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The Origin of Faunas.
Evolution of Lizard
Congeners in a Complex
Island Fauna:
A Trial Analysis

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INTRODUCTION

The history of faunas, whether studied by paleontologists and zoogeographers or by systematists, has customarily been described in terms of phylogeny or colonization—in terms, therefore, of the origin or arrival of species. However, a major element permitting the build-up of faunas has been the coadaptation of their species—the fact that they are ecologically fitted together. Study of this coadaptation among living species is, in fact, a major part of modern ecology. Yet ecologists have, on their part, avoided history; they have avoided any attempt to look closely, theoretically or empirically, at the historical sequence of events in the build-up of a complex coadapted fauna.

In order to test whether a historical ecology for complex faunas is possible, I here endeavor to provide the necessary analysis in one well-documented case, taking as my starting point some empirically determined rules of size change in a lizard genus that has colonized many islands and has radiated on some of them to form complexly coadapted congeneric faunas.

Schoener (1970) has provided evidence that in the lizard genus *Anolis* species living without congeners—"solitary anoles"—on the Lesser Antillean islands tend

to fall within a characteristic small size range. Again he has shown that, when two anole species occur on any Lesser Antillean island, there is always marked difference in size. His unpublished data also show that, in general, the greater the diversity of island anole faunas, the greater the disparity between the largest and smallest species. I shall call these empirically discovered relationships the *Schoener rules*.

Schoener has discussed these phenomena in terms of competition for resources, primarily food (Schoener, 1969a, 1969b, 1969c, 1970), and has proposed an elaborate model (Schoener, 1969a) predicting optimal sizes for solitary predators, and, as well, convergence and divergence of size changes in complex faunas.

He has not, however, attempted to trace or explain the historical sequence of events in any complex fauna. In all his explicitly predictive statements he has avoided anything beyond simple interactions (species pairs or, more rarely, trios).

I shall here endeavor to explore the possibility of expanding the Schoener rules and their proposed ecological explanation into a model of the historical sequence of size change that can be matched against the probable history of an actual fauna—that of the island of Puerto Rico. The model will be as simple as possible. It will take the classical expectations of character displacement for species pairs and, carrying these forward for increasingly larger faunas, will endeavor to explain some of the complexities in evolution (not only of size) in complex island faunas with as few supplementary assumptions as possible. The proposed model will derive directly from the empirical base of the Schoener rules. What Schoener has shown to be true for the Lesser Antilles—islands of small to moderate size and all of modest age—I here extrapolate in quite literal fashion to an island—Puerto Rico—of much greater size and age.

The choice of Puerto Rico as the test of the proposed model is an inevitable one. For this island, far better than for any other, there exists a phylogeny of the anoline lizards constructed in classical fashion on morphological and other grounds independently of any ecological hypothesis whatever. This phylogeny therefore provides a framework not susceptible to manipulation or distortion to which any ecological hypothesis must be fitted.

WEST INDIAN ANOLES, SIZE, AND ECOLOGICAL PRINCIPLES

West Indian anoles provide good data to an extent that is only beginning to be appreciated. They are taxonomically well known (although new species are probably still to be discovered on the two largest islands, Cuba and Hispaniola). Ecologically their study has begun to be quite sophisticated. Large museum collections exist for most species, permitting collection of accurate metrical data.

Beyond this, however, the distribution of so many species (more than 70) over so many islands (Fig. 1) with varying degrees of diversity allows one to treat the island faunas as "experiments of nature," testing each hypothesis as it is devised.

One other fact makes West Indian *Anolis* especially favorable for ecological discussion. They occupy the diurnal arboreal lizard niche in the West Indies essentially alone. They came to the Antilles from the complex faunas of the mainland, where they primitively occupied the tree crown, and where they share this niche with some other lizards and also birds and mammals. In the West
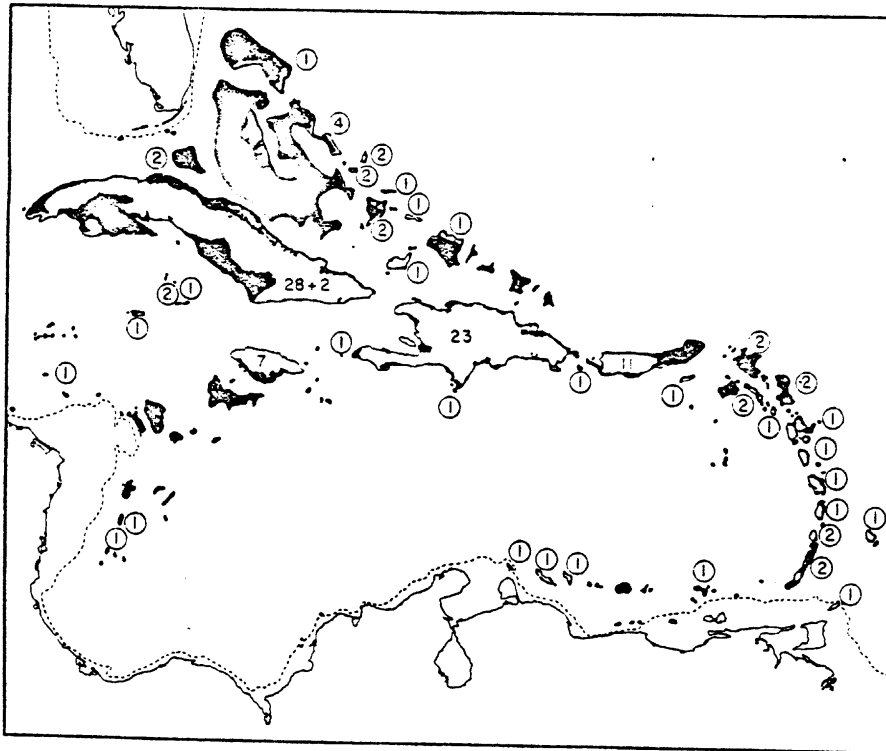

Fig. 1. The West Indian islands and the number of Anolis *species per island or island bank. (The additional two on Cuba are species of the related genus* Chamaeleolis.*)*

Indies they have usually no lizard competitors in vegetational niches, and there are far fewer birds and even fewer mammals. On these islands all erect vegetation from grass to trees—everything that provides a perch—is essentially the domain of *Anolis*. In consequence, competition is almost wholly intrageneric, and West Indian *Anolis* can be treated as if they were evolving alone. Figure 2 indicates some of the most common niches filled by *Anolis* on the largest, most complex islands (cf. Rand and Williams, 1969).

For West Indian *Anolis* we have the addtional good fortune that Schoener has done the basic work of measurement. He has tabulated measurements for the largest third and the largest sixth of the available samples and also maxima of head length, snout-vent length, and tibial length for all West Indian species
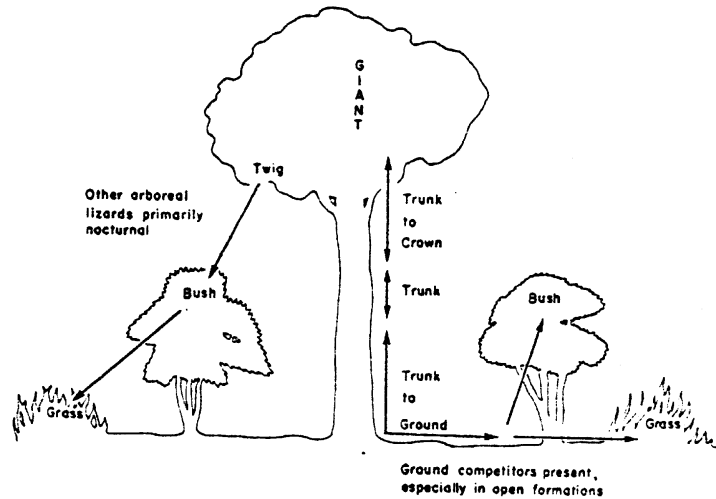

Fig. 2. The most common ways in which the vegetation of the larger Caribbean islands may be utilized by members of the genus Anolis. *Niches are named according to the usage of Rand and Williams (1969). It is shown that the bush and grass niches can be reached from two directions.*

(specimens in the Museum of Comparative Zoology, supplemented when desirable by other major collections). Schoener's tabulations are the solid base upon which all discussions of size in this paper are built.

Schoener has preferred in his own analyses (Schoener, 1969c) to use the mean of the largest third. In the present paper, with access to his original tabulations, I shall most often use maxima. My choice rests on the following considerations: (1) Schoener's tables make clear that the maxima do not differ in trend or significance from the means of the largest third. (2) The maximum is a convenient datum easily obtainable when Schoener's tables require to be suplemented. (3) Maxima, as an additional statistic, test for the inclusion of taxa that have been mistakenly ignored. (The very few extreme individuals that initially seemed out of line with the rest of certain species samples have proved in one case to be representative of a distinct, and at the time of measurement, unrecognized species, and in another of a valid subspecific difference—see below.)

Schoener's data on species difference in size is supplemented by limited evidence on the sizes of insect prey taken by size classes within species (primarily from stomach analyses of two competing species, *A. aeneus* and *A. richardi*, on the Lesser Antillean island of Grenada (Schoener and Gorman, 1968)). The data, though meager, are quite suggestive. The following conclusions are well-supported by the present evidence:

(1) Adults of species that differ in adult size eat prey of different average size. The range of prey size is always great, but larger species eat significantly larger prey than smaller species (Schoener and Gorman, 1968).

