed significantly from each other. Where sufficient data were available for assessment, small islands tended to be similar to adjacent larger ones. An exception was Sandy Spit, which had higher values than Tortola.

On Puerto Rico most localities were similar, although Coamo had significantly lower values.

Rows between infralabials.—Inter-island variation showed no consistent geographic trend although several of the adjacent larger

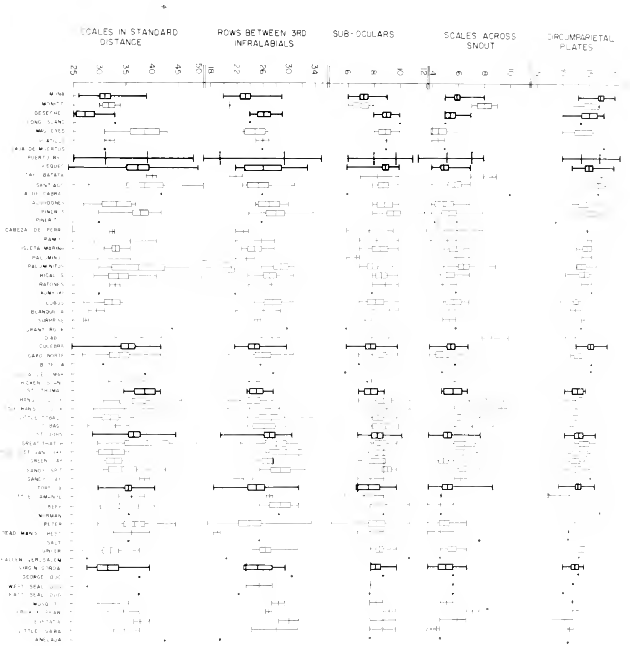

FIG. 5.—Variation in five characters of members of the *Anolis cristatellus* complex among various islands of the Puerto Rican-Virgin Island Archipelago. Symbols as in Fig. 4, except for those for the island of Puerto Rico, for which the horizontal line represents the total range of values obtained from all populations, and the two vertical lines in each figure indicate means of the localities with the highest and lowest values respectively.

islands displayed significant differences, e.g., Mona-Desecheo, St. Thomas-St. John (Fig. 5). Most of the smaller cays were similar to adjacent larger ones, although several north of Tortola had significantly higher values than did Tortola. The series of cays between Puerto Rico and Culebra were highly variable, with some of the inter-cay differences, as well as most of the differences between those cays and Culebra, being significant.

On Puerto Rico values were quite variable along the eastern coast, both the highest and lowest values being found there. The extreme values were not a result of gene flow from the east in this case as the eastward islands had values close to the less extreme ones of Puerto Rico. Elsewhere there was an increase in values along the northern coast and central mountains into the Luquillo range in the northeastern part of the island. Southern coast values tended to be lower than those from the mountains.

Scales in standard distance.—When the larger islands are compared, a very marked geographic pattern is noted. Mona and Desecheo have values which are greatly, and significantly, lower than any of the other large islands nearby. Desecheo is significantly lower than Mona. The islands east of Puerto Rico show a cline of decreasing values from west to east, the extreme eastern end (Virgin Gorda) reaching values as low as those of Mona. In contrast to the usual condition, the cays between Puerto Rico and Culebra do not differ significantly among themselves (except for Piñeros which has a higher value than most of the others) though several have significantly lower values than either Culebra or Vieques. Several of the cays north of St. Thomas-St. John-Tortola show significantly lower values than these islands. This is the only character studied in which significant differences were found between Virgin Gorda and Tortola (and the southern chain of smaller islands). Ginger Island which lies in the eastern part of the chain has a population with similar counts to those of Virgin Gorda but significantly different from those of Tortola. By contrast, a more western island in the chain, Peter Island, is like Tortola but significantly different from Virgin Gorda. Values presented here are consistently lower than those of Gorman *et al.* (1968) for some of the same islands; this may be a result of differences in methods of making counts in the two studies.

On Puerto Rico, extreme interlocality variability coupled with lack of geographic trend occurred on the eastern coast. Elsewhere there seems to be a peripheral reduction in values away from the central mountains, especially on the southern coast, although certain localities constitute exceptions.