(2) Smaller size classes within a species in general take smaller prey than the larger size classes of the same species (Rand, 1967; Schoener, 1967, 1968; Schoener and Gorman, 1968).

(3) Equally sized juveniles of species that differ in adult size already differ in prey-size preferences in the same way that the adults differ (Schoener and Gorman, 1968).

(4) The sexes of dimorphic species differ in prey size preference (Schoener, 1967; Schoener and Gorman, 1968).

(5) Equally sized juveniles of the two sexes tend already to differ in prey size preference in the same way that the sexes of the adults differ (but special growth or energy requirements in differing seasons may complicate this simple statement; see Schoener and Gorman, 1968).

These observations provide functional background for the interpretation of the size relationships seen in the Schoener rules as classical character displacement by divergence. Hence they provide also the empirical foundation for the edifice of inference erected in this paper.

THE LESSER ANTILLES: MODEL FOR A MODEL

I am here deliberately choosing the anoles of the Lesser Antilles as the model for a model. I am postulating that the mechanism which resulted in the Schoener rules accurately mirrors that which operated in the first stages of the more diverse faunas of the Greater Antilles. The Schoener rules provide quantification and example; we go beyond them to analysis of more complex faunas by step-by-step employment of the same rules. However, we will first need to look closely at the Lesser Antillean data to determine whether the causal explanation I propose does in fact fit the data in all regards. Figure 3 maps the area and names the islands and species discussed.

Schoener's First Rule: The Size of Solitary Species

Schoener's Rule 1 states that an anole occupying an island without congeneric
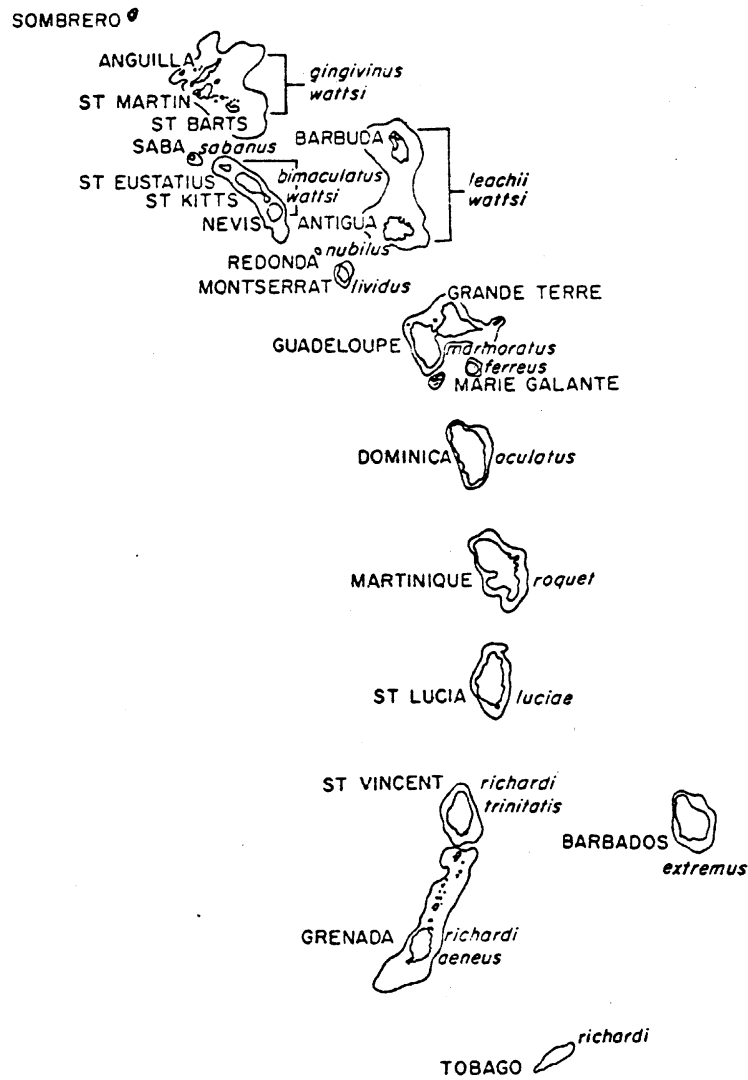
Fig. 3. The Lesser Antilles: species and islands.

competition tends to a range of sizes with maximal head lengths of between 20 and 25 mm and maximal snout-vent lengths of between 65 and 95 mm. Table 1 records the maximal sizes for the solitary anoles in the Lesser Antilles for which the Schoener rule was formulated. The two phyletic groups—*Anolis roquet* and *bimaculatus*—are treated separately. Inspection shows immediately (1) there is strong sexual dimorphism; (2) head sizes are similar in magnitude and range in both phyletic groups; (3) body length (snout-vent length minus head length) is greater by 8 mm in the *roquet* group than in the *bimaculatus* group; (4) the

spread between largest and smallest is very similar in both groups and for both measurements (5 mm for head size in the *bimaculatus* group, 3 mm for the same measurement in the *roquet* group; 13 mm for snout-vent length in the *bimaculatus* group, 17 mm for the same measurement in the *roquet* group).

In Table 1 I have, however, carefully omitted those species and islands which pose some difficulty for the Schoener rule. These, unquestionably, are crucial. Let us first propose a mechanism explaining the Schoener rules and then see whether the anomalous examples are reconcilable with this explanation.

Table 1. Maximal Sizes for Solitary Species of *Anolis* in the Lesser Antilles

Island	Species	Head Length	Snout-Vent Length	N
A. roquet Group (Omitting *richardi* on Tobago and *aeneus* on the Grenadines) (See Below in Text)				
Martinique	*roquet*	20♂/15♀(1.3)	79♂/59♀ (1.3)	50/20
St. Lucia	*luciae*	25/16 (1.6)	91/62 (1.5)	49/13
Barbados	*extremus*	20/15 (1.3)	74/60 (1.2)	43/18
A. bimaculatus Group (Omitting *marmoratus* on Guadeloupe) (See Below in Text)				
Saba	*sabanus*	20♂/14♀ (1.4)	67♂/51♀ (1.3)	70/34
Montserrat	*lividus*	21/15 (1.4)	69/51 (1.3)	55/41
Redonda	*nubilus*	23/15 (1.5)	79/52 (1.5)	21/5
Dominica	*oculatus oculatus*	23/16 (1.4)	75/55 (1.4)	21/10
	o. cabritensis	22/16 (1.4)	75/57 (1.3)	24/11
	o. winstoni	23/18 (1.3)	77/61 (1.3)	23/7
	o. montanus	25/17 (1.5)	95/64 (1.5)	15/12

I assume, out of hand, that size is under the control of natural selection and always tends to an optimum for each species, maintaining it if reached, pushing toward it if not yet attained. The explanation, then, for similar sizes in solitary anoles should be intraspecies competition, leading to similar selective forces acting upon species with similar but not necessarily identical initial adaptations.

Note that the anoles that populated the Lesser Antilles came from complex faunas (Puerto Rico to the north, South America to the south; Gorman and Atkins, 1969), which were diverse in sizes as in other features. There is thus no ground for predicting for an invader at the time of invasion any particular size.[1]

[1] Schoener (1969c) has discussed the possibility that "solitary size" is itself significant for colonization, pointing out that *carolinensis*, *grahami* and *cristatellus*, colonists of islands satellite to the Greater Antilles, are of solitary size on their home islands. But, as he also points out, *sagrei*, one of the two major colonizers (the other is *carolinensis*, of Williams, 1969) is smaller than solitary size on its home island (Cuba) but has apparently evolved to solitary size on Swan Island, where it may have been long resident. Two colonists of the Bahamas—*angusticeps* and *distichus*—are also smaller than solitary size on their respective ports of origin, Cuba and Hispaniola.

In any event, selection for a new size optimum begins with the fact of invasion. Attainment of a size optimum will, however, take time. Some cases, therefore, should exist in which the time since invasion has not been long enough, the size optimum has not been reached, and the first Schoener rule is apparently violated.

Problem Cases Under the First Schoener Rule:
Solitary Species That Are Too Large

We have admitted a considerable range for solitary species. The largest species, indeed, may in snout-vent length be almost one-and-one-half times the smaller, or in head length 1.3 times the smaller. Most solitary anoles do in fact fall in the range 65 to 80 mm in body length. Two populations fall 11 and 15 mm respectively beyond this, *luciae* with a maximum body length of 91, *oculatus montanus* with a maximum of 95 mm. As Table 1 shows, *montanus* is only one exceptional population within a species which otherwise falls near the center of the size range of solitary anoles. I have no ready explanation for the size of *luciae* or *montanus*. It would be facile but no real explanation to ascribe the size discrepancy of the aberrant population of *oculatus* to the fact that it is montane. We must apparently acknowledge the existence of unknown accessory factors that spread out the size range that is adaptive for solitary species.

However, two other populations have body size maxima 24 and 33 mm respectively beyond the extremes already set by *luciae* and *montanus*. To admit these as falling under the first Schoener rule would seem destructive of the rule itself. I propose that both in fact have only recently become solitary.

Recall that we have not regarded the size of solitary anoles as primitive but as something evolved. If, therefore, a species not of solitary size either has arrived on a land mass that has no congeners or if its competing congeners have, for whatever reason, gone extinct, that species will be under selection to become of solitary size. Evolution, however, takes time and, if the present time transect finds the newly arrived or newly solitary species in the initial stages of its evolution, it will not yet have undergone evolution. It will still be of nonsolitary size.

The explanation that it is newly arrived seems the plausible explanation for the size of *Anolis richardi*, solitary on Tobago. This population has a maximum head length of 32 mm and a maximum snout-vent length of 128 mm.[2] These measurements are far out of line with the ranges of 20 to 23 mm for head length and 74 to 91 for snout-vent length found in other solitary anoles of the *roquet* group. However, *A. richardi* on Tobago is judged by taxonomists to be subspecifically identical with a population on Grenada that is a member of a species pair. As Table 2 indicates, *richardi* on Tobago is comparable in size with

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[2] Lazell (1971) reports a male with a snout-vent length of 140 mm. This exceeds all known dimensions for the larger of a species pair. I must admit again that I have no ready explanation for this.

Table 2. Male and Female Maxima for Solitary and
Paired Populations of Anolis richardi

	♂	N	♀	N
Tobago (solitary)	32 – 128	(42)	21 – 80	(20)
Grenada (paired with *aeneus*)	28 – 108	(49)	19 – 73	(25)
St. Vincent (paired with *trinitatis*)	34 – 122	(38)	23 – 84	(27)
Bequia (paired with *aeneus*)	31 – 108	(30)	20 – 71	(9)
Carriacou (paired with *aeneus*)	31 – 120	(13)	19 – 71	(5)

those populations of *richardi* which are members of a species pair. If we may infer that *A. richardi* evolved its size as a member of a species pair and has only recently colonized Tobago, no anomaly exists. Much other data fit this hypothesis. Gorman and Atkins (1969) have shown that the direction of colonization for the *roquet* group in this part of its range has been *from* north to south. *Anolis richardi*, according to this, came from Grenada to Tobago. Since the Tobago population does not differ in squamation, color, or in the electrophoretic properties of those of its proteins which have been tested from the Grenada population, we may safely say that it appears to have undergone very little evolution in situ. We may then reasonably infer that the Tobago population has not had time to evolve to the solitary optimum and find in this an adequate explanation of its failure to conform to the Schoener rule.

It is worth noticing (Table 3) that *A. aeneus*, one of the smaller species pairs with *A. richardi*, does occur alone on some of the Grenadines and in these cases keeps the same size that it has on Grenada. Again, the historical explanation seems adequate: the solitary populations of *aeneus* in the Grenadines have not been isolated long enough.

In the Guadeloupean microarchipelago, on Guadeloupe itself, and on Desirade and Les Saintes, there is a series of populations differing strikingly in color and also in some scale characters. All these populations (maximal snout-vent lengths 71 to 80 mm) conform to the first Schoener rule for the size of solitary anoles. Off the Guadeloupe bank to the southwest is the island of Marie Galante. The only species collected there by recent expeditions—*A. ferreus*—has a size, like that of Tobago *richardi*, corresponding to that of the larger of a species pair (Fig. 4) and very unlike the related adjacent populations. Schoener (1969c) and Williams (1969) have commented on this problem. Schoener (1969c) suggests

Table 3. Maximal Size of *Anolis aeneus* on the Grenada Bank

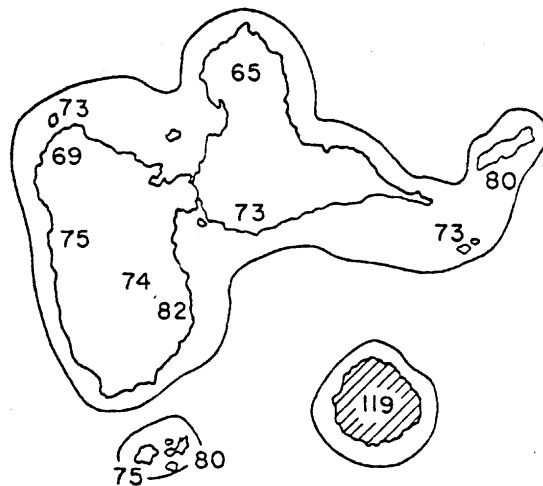| Paired with *richardi*	Head Length	Snout-Vent Length	N
Grenada	19♂/14♀	71♂/51♀	49♂/19♀
Bequia	18/13	68/49	36/3
Carriacou	18/13	70/48	29/12
Solitary			
Mayreau	17♂/13♀	65♂/48♀	22♂/7 ♀
Petite Martinique	17/12	61/45	24/12
Petite St. Vincent	19/13	70/48	9/4
Union	18/13	69/50	13/8

Fig. 4. The Guadeloupean microarchipelago. Numbers are maximum adult male size in each of the named populations. (Data corrected according to Lazell, 1971.)

several hypotheses but characterizes as "*ad hoc*" and "unfalsifiable" the hypothesis favored by Williams (1969) of the former presence of a second species on the island.

Clearly, if the second species is not now present (and there is no current evidence that it is) the idea of its former presence may seem merely an *ad hoc* escape from a conclusion damaging to the hypothesis. But the belief that all ecological conditions must be explained by present conditions *only* is itself fallacious, and historical explanations cannot safely be disregarded out of hand. The postulation of a second species is not literally unfalsifiable: it could be

demonstrated by fossils or by old collections. In the present case, the hypothesis might be reinforced by evidence on vegetational history: Marie Galante is an arid island; was it always so, or has climatic deterioration eliminated the wet-adapted of two species?

One fact about Marie Galante may speak against the hypothesis of a second species: Marie Galante is on its own bank, and Williams (1969) has postulated that two species have been established in the Lesser Antilles only on emerging complex banks that permit both species to have a secure foothold before coming into contact and competition. However, Williams (1969) has also suggested that even failed invasions might leave their mark upon a resident species. (Schoener, 1969c has suggested for *ferreus* an explanation which might apply as a reason for the failure of *ferreus* to return to solitary anole size after extinction of the putative second species: "It may be just as advantageous for species to have females at the size normal for males, which they are in *richardi* or *ferreus*, or at least not feasible to move them off on adaptive peaks in favor of males.")

A still unresolved question is crucial to the second species hypothesis. The second species would on the grounds of proximity have to be a member of the *marmoratus* complex, while *ferreus* on Marie Galante, clearly related to that complex, must be supposed to have reached species status. If *ferreus* were not a full species, competition would not "nudge" it (Williams, 1969) into larger size. Instead, gene flow should reduce any trend to large size. Lazell (1964), the last reviser of the *marmoratus* complex, is vehement that *ferreus* is merely a subspecies of *marmoratus* and in fact he sees it as a participant in a size cline with adjacent island populations. The cline is less obvious on its face than Lazell makes out, but the issue is not easily settled. In such a case, biochemical taxonomy may very well assist: if *ferreus* is a species, it may plausibly differ from the other members of the *marmoratus* complex when studied by electrophoretic analysis of proteins.

The Marie Galante anole is on any hypothesis a special case; there are no genuine parallels. It is on its own bank and thus ought to have the characteristics of a solitary anole; however, its bank is special in that it is very close (almost uniquely close) to another larger bank. Compare, however, the similar proximity of the St. Vincent and Grenadan banks which (Williams, 1969) is involved in the major evolutionary events in the *roquet* group (Gorman and Atkins, 1969). It is tempting to seek the explanation of the one special feature in the other: the distance may be just far enough to have permitted *ferreus* to reach species status and just close enough to permit a high frequency of failed invasions. (Baskin and Williams [1966] have suggested similar "threshold" invasions as the explanation of the striking difference in neighboring island *Ameiva*.)

Schoener's Second Rule: Coadjustment of Species Pairs

Schoener's second rule predicts that, if two anole species occur on an island, one will be smaller and the other larger, the ratio of the two sizes ranging from
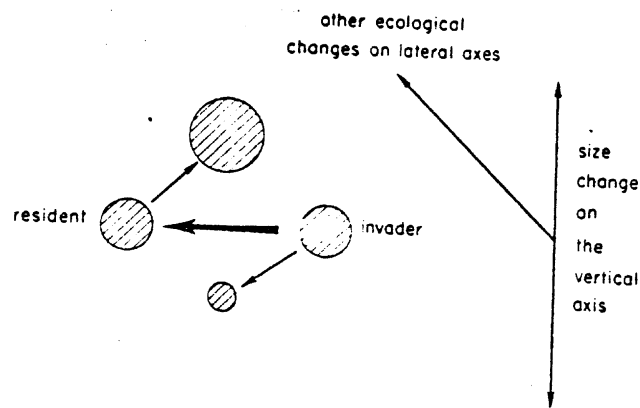
Fig. 5. Diagram of the possible effect on a resident solitary anole of an invader of the same size.

1.5 to 2. A simple model of classical character displacement provides a mechanism for this result: assume the invasion of the domain of a solitary anole by successful propagules of another solitary anole. The two are initially *ex hypothese* similar in size (Fig. 5). They compete for food and other resources. The classic expectation is divergence (character displacement) in order to avoid or lessen the effects of competition. Among the possible kinds of divergence will be size divergence, which has been shown to correlate with utilization of different sizes of food (Schoener and Gorman, 1968). Other modes of divergence are, of course, possible, but as a simplifying assumption we will *at first* ignore these. Our model and our prediction then is that, as a result of interspecies competition, one species will become larger and the other smaller.

No prediction is made in this model regarding the magnitude of size change. The striking empirical discovery of the Schoener rule for Lesser Antillean anoles is the extent of size difference.[3] In all cases in which two species are truly syntopic, i.e., both found widely dispersed and intermixed all over an island, the species differ in size by an impressive factor. Physically adjacent species in complex anole faunas may differ by much less or may not differ at all.