Scale rows across snout (scale rows between canthals).—None of the larger islands show significant differences among themselves except Vieques had significantly lower counts than Culebra and Mona. By contrast many of the small cays had populations quite different from those on adjacent larger islands. Monito differed greatly from either Mona or Desecheo. Various of the small cays between Puerto Rico and Culebra differed significantly among themselves, several having significantly higher counts than either Vieques or Culebra or both, though there was no geographic consistency to the pattern of variation among cays. Finally, the cays to the north of St. Thomas-St. John-Tortola generally show higher counts than the three mentioned larger islands, with most of the differences being significant.

On Puerto Rico the higher values occurred on the eastern coast with lower or similar ones elsewhere. A notable exception was the

San German population with a mean value much higher than any other locality in Puerto Rico.

In summary it can be stated that each character studied shows its own independent pattern of variation. Within Puerto Rico, sharp discontinuities in scutellation do not necessarily occur where there are abrupt changes in dewlap color; conversely, scale characters may change markedly within an area where dewlap color is uniform.

Discussion of Patterns of Variation

Several biogeographic interpretations can be made from this study of variation.

1.—Gene flow is great among the islands, mostly occurring from east to west and predominately under the influence of direction of water currents. Several lines of evidence converge in indicating this. First of all *A. c. cristatellus* has had little success in spreading eastward (against prevailing water currents), whereas *A. c. wileyae* has been able to move westward much more easily. This is evidenced by the fact that influence of *A. c. cristatellus* on dewlap color of small insular populations is not felt more than 2 km off the east coast of Puerto Rico, whereas the *A. c. wileyae* pattern is found on islands in a widely dispersed area and westward immigrants have been numerous enough to influence dewlap color of even the large, eastern-coastal population of the Puerto Rican mainland. An almost identical distribution pattern of two color forms of the millipede, *Orthocricus arboreus*, has been found by Dr. Manuel Velez (personal communication). Heatwole and Torres (1967) have previously interpreted patterns of geographic variation of the lizard, *Ameiva exsul*, in a similar way.

The great variability in some scutellation characters along the eastern coast of Puerto Rico as compared to the rest of the island may be the result of gene flow from a number of sources, each with quite different characteristics. As previously shown, there is almost a random pattern of variation among the small eastern cays. These would make different relative contributions to immigration along specific sections of the eastern coast and thereby contribute to high interlocality variation there.

Second, the fact that the cays north of Tortola and St. John, and to a lesser extent those north of St. Thomas, tend to differ from these larger islands, whereas small islands in a more east-west alignment with the larger ones do not, suggests that water currents influence degree of immigration (or conversely isolation). Information concerning the chain of islands south of Tortola would be instructive on this point.

2.—Island size seems to influence degree of divergence. Most of the large islands from Puerto Rico eastward are very similar, often showing no significant differences or only gradual clinal trends. This indicates considerable genetic exchange among their populations (all are aligned roughly east to west except Anegada, from which inadequate samples of material were obtained). The smallest of these islands, Culebra and Vieques, which are also more distant on an east-west basis from other large islands than is true of adjacent islands in the Virgin group, tend to diverge from each other (aligned north and south) and from nearest large neighbors more than do the other large islands, except the special cases of Mona and Desecheo discussed later. Thus, the combination of relatively great distance between islands and small size seems to result in a great degree of divergence. The effect is most strongly seen on the cays between Puerto Rico and Culebra which, even though near to each other and to larger islands, have, presumably because of their small size, undergone considerable divergence and in an almost random way.

Mona and Desecheo should be discussed in terms of the above two generalizations. Although they are on an east-west alignment with Puerto Rico, the populations tend to diverge from those of Puerto Rico; also the Mona and Desecheo populations are significantly different from each other in many characters. The apparent paradox is resolved by the facts that (1) the current sweeps northward in the Mona channel (Kaye, 1959), thereby greatly reducing the probability of flotsam transport between Puerto Rico and the two western islands or among themselves, (2) interisland distances involved are greater than among the eastern islands, and (3) isolation time has been much greater, Mona and Desecheo not having been connected with each other or with Puerto Rico at least since the end of the Pliocene (if ever), whereas the Virgins were connected with each other and with Puerto Rico as recently as about 9,000 years ago (Heatwole and MacKenzie, 1967).

Isolation time, however, does not account for the greater divergence noted for Culebra, Vieques and the small cays just east of Puerto Rico, as all of these were connected with each other and with Puerto Rico as recently as about 6,000 B.P. except for Culebra which was connected as late as 8,000 B.P. (Heatwole and MacKenzie, 1967).