In most cases—taking mean solitary anole size as the initial size—both members of a species pair have changed size. As in the case of solitary anole size, there appears to be a phyletic factor in size change (Table 4).

[3]The size differences found by Schoener for *Anolis* are impressively greater than those found empirically for birds, as Schoener has himself commented. There is, however, an obvious difference in life history between birds, which characteristically exercise parental care of their young and lead or actively feed them, and reptiles, in which their young may be active competitors. All the discussion in this paper is in terms of adult sizes. In order genuinely understand the competitive significance of size for *Anolis* and other reptiles, we should know sizes and their food from hatchlings to old adults. No data adequate to this issue exist.

Table 4. Divergence from Average Solitary *Anolis* Species Size in Two-Species Islands (Figures Rounded; Males Only. Unpublished Data from Schoener.)

Head Length

1. *bimaculatus* group (average solitary size ca. 22 mm head length)

	Larger	Smaller	Larger/Smaller
Anguilla bank	-1,-2,-2	-8,-8	1.4, 1.4
St. Kitts bank	+4,+7,+9	-7,-7,-7	1.7, 1.9, 2.1
Antigua bank	+9,+11	-6,-6,-6	1.9, 2, 1

2. *roquet* group (average solitary size ca. 21 mm head length)

	Larger	Smaller	Larger/Smaller
St. Vincent	+13	-3	1.9
Grenada bank	+7,+10	-3,-3	1.6, 1.7

Snout-Vent Length

1. *bimaculatus* group (average solitary size ca. 71 mm snout-vent Length)

	Larger	Smaller	Larger/Smaller
Anguilla bank	-3,-6,-7	-25,-24	1.4, 1.4
St. Kitts bank	+17,+31,+35	-20,-22,-22	1.8, 2, 2.1
Antigua bank	+31,+42	-17,-19	1.8, 2.2

2. *roquet* group (average solitary size is 81 mm snout-vent length)

	Larger	Smaller	Larger/Smaller
St. Vincent	+41	-10	1.7
Grenada bank	+27,+39	-10,-11	1.5, 1.7

In the *bimaculatus* species group in the northern Lesser Antilles, the smaller of the species pair diverges from solitary size substantially and rather uniformly, the larger to a variable degree, on one bank to an extreme degree, on another variably. In one case (*wattsi-gingivinus* on the Anguilla bank), there is no departure by larger species from solitary size. This is a special case, to be discussed below as a problem.

In the southern Lesser Antilles, the very distinct *roquet* species group (Underwood, 1959; Gorman and Atkins, 1969) has its smaller species relatively little reduced from solitary anole size (there is near overlap with the lower range of solitary species of *roquet* or *bimaculatus* groups) and the larger is much larger in absolute terms (always more than 50% greater than solitary size).

One other fact is of importance: Schoener and Gorman (1968) have shown

that on Grenada, in addition to substantial size divergence between the two syntopic species, there is real if less striking difference in thermal habitat and hence physiological adaptation. There is anecdotal evidence for similar climatic difference (or difference in climatic range) between other pairs of Lesser Antillean anoles. Thus, *wattsi* on St. Kitts and on Barbuda is known to include in its habitat darker areas than any utilized by *bimaculatus* on St. Kitts or *leachii* on Barbuda.

This is a noteworthy phenomenon: though the Lesser Antillean data demonstrate in two distinct phyletic groups that one of the first adjustments between syntopic anoles is size divergence (and substantial size divergence at that), probably in all cases there is divergence also in another parameter. Thus, if we view size divergence as movement on a vertical scale to avoid competitive collision, there is apparently always movement also sideways in another ecological dimension. Clearly, to fully fit our model to the Lesser Antillean facts, we must amend it to include the possibility (in fact, high probability) of ecological adaptations in factors other than size. Nevertheless, we shall as a matter of method always look *first* for size change as the adaptive reply to interspecies competition—finding something of an empirical justification in the striking extent of size change in the adaptive shift from Lesser Antillean solitary species to Lesser Antillean species pairs.

A Problem Case Under the Second Schoener Rule: A Member of a Species Pair That Is Too Small

Anolis gingivinus of the Anguilla bank, as already mentioned, has the size of a solitary anole, although a second species, *A. wattsi*, occurs on the same bank. On St. Martin, *A. gingivinus* males have a maximum head length of 22 mm and a maximum snout-vent length of 68 mm. They are, in fact, at the lower end of the range of size for solitary species. *A. wattsi* on the same island is indeed smaller (the same maxima, 14 and 47 mm, respectively) and hence there is not in a strict sense a violation of the Schoener rule. However, the ratio between larger and smaller species is the lowest (1.5) in any Lesser Antillean species pair and *wattsi* is as large on St. Martin as on the St. Kitts or the Antigua banks. There should be some special aspect of the relations of the two species on the Anguilla bank that explains the anomalous ratio.

Anolis wattsi, which on the other banks on which it occurs is widely syntopic with a larger species, is on St. Martin strikingly localized. *Anolis gingivinus*, like the larger species of the other banks, is widespread over all the island, but *A. wattsi* is restricted to certain ravines (Lazell, Ruibal, personal communications). In fact, the restriction of *A. wattsi* on St. Martin corresponds to its general tendency on other islands (see above) to occur most frequently and abundantly in damper and shadier places than the larger species, whichever that may be. But the restriction on St. Martin is severer, more complete, such that *wattsi* does not occur outside the damper, shadier places. It is impressive for our

argument that though this special sort of overlap implies minimal size change, there is still size change. *Anolis wattsi* is a derivative of *A. acutus*, solitary and of solitary size on St. Croix; the most impressive change externally in *wattsi* is size.

From the Lesser Antilles to Large Complex Islands: The Model Stated

According to the hypothesis here set forward, the size ratios seen on the two-species islands of the Lesser Antilles give us the correct image of the magnitude and nature of the size differences that evolved between the first two species of any of the Greater Antilles.

Again, the thermal difference so clearly demonstrated on Grenada by Schoener and Gorman is a model of sorts of alternative differences to be expected in the two species stage of the colonization of the Greater Antilles.

The two-species stage on the Greater Antilles is long past. The Lesser Antillean story is the only clue we have to it. Contrariwise, the one-, two-, three-, or four-species islands that we see among the Caribbean satellites to the Greater Antilles (cf. Williams, 1969) do not provide any comparably useful model of these earliest stages in the evolution of the fauna of the large islands. *All* these satellite islands have animals that are too recently arrived and too little evolved since their arrival to provide any light on the radiation within the large islands.

We must begin then with the Lesser Antillean model. We can, as a thought experiment, add to a fauna (coadapted as in the Lesser Antilles) various sizes of new colonizers (Fig. 6).

Thus (1) if we add a new anole of appropriately solitary size, it will be intermediate between the two resident species. The easiest adjustment would seem to be change in size of one or both resident species—a spread of extremes. (We assume, according to the Lesser Antillean model of the species pair, that after evolution of size adaptation, the largest of the series of three will be about twice the size of the invader and the smallest about half its size; i.e., that syntopic species adjacent in size will, whenever possible, differ in size by a ratio of 2 to 1.) Note that in the simplified competitive scheme that we have set up the invader will *not* change size. If it were to do so, it could only come closer in size to one or the other of the two resident species.

(2) If we postulate a single invader as large as the larger of the pair (and we allow only size change), we again expect a spread of extremes. The amount of change and whether one or all will change will depend upon the genetic potentialities of each. An essentially similar result is expected if the invader is as small as the smaller of the resident pair.

(3) We will expect no size change—all other things being equal—only if the single newly arrived species is sufficiently larger or sufficiently smaller than the resident species to avoid or relieve competition on that ground alone. Such size disparity is to be expected in the colonizer only if it comes from a complex fauna where alone extreme sizes, according to our hypothesis, will have evolved.

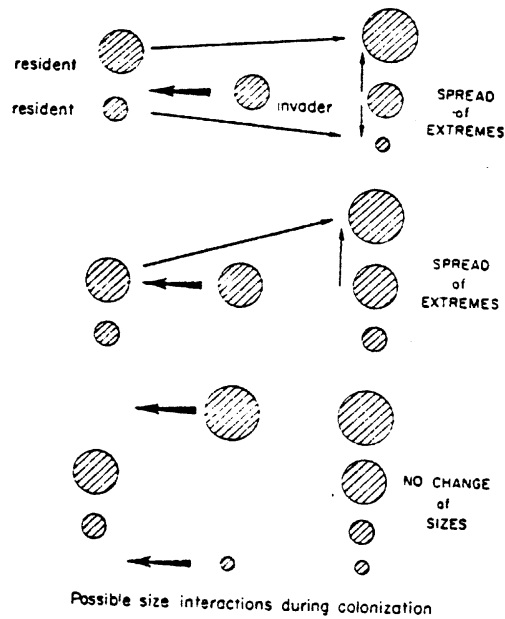In any event, with three species present we expect a graded series of

Possible size interactions during colonization

Fig. 6. Possible size interactions during colonization of a two-anole island by invaders of various sizes.

sizes—large, middle, and small—such that they are far enough apart in physical dimensions to be noncompetitors. I emphasize again that as a first hypothesis we assume the size ratio seen in two species islands of the Lesser Antilles to apply to adjacent species in multispecies series.

We are ignoring here, again deliberately, some real possibilities of size convergence (Schoener, 1970). We may be compelled to invoke size convergence or at least limitation of size divergence later under special conditions of resource distribution. We set this aside here as not a *first* expectation.

If now, following our simplified model, we add still another species, we see that again unless it fits at the extremes it will compete in size with some resident and indeed the more the size series is spread, the more difficult will it be for a new invader to avoid competition by change of its own size. Again we expect size change only at the extremes.

THE MODEL TESTED

The First Test: A General View of Size in the Greater Antilles: The Model Elaborated

To test and amplify these hypotheses, we have only to look at the largest and smallest species on each of the four Greater Antilles Table 5. The extremes are indeed further apart the larger the fauna. This we have in fact defined as the third Schoener rule.

Table 5.

Island	Faunal Size	Males of Largest Species	Males of Smallest Species	Size Spread
Cuba	28 species	191[a]	38	-153
Hispaniola	23 species	175	38	-137
Puerto Rico	11 species	137	40	- 97
Jamaica	7 species	124	57	- 74

[a]Data not from Schoener but from Schwartz and Garrido (1971). Dealing with much larger samples than those available to Schoener, they divide the *equestris* complex into five species, the maxima of which are 191, 190, 188, and 172.

But note that some constraint seems to exist at the lower end of the scale: on Cuba the smallest species is not significantly smaller than the smallest on Hispaniola or Puerto Rico. Only on Jamaica is there a difference. Here the smallest species is 17 mm larger, thus appearing to imply that the pressure toward small size is not as great as on the larger, faunally richer islands.

Apparently, however, there is some floor at ca. 38 to 40 mm male snout-vent length; below this size, change is not possible to an anole: no pressure of adjacent species can push the smallest species further. Note also that size change *upward* does not have a simple and direct relation to the number of species; it is slowed in the larger islands.

What, then, are the factors that provide upper and lower limits to size change?

Obviously one upper limit is provided in energetic terms by available food resources. We find, therefore, that giants tend to be allopatric (the "races" of *A. ricordii* or species of *A. equestris*). In addition, Schoener has provided evidence that giant anoles may extensively supplement their insect diet with fruits. It is reasonable to suspect that this may be a general phenomenon. Note, however, that the *equestris* complex on Cuba is larger than any anolines on any part of North, Central, or South America. Clearly, on the mainlands constraints on large anoline size are greater than on the islands. Presumably, mainland anoles are affected by the competition of other arboreal forms such as other lizards but probably also birds and mammals. (Some birds compete with anoles in the West Indies, but critical groups present on the mainland are absent.)

Lower limits—which seem in anoles to be even more rigid than the upper limits and are *the same on the mainland and the islands*—are perhaps provided by competition with insects and by vulnerability to insect and other arthropod predation.

In any event, such constraints apart, we expect and find the spread of extremes. But on the Greater Antillean islands, the spread of extremes does not keep pace with the size of the fauna. The initial distance as exemplified on two species islands in the Lesser Antilles was considerable: the larger species might be half again the size of the smaller. Clearly, between adjacent middle sized species

in large faunas, this distance has been severely compressed and, if we look at actual faunal sizes on each of the Greater Antilles, we find much duplication of middle sizes.

We should expect this on our model. The extremes clearly have a free direction in which to move. The middle, however, is always crowded (Fig. 7). An animal at the middle cannot readily adapt in size. It cannot easily grow larger because a range of upper sizes is already preempted; it cannot grow smaller because a range of smaller sizes is already preempted. For it, adaptation (coadjustment) must involve another ecological dimension.

the
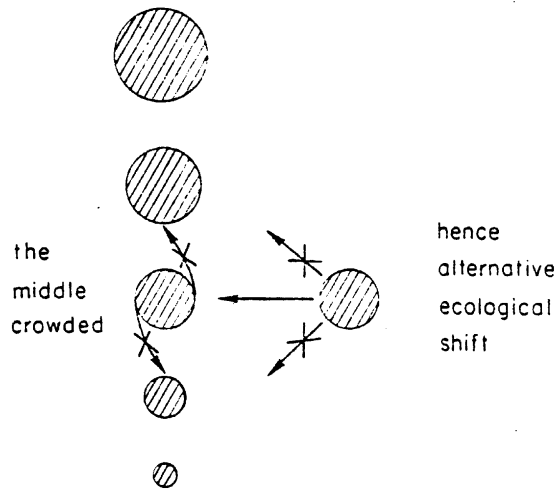middle
crowded

hence
alternative
ecological
shift

Fig. 7. The "crowded middle" in the later stages of colonization or radiation.

In fact, we have already seen on two species islands of the Lesser Antilles that even two species do coadjust in other regards than size. They move apart on other ecological dimensions as well—in the analyzed case in a microclimatic dimension.

We emphasize then again the two phenomena—vertical movement on the size scale with spread of extremes and sidewise movement on other ecological dimensions.

If we look at the vertical movement on the size axis, we see that this is freest for extreme species. Until there are other constraints, these species need not move sidewise: the larger may become larger and the smaller smaller. If this be true, the largest and the smallest species should have retained their original microhabitat. They will be syntopic because their adjustment has been in absolute size.

This is not true at all, however, for the middle-sized species. The crowded middle requires that these species must move apart in some ecological dimension

other than size. We must expect these species of intermediate size, then, to be ecologically very diverse; we may also expect some of these species to be allotopic or allopatric.

Let us now test these hypotheses against an actual fauna.

Puerto Rico: The Test By Reconstruction of History

On the basis of the model just constructed, it should be possible to set up a series of sequential steps which lead to a fauna of any desired complexity—5, 10, 20, 25. But how shall we test these presumptive patterns? They are historical patterns not directly verifiable. Obviously we can test our model and the patterns it generates only if we have some solid independent ground for inferring the sequence of events in faunal history, some island fauna for which we are confident that we know phyletic relationships, know which species are primitive and which derived, know in fact the total sequence.

Very fortunately the Puerto Rican anole fauna is known and understood to the desired degree. No other of the Greater Antilles fits the stringent requirements of the test. Jamaica, with seven species, all the result of a single radiation, might rival Puerto Rico, but the sequence of phyletic branching among the endemic species is so unclear that several phylogenies might be proposed with no grounds for choice among them. In Cuba and Hispaniola, there are still a number of species incompletely known and probably also species still to be discovered. Their faunas also are mixtures of more than one phyletic group and involve endemic radiations complicated by one or several later invasions. Certainly we can only hesitantly speak of the phyletic sequences in either of these islands.

Even for the Puerto Rican bank (Fig. 8) there is still one species which is very poorly known. Ten species are ecologically well studied on the mainland of Puerto Rico (Fig. 9): *A. cuvieri*, a giant anole; *A. occultus*, a dwarf; *A. evermanni*, a green tree anole; *A. stratulus*, a grey-brown smaller tree anole; *A. gundlachi*, *A. cristatellus*, *A. cooki*, brown or grey anoles of the lower tree
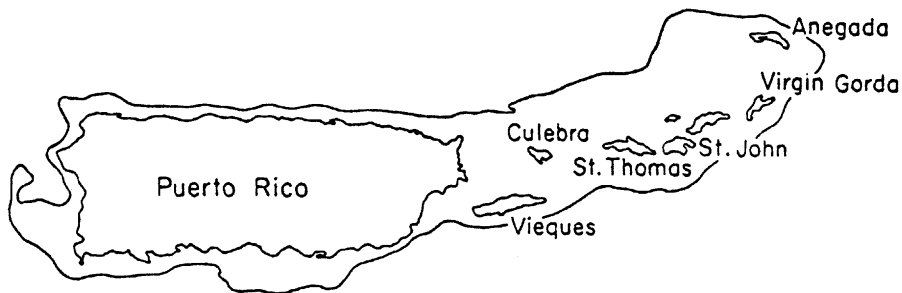

Fig. 8. The Puerto Rican bank, showing the Puerto Rican mainland and the smaller Virgin Islands to the east.
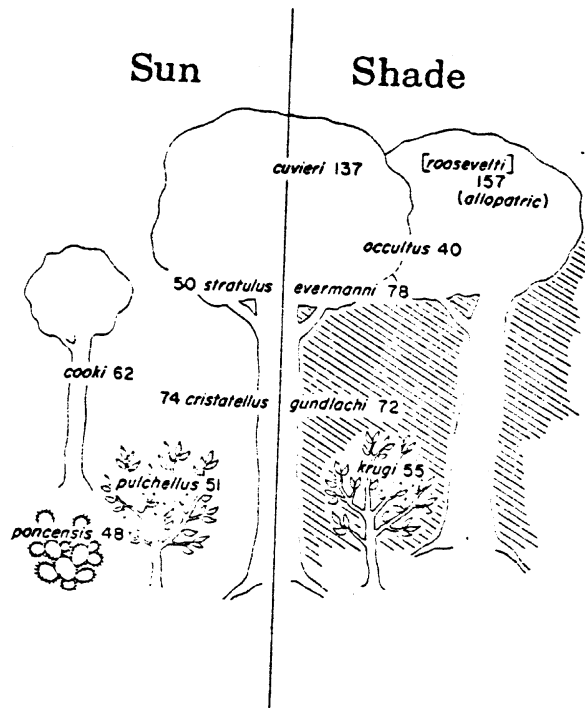
Fig. 9. The 10 Anolis of the mainland of Puerto Rico placed diagrammatically according to their spatial and climatic niches. Number is maximum male size. In brackets is an eleventh species, A. roosevelti, isolated on the small island of Culebra (see Fig. 8).

trunk; and *A. krugi, A. pulchellus* and *A. poncensis*, striped anoles of bushes and grasses. These can be discussed with confidence. However, on the small island of Culebra to the east, an eleventh species is known from two specimens: *Anolis roosevelti*. It may now be extinct. Fortunately its relationships and phyletic position are clear (it is a giant, related to but more primitive than the common giant species of Puerto Rico—*A. cuvieri*) and, though nothing is directly known of its ecology, much may be inferred from its structure, so very similar to *A. cuvieri*. The incompleteness of our knowledge is in this instance minimally inconvenient. (See further below.)