Taxonomic Assessment

If each insular population that showed significant differences from those of all neighboring islands in one or even several characters were described as separate named subspecies, almost every small cay between Puerto Rico and Culebra for which an adequate sample was obtained, would have its own endemic, the larger Virgins would have at least one subspecies, the cays north of Tortola–St. John one or more, and Puerto Rico several; the geographic boundaries would depend on which characters one chose as diagnostic. But, such a treatment would tend toward compartmentalization into an overly rigid classification, which would obscure evolutionary dynamics. One might suspect that over a period as short as several decades the characteristics of a small population on a tiny cay would change significantly by genetic drift, or that local extinction followed by recolonization and establishment of a new population with different characteristics (because of the founder effect) might repeatedly occur. Consequently, I prefer to maintain all the populations east of Puerto Rico as *Anolis cristatellus wileyae* without further nomenclatural proliferation, simply recognizing that (1) populations on relatively isolated small cays diverge widely from those on the larger islands, (2) that the cays north of Tortola-St. John tend to diverge from the larger islands, and (3) that a zone of intergradation with *A. c. cristatellus* occurs along the northeastern coast of Puerto Rico and some of the islands within 2 km of that coast.

Because of their distinctiveness from Puerto Rico and from each other in many characters, nomenclatural recognition should be given to the populations of both Mona and Desecheo. In the absence of data on hybridization potential, it is perhaps a toss of the coin whether to consider them full species or subspecies. I choose to do the former because of karyotypic differences between the Mona and Puerto Rican forms (Gorman and Stamm, 1975). In fact, Gorman and Stamm consider the Mona form more closely allied to *A. cooki* than to *A. cristatellus.* The Mona and Monito populations should thus be designated by the name *Anolis monensis*; the form on Desecheo is described as new.

Anolis desechensis new species

Holotype.—No. 159396, Museum of Natural History, The University of Kansas. Adult male collected by H. Heatwole, Desecheo Island, Puerto Rico, 28 March 1961 (Fig. 6).

Diagnosis.—A species of *Anolis* with a uniformly yellow-orange dewlap, 8-10 suboculars (mean 9); 24-29 scale rows between the third infralabials (mean 26.2); 25-33 scales in the standard distance (mean 27.2); 5 postrostral scales.

Range.—Known only from the type locality, Desecheo Island, Puerto Rico.

Description of Holotype.—Dorsum uniformly deep brownish-gray becoming lighter on the venter; nuchal crest slight but tail crest prominent, as high as the diameter of the tail and extending approximately half the tail's length; dewlap uniformly yellow-orange (in life) becoming dull gray (in alcohol); 6 loreal rows of scales; 20 lamellae under the 4th (left rear) toe; 18 forearm scales;

FIG. 6.—Holotype of *Anolis desechensis.*

14 circumparietal scales; 8 suboculars; 6 scales across snout between canthals; 28 rows of scales between the 3rd infralabials; 5 postrostrals; 25 scales in standard distance; snout to vent length 57 mm.

This leaves the status of the forms on the Puerto Rican mainland to be considered, for which the name *A. c. cristatellus* is applicable at least to the populations of the north coast and central mountains with orange and green dewlaps. The form on the southern coast with yellow dewlaps cannot be grouped with either *A. monensis* or *A. desechensis* even though it shares dewlap color with them, because it differs in many scutellation characteristics. Such a grouping would obscure true relationships. In most characteristics the southern population of Puerto Rico is certainly much more closely related to *A. c. cristatellus* than to either *A. monensis* or *A. desechensis* and there is a broad zone of intergradation between *A. c. cristatellus* and the yellow dewlapped form in southwestern Puerto Rico. Consequently, the most realistic approach would be to simply list the latter as a color variant of *A. c. cristatellus* and not give it nomenclatural status. Indeed, in view of the correlation of uniformly yellow dewlaps with hot dry environments (southern Puerto Rico, Mona and Desecheo being hotter and drier than the other areas under consideration), one might suspect that this character is environmentally controlled, i.e. against the genetic background common to members of the complex, hot and/or dry environments favor development of the yellow-orange pigment or, conversely, inhibit formation of the green and red components. However, experimental work on environmental effects on development of dewlap pigment would have to be carried out before this could be tested.