Before going on, let us establish unmistakably that we have all the information needed to determine and verify the historical sequence of ecological change in the Puerto Rican anole fauna that we are attempting to reconstruct. For our purpose we need:

(1) *Detailed information on the ecology of the Recent species.* This we have for Puerto Rico from Rand (1964), Schoener and Schoener (1971b) and Webster (1969) as well as unpublished notes on *Anolis cooki* by Webster.

(2) *A clue to the ecology primitive for the group.* We can infer this from the

basic adaptations of the genus. The adhesive toe lamellae which define the genus are devices for arboreal life high in the trees on leaves and branches. *Anolis* came to the islands from the complex faunas of the mainlands; it was there primarily and primitively an animal adapted to the tree crown. Of the modern niches on Puerto Rico, therefore, the crown niche should be most like (but not identical to) the niche of the anole that first invaded Puerto Rico.

(3) *A clue to the first stages of complexity.* At a minimum we must know the two species stages and the rules for transformation from the one species stage. We have this, of course, in the Lesser Antilles in Schoener's rule 2. It would help, no doubt, if we had direct empirical evidence on stages of three or four species, but in *Anolis*, as I have pointed out above, we have no such stages, evolved *in situ*, available to us. Our model is the device by which we bridge this gap in our evidence.

(4) *A test of the temporal sequence in ecology that we are endeavoring to set up.* The usual test will be phylogeny. It would be best were there a fossil sequence that would really give us in successive layers and ages the sequence of sizes that did occur. But no such sequence is known for *Anolis* in Puerto Rico—or anywhere. We must operate, therefore, in the customary way by inference from the morphology of Recent species. Fortunately, in Puerto Rico the morphological evidence seems unusually solid and unambiguous. As we shall see below, there are few loose ends. For Puerto Rican anoles we can construct an exceptionally believable phylogeny.

Figure 10 constructs this phylogeny in terms of the evidence provided by the investigations of Etheridge (1960, 1965) on osteology, of Gorman and Atkins (1969) on karyotypes, and of Maldonado and Ortiz (1966) on electrophoretic patterns. This evidence is discussed in some detail below.

However, Fig. 10, like most dendrograms, does not carry on its face all the information that is needed to justify or even to construct such a phyletic diagram. In addition to the specific features cited above and labeled in Fig. 10, there are two sorts of background information utilized that are always implicit for the specialist who makes and is competent to make such a phyletic diagram:

(1) *Narrow relationships.* Always in a phyletic study some species appear on the totality of obvious external characters and on habitus and often on geographic proximity to be so closely similar, that any more elusive character—skeletal, chromosomal, biochemical, or behavioral—that contradicts that relationship is itself put in question. We deal in such cases with species pairs and species series, in which the problem is *not* a problem of establishing affinity but may involve, instead, a problem of finding valid differential characters.

In Puerto Rico the narrow relationships of the anoles are easy to recognize. To the experienced eye and especially in life, all Puerto Rican anoles are readily distinguishable by conventional external characters: dewlap and body color, scale size, etc., but despite the differences, species pairs and series are obvious: *A. cristatellus* and *A. cooki* are such an obvious pair and have in the past been
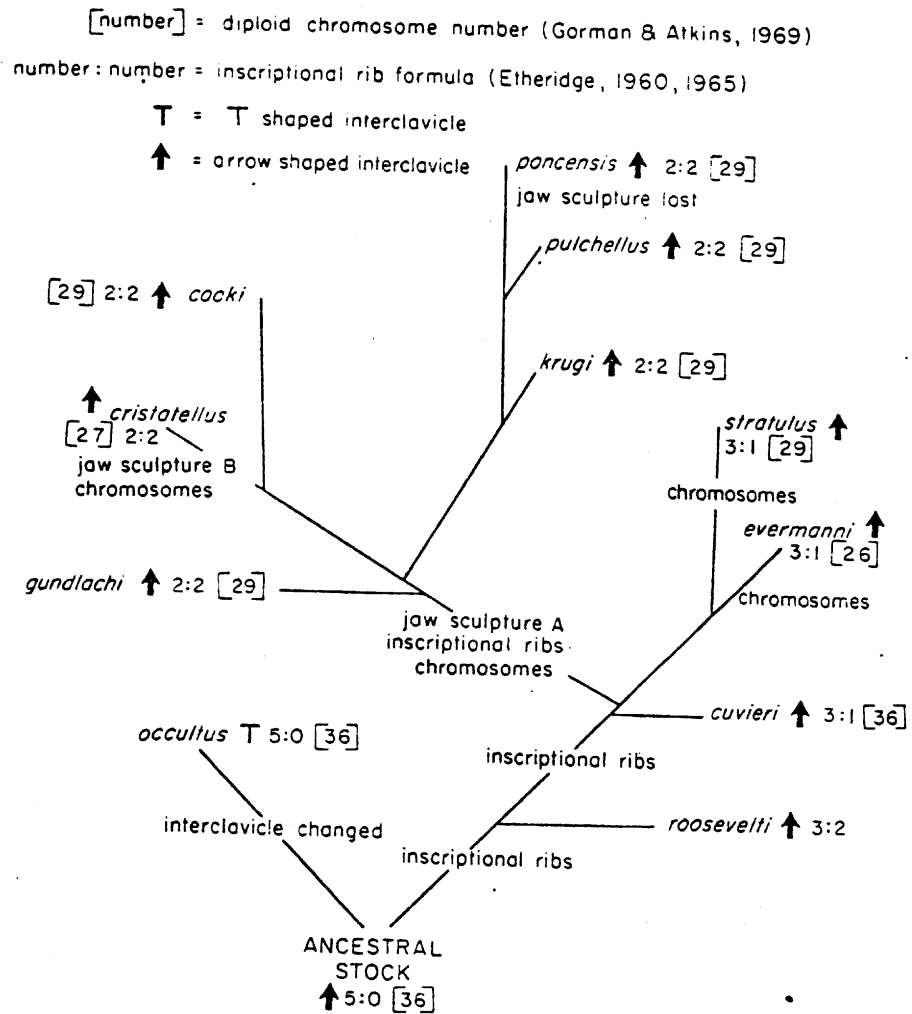
[number] = diploid chromosome number (Gorman & Atkins, 1969)

number : number = inscriptional rib formula (Etheridge, 1960, 1965)

T = T shaped interclavicle

↑ = arrow shaped interclavicle

poncensis ↑ 2:2 [29]
jaw sculpture lost

pulchellus ↑ 2:2 [29]

[29] 2:2 ↑ *cocki*

krugi ↑ 2:2 [29]

↑ *cristatellus*
[27] 2:2
jaw sculpture B
chromosomes

stratulus ↑
3:1 [29]
chromosomes

evermanni ↑
3:1 [26]
chromosomes

gundlachi ↑ 2:2 [29]

jaw sculpture A
inscriptional ribs
chromosomes

cuvieri ↑ 3:1 [36]

occultus T 5:0 [36]

inscriptional ribs

interclavicle changed

inscriptional ribs

roosevelti ↑ 3:2

ANCESTRAL
STOCK
↑ 5:0 [36]

Fig. 10. A dendrogram for Puerto Rican Anolis *indicating the points at which chromosomes and skeletal morphology change.*

confused; *A. gundlachi* is similar to them in habitus, including tail crest, but quite distinct in body color and especially scale size. *A. cuvieri* and *A. roosevelti* are as clearly similar to each other in their middorsal and tail crests but they differ in color and in smaller details. *A. evermanni* and *stratulus* are not so obviously paired, differing strikingly in color. They are united as much by the absence of the scale specializations of the other series as by any positive feature. *A. krugi*, *A. pulchellus*, and *A. poncensis* form an obvious series, similar in habitus but differing sharply in scale size and dewlap color.

Many of the characters ("character states") that unite such species pairs and series reflect direct ecological adaptations to the environment in which they live. Thus, *poncensis, pulchellus,* and *krugi* are strikingly similar in their relatively slender body habitus and in the dorsolateral light lines that further emphasize their slenderness. Both features are directly adaptive (cryptic) in the grass-bush habitat of these three species. It would seem reasonable to suspect circularity in any phylogenetic hypothesis that uses groups partly defined on ecological grounds in such a test as we propose of the *origin* of ecological adaptations. But such ecological adaptations by themselves neither affirm nor deny phyletic relationships. Clearly the unity and validity of groups partly recognized on directly adaptive features needs to be confirmed by independent evidence, i.e., the evidence of characters *not* directly adaptive. However, ecological adaptations may be those of a common ancestor or they may have been separately acquired by diverse phyletic lines. If, however, the independent evidence—karyotypic, biochemical, osteological—is congruent with the hypothesis of common ancestry, there will be no ground for discarding groups partly ecological in nature from our test phylogeny. What we will seek in the phyletic parallel to our ecological diagram is a *sequence* of morphological adaptation to be compared with a *sequence* of ecological adaptations, and a sequence is given by the connections *between* "narrow" groups not by the groups themselves.

How do we connect these narrow groups with one another? Clearly again by similarity. Of any species pair or series, one member is closer to other species in the relevant complex. Here ecological adaptations are no longer involved; we deal strictly with characters that transgress at least minor ecological boundaries: we here use evidence such as that labeled in Fig. 10, not in despite of "narrow relationship" but as a complement to it. We use karyotypic, biochemical, or osteological evidence for whatever leads they provide. Thus, no habitus or ecological features make obvious a particularly close relationship between *gundlachi* and the *poncensis-pulchellus-krugi* series; however, the electrophoretic evidence of Maldonado and Ortiz insists on this relationship. Chromosomal evidence (Gorman, Thomas, and Atkins) again shows a closer resemblance of *gundlachi* with the grass-bush series than with *cristatellus*, which in habitus and habits would seem a closer relative. Similarly, jaw sculpture suggests that the grass-bush series may form a larger unit with *cristatellus, gundlachi,* and *cooki,* and even with *Anolis cybotes* on the adjacent island of Hispaniola.

(2) *Wider relationships.* Just as the evidence of narrow relationship is not explicit in Fig. 10 and yet was essential to its making, so there is another side of background evidence of as great importance but again not explicit on the diagram itself. Figure 10 was not constructed *in vacuo* on evidence provided by Puerto Rican anoles alone; implicit in it are many stated judgments on the phylogeny of *Anolis,* of iguanids, and of lizards. This is necessarily true. In the present stage of taxonomic biology, it cannot be successfully pretended that any scheme of classification or any phyletic diagram, however restricted in scope, is

independent of the thousands of analyses that have gone before it. We necessarily (and despite pretensions to the contrary) examine all cases in the context of accumulated knowledge. Only from such wider viewpoints can we get clues to primitive character states whether in Puerto Rican anoles or in other groups. Etheridge (1960) assessed the phyletic sequence of skeletal features *within Anolis* on the basis of a careful consideration of the interrelationships of all iguanids (and for certain features, all lizards). His analysis itself relied heavily upon the prior work of Cope and Boulenger—and of others of lesser competence. Similarly, the judgment central to the discussion below of karyotype evolution, that the karyotype with 12 macrochromosomes and 24 microchromosomes is primitive *within Anolis*, rests upon considerations derived from a review of known iguanid and other lizard karyotypes (Gorman, Atkins, and Holzinger, 1967). Such overviews of the information on one or several higher levels are imperative preconditions for phyletic analysis. In analysis of the Puerto Rican anoles we would have no firm foundation for our phylogeny except that we have such overviews. Direction of evolutionary change is never unequivocally indicated within any narrow group; it only begins to be indicated by the connections between narrow groups and may only be satisfactorily indicated by the *congruence* of trends in a wide-ranging comparison going far beyond the level of the narrow groups.

Let us consider for a moment one character state peculiar to one species—the body scales of *poncensis*. They are larger and more heavily keeled than in any other Puerto Rican anole. Are they primitive, i.e., temporally antecedent to the other compared character states, or derived, i.e. the result of relatively recent divergence? Clearly the condition is at one end of a series of evolutionary stages, but which end? Clearly there is a sequence *poncensis-pulchellus-krugi* in which *krugi* is more similar to other Puerto Rican anoles than are the other grass-bush anoles, but what is the direction of the sequence? There is no answer within the sequence itself. The answer comes from the evidence of inscriptional ribs and of karyotypes, and especially from the *congruence* of these two quite independent kinds of evidence, each of which depends on information not only outside the Puerto Rican radiation but outside the genus *Anolis*. On this evidence, quite outside the *poncensis-pulchellus-krugi* series, there can be no question but that *poncensis* is an extremely specialized animal, the most specialized species of the whole Puerto Rican radiation.

I emphasize that Fig. 10 has built into it as background information much that derives from both the wider and the narrower view. With this understanding, the specific characters most used in the construction of the figure can now be commented upon.

The characters used in the construction of Fig. 10 deserve brief comment:

(1) *Number of inscriptional ribs* (Etheridge, 1960, 1965). "Inscriptional ribs" are the endochondral abdominal skeleton of lizards, and in *Anolis* involve numbers of fixed and floating abdominal "chevrons" that are species- and

species-group-specific. South American *Anolis* of the alpha section, to which all Puerto Rico anoles belong, have high numbers of such chevrons (5 to 6), all of which are fixed. (High numbers are believed to be primitive; see Etheridge, 1960, pp. 110-115). In the West Indies. most species have reduced numbers of chevrons, some of which become free in advanced forms. On the basis of inscriptional ribs, Puerto Rican anoles sort into the following groups, arranged in the order of increasing specialization (data on *A. occultus* [undescribed in 1960] and *A. cooki* [not then recognized as a full species] have not previously been published and derive from Etheridge. in litt.):

I	*A. occultus*	5 to 6 fixed; 0 free
II	*A. roosevelti*	3 fixed; 2 free
III	*A. cuvieri*	
	A. evermanni	3 fixed; 1 free
	A. stratulus	
IV	*A. cristatellus*	
	A. cooki	
	A. gundlachi	2 fixed; 2 free
	A. krugi	
	A. pulchellus	
	A. poncensis	

Anoles on other islands would be included in each of these groupings except I, e.g., *A. ricordii* of Hispaniola in group II, and many species on Hispaniola, Cuba, and Jamaica in group III, fewer on each of the islands in group IV. Occurrence of groups III and IV o Jamaica. all the anoles of which belong to the beta section of Etheridge (1960), demonstrates that groups III and IV have separately evolved in these two sections. Since these groups have evolved twice, they may have evolved independently still other times. It requires other evidence to settle the point.

But the sequence from primitive to specialized seems clear, however many times it may have occurred; and this evidence is of primary importance for the placement of *occultus* and *roosevelti* in the dendrogram of Fig. 10 and puts them clearly at the base of the phyletic tree.

(2) *Interclavicle type* (Etheridge, 1960). All Puerto Rican anoles belong to the alpha section as distinguished by Etheridge (1960, 1965)—the autonomic caudal vertebrae are without or have only very small transverse processes. Within the alpha section, two major subsections differ in the shape of the interclavicle and its relationship to the clavicle. The two kinds of interclavicle have been distinguished as "arrow" and "T"—a convenient phraseology which somewhat exaggerates the actual difference. An "arrow" interclavicle has the lateral arms divergent from the clavicle in their whole extent; a "T" interclavicle has these arms proximally closely applied to the clavicle. The phyletic sequence within the alpha anoles is clearly from "arrow" to "T." Nonanoline iguanids have the arms

of the interclavicle more widely divergent from the clavicle than in any anole, and among anoles most of those which are primitive in regard to inscriptional ribs have arrow-shaped interclavicles.

Within Puerto Rico, only *occultus* has a T-interclavicle. In inscriptional ribs it is quite primitive and it is a plausible hypothesis that the first anoline split within Puerto Rico occurred between the ancestors of *occultus*, which evolved the T-shaped interclavicle, and the ancestors of *roosevelti-cuvieri*, which retained the primitive arrow-interclavicle.

(3) *Jaw sculpture* (Etheridge, 1960). Jaw sculpture occurs only in adult anoles of a few species in Puerto Rico and Hispaniola, and one in Cuba. Etheridge distinguished three types of sculpture, two of which occur in Puerto Rico: (a) the *cristatellus* type (B of Fig. 10): "the outer and lower parts of the dentary are swollen and irreguarly scored with deep horizontal excavations." This is known in *cristatellus* (and the very similar species *scriptus* from the Caicos, Inagua and Mariguana banks west of Puerto Rico).

(b) the *krugi* type (A of Fig. 10): "along the ventral surface of the dentary there is a series of from seven to ten large, deep, semi-lunar excavations." This occurs in *A. krugi, A. gundlachi,* and *A. pulchellus.*

The groupings here are clearly minor ones, but the specific kind of sculpture seen is distinctive enough to be probably monophyletic and hence useful at the species group level. *Anolis cooki*, not distinguished as a species at the time Etheridge wrote, has the *krugi* type jaw sculpture (MCZ 93434).

(4) *Electrophoretic patterns.* A. A. Maldonado and Evelina Ortiz (1966) subjected blood sera from *A. cristatellus, A. gundlachi, A. krugi, A. pulchellus, A. evermanni,* and *A. cuvieri* to electrophoresis. Patterns of mobility and of concentration of four globulins and of albumin were obtained. The most similar patterns were those of *A. pulchellus* and *A. krugi,* and *A. gundlachi* was next in its resemblance to these. *Anolis cristatellus* was distinctive among Puerto Rican anoles in the relatively slower mobility of its third globulin. *A. cuvieri* and *A. evermanni* were distinctive in the higher mobility and greater concentration of the first globulin. These results are readily interpretable in terms of our dendrogram, and, like karyotypes and in contrast to external morphology, indicate a closer relation of *A. gundlachi* to the grass anoles (*A. krugi, A. pulchellus, A. poncensis*) than to *A. cristatellus.*

(5) *Karyotypes* (Gorman and Atkins, 1969). A karyotype with 6 pairs of macrochromosomes and 12 pairs of microchromosomes has been regarded as primitive for lizards generally and specifically for the family Iguanidae (Gorman, Atkins, and Holzinger, 1967). This pattern is retained in only two Puerto Rican anoles but the other rather diverse karyotypes in Puerto Rican anoles may be derived from this most primitive one (Gorman and Atkins, 1969). The karyotypes sort into the following groups:

I   (primitive): *A. occultus, A. cuvieri,* $2N = 36$
II   (advanced): $2N$ reduced from 36:
    a. *stratulus, gundlachi, krugi, pulchellus,*
      poncensis, cooki $2N = 29$
    b. *cristatellus* $2N = 27$
    c. *evermanni* $2N = 26$

Analysis at this level (diploid number only) is, of course, very incomplete and includes in one group karyotypes not closely related.