Discussion

Gorman *et al.* (1968), Gorman and Atkins (1969), and Gorman and Stamm (1975) have pointed out that *A. cooki, A. monensis,* and the Puerto Rican grass and forest species in the *cristatellus* group all have 29 chromosomes; *A. cristatellus* (including the subspecies *wileyae*) is exceptional in having 27. On the basis of detailed karyotypic studies, the first authors provide two alternative hypotheses for the evolution of the *cristatellus* complex. One is that *A. cooki* (and consequently also *A. monensis* since these two species are karyotypically indistinguishable; Gorman and Stamm, 1975) has the more primitive karotype and *A. cristatellus* is derived from an ancestor with that karyotype. The second hypothesis is that *A. cristatellus* was derived by chromosome loss from an ancestor with a *gundlachi*-type karyotype and that *A. cooki* was a further derivative (by centric fusion) from the *cristatellus* type. The former interpretation is favored in the present paper and the phylogenetic history of the complex in the Puerto Rican-Virgin Island area is postulated to have been as follows:

When Puerto Rico and the Virgin Islands were one continuous land mass, a proto-*cristatellus* ancestor (with the *cooki-monensis* karyotype) covered the entire area. The southwestern part of Puerto Rico was considerably larger and extended well into the Mona Channel, deflecting currents more to westward than at the present time (Heatwole and MacKenzie, 1967) resulting in colonization of Mona and Desecheo by flotsam transport from southwest Puerto Rico. Following the receding of the southwestern Puerto Rican coastline with rising sea level, Mona and Desecheo became relatively isolated even from flotsam transport (Heatwole and MacKenzie, 1967), and divergence proceeded independently on the two islands. The common dewlap color that populations on Mona and Desecheo share with those of southwestern Puerto Rico may reflect the fact that Puerto Rico was probably the origin of the founders of Mona and Desecheo (but see alternate explanation above). After the isolation of the Mona and Desecheo populations, the mainland Puerto Rican-Virgin Island stock underwent chromosomal loss to form the present day karyotype of *A. cristatellus.* Continuous gene flow among *cristatellus* populations has maintained them close together up to the present time. Separation into *A. c. cristatellus* and *A. c. wileyae* has been extremely recent (only about 8,000 years ago), when rising sea level isolated the Virgin Islands from each other and from Puerto Rico (Heatwole and MacKenzie, 1967). There may well have been geographic clines in dewlap color or other characteristics well before physical separation of the islands, however. Isolation is very incomplete even today because of flotsam transport of individuals from east to west.

Exactly when and under what circumstances *A. cooki* split off from the proto–*cristatellus* stock is uncertain. If the events postulated here are correct it would have had to have occurred prior to the loss in chromosome number by the mainland Puerto Rican stock, and was probably much earlier, perhaps even antedating the isolation of the stocks which gave rise to *A. monensis* and *A. desechensis.* By contrast, the origin of *A. scriptus* must have been after chromosomal loss by the *cristatellus* stock, as *scriptus* also has only 27 chromosomes (Gorman *et al.,* 1968). It is undoubtedly a form which has differentiated on the Bahamas after relatively recent dispersal and colonization of that area by a form from Puerto Rico very near to modern *A. cristatellus.*

Williams (1969) has considered the problem of dispersal of Caribbean anoles from one island to another and the factors that affect their subsequent establishment. He points out that successful colonists of new islands are a small fraction of the number of species available for colonization and that they are rather versatile, broadly tolerant species. Once a colonist has become established on a new island it may exclude later potential colonists; a single, broadly-adapted population may be more resistant to invasion than a more complex fauna of specialists. The *cristatellus* complex supports these views. *A. cristatellus* is the most common, widespread, and eurytopic anole on Puerto Rico and it is consequently the most likely candidate for overwater dispersal to, and colonization of, new islands. Its derivatives are the only anoles present on Mona and Desecheo. *A. scriptus* is the only species derived from a Puerto Rican source that occurs in the Bahamas, although separate invasions of other stocks have taken place there from other Antillean sources. At present *A. monensis* on Mona has a structural niche and general ecology almost identical to that of *A. cristatellus* on Puerto Rico (Gorman and Stamm, 1975). My casual observations suggest the same is true of *A. desechensis.*

Electrophoretic and biochemical techniques have been extremely fruitful in examining genetic relationships of closely related populations. For example, such studies on what previously had been considered a single species of anole with geographically variable dewlap color, permitted identification of 3 sibling species (Webster and Burns, 1973). Application of similar techniques to *A. c. cristatellus* on Puerto Rico would perhaps lead to a more precise assessment of the taxonomic status of the populations with different dewlap colors.

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