Further analysis (Gorman and Atkins, 1969) sorts II into 2 series: (a) a *cristatellus* group with a primitive subseries containing *gundlachi, cooki, krugi, pulchellus*, and *poncensis*, and a more advanced subseries including only *cristatellus* on Puerto Rico plus *scriptus* in the Bahamas; (b) an *acutus* group (named after a related species on St. Croix) with only *stratulus* and *evermanni* as Puerto Rican members.

The *cristatellus* series is well defined: all have a sex trivalent $(X_1 X_2 Y)$. The diploid number is therefore odd in males, but *cristatellus* and *scriptus* lack two microchromosomes present in more primitive members of the series (Gorman, Thomas, and Atkins, 1968).

The *cristatellus* group differs from *stratulus* in having 6 macro-, 2 intermediate, and 5 microbivalents and the sex trivalent; whereas *stratulus* has 6 macro-, *one* intermediate, and 6 microbivalents; and the sex trivalent—i.e. the 8th chromosome—is metacentric in the *cristatellus* group, acrocentric in *stratulus. Anolis evermanni* differs from both the *cristatellus* series and *stratulus*. It lacks the sex trivalent but has a heteromorphic pair of sex chromosomes. As in *stratulus* there is a sharp break between 6 macrobivalents and the seventh (intermediate), which is metacentric. The 8th chromosome pair (acrocentric) are the sex chromosomes. There are only 26 chromosomes in both males and females.

Clearly in the advanced Puerto Rican species certain of the original 12 pairs of microchromosomes have undergone fusion to produce intermediate metacentric and sex chromosomes, and there apparently has been loss of chromosomes as well. The intermediate steps are missing in these rather impressive changes, and it is not on the face of the evidence possible to determine at what point the *cristatellus* group branched off relative to *stratulus* and *evermanni*. If, as Etheridge (1960) believes on osteological grounds, *A. cybotes* of Hispaniola is a member of the *cristatellus* series, then, since the karyotype of *cybotes* is primitive (6 pairs of macro-, 12 pairs of microbivalents), the sex trivalent must have evolved twice. The dichotomy between *cristatellus* and *acutus* would have been very early and *evermanni* may have diverged before the sex trivalent evolved in the *acutus* group. Alternatively, if, as Gorman and Atkins believe, the sex trivalent evolved only once, *cybotes* cannot be part of the *cristatellus* series

(see their dendrogram, 1969, p. 77) and *evermanni* may have lost its sex trivalent secondarily.

The important point appears to be that the *cristatellus* series is very much a small radiation on Puerto Rico, compact and clearly delineated, and quite separate now from the *acutus* group, which is relict on Puerto Rico but achieved its own flowering out in the *bimaculatus* and *wattsi* series of the northern Lesser Antilles. Whether the *cristatellus* series branched off *before* the *acutus* series or at some point *from* the *acutus* series cannot now be determined. Figure 10 rather arbitrarily chooses the point of divergence early, following the osteological rather then the karyotypic evidence.

The several kinds of evidence are in very good agreement and the dendrogram can be taken to be a highly probable representation of real relationships.

Compare now Fig. 11, which indicates the ecological and size changes correlated with the phyletic branching. Inspection of this diagram leads to the following comments:

(1) The first dichotomy within the dendrogram involves size change primarily. The two species that are the surviving representatives of that dichotomy in the modern fauna are basically in the same habitat and climatic niche.[4] They both may crudely be described as crown animals of the shaded forest. It is possible to quibble a bit about this but the same modal situation describes both. A giant anole such as *cuvieri*, though it is, in fact, seen some of the time at every level (personal observation), is most often seen high in the crown. A dwarf anole such as *occultus* is seen on branches and twigs of small diameter (Webster, 1969) and therefore not infrequently on bushes and vines, but certainly its modal structural niche includes the crown.

The size ratio between these two species is the most extreme seen within the whole Puerto Rican sequence. It far exceeds the size differential seen on the two-species islands of the Lesser Antilles. We may reasonably doubt that the size differential seen now is the original size differential when these species first coadapted; rather it must represent the "spread of extremes."

The dendrogram of Fig. 10 now appears to require that there be a second dichotomy derived from the *cuvieri-roosevelti* stock and resulting in (1) the *evermanni* sequence (which gave rise to the *bimaculatus* sequence in St. Croix and the Lesser Antilles) and (2) the *gundlachi* sequence (more important in Puerto Rico). However, the apparent implication of Fig. 10 that there was a true dichotomy (appearing to imply simultaneity of origin of the *evermanni* and *gundlachi* stocks) is not necessary in terms of our model.

Our model, based as it is on the primary importance of size, implies that the next step in the sequence would be the addition of only *one* new species. Such an addition would have the result suggested in Fig. 6—a species of middle size

[4]*A. occultus* and *A. cuvieri; roosevelti* is here ignored since it is an isolated relict not syntopic with *occultus*. See below.
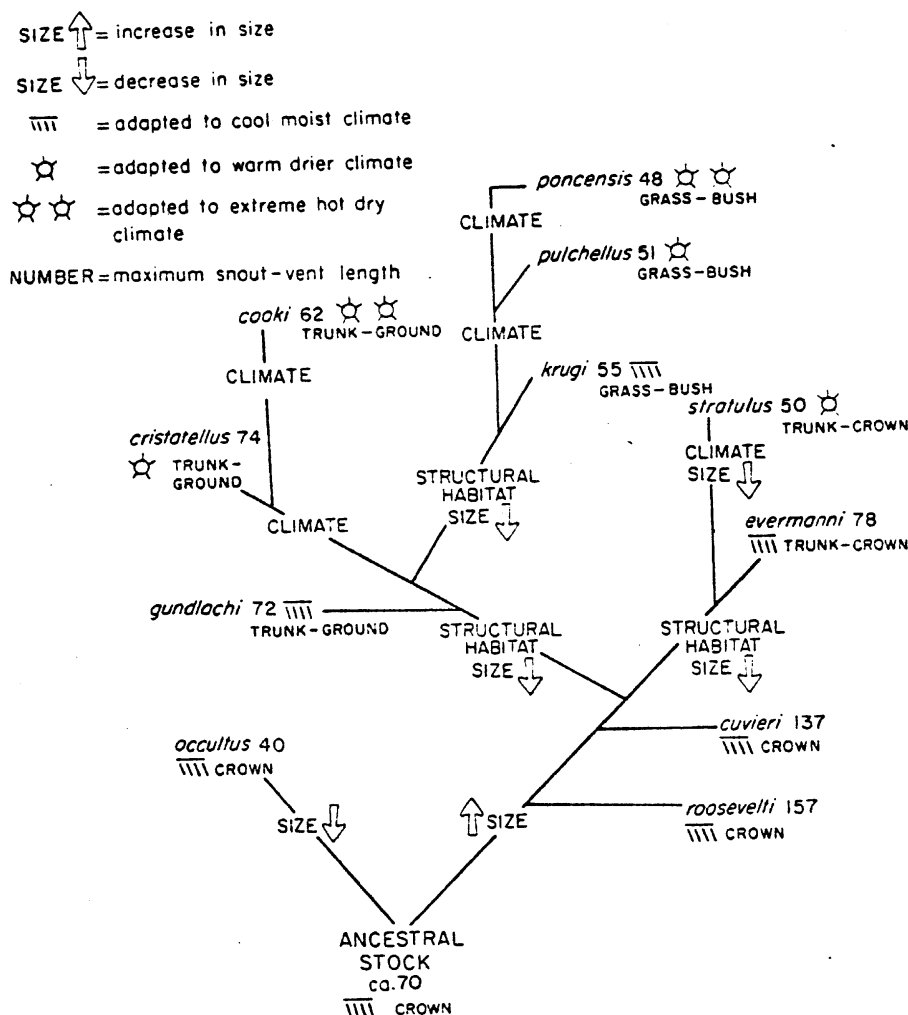
Fig. 11. A dendrogram for Puerto Rican Anolis showing the points at which size or other ecological change have occurred.

inserting between two already divergent species, which thus become more extreme in size ("spread of extremes").

Anolis evermanni fits our expectation for this third species. It is intermediate in size between *cuvieri* and *occultus* and it is again basically a crown animal of the shaded forest. When now we examine the size ratios of these three crown species, we find that the size ratios between adjacent species (i.e., those most similar in size) are quite within the range of the ratios of the anoles of two species islands in the Lesser Antilles:

cuvieri	137	
ratio *cuvieri:evermanni*		1.8
evermanni	78	
ratio *evermanni:occultus*		1.95
occultus	40	

Let us at once admit that *evermanni* as the third species was not at its first origin ecologically equivalent to *evermanni* in the modern fauna any more than the giant and dwarf were at the time of their dichotomy identical to modern *cuvieri* and *occultus*. In size *evermanni* may have been essentially what it is now; but it may have used more of the tree trunk then than it does in the presence of the additional species of the Recent fauna.

It must again be emphasized that, while we are here stressing size adjustment to every extent possible, other adjustments to the presence of competing species do in fact always occur. Thus, although in the crown size change was primary, other ecological adjustments did in fact occur in the trio *occultus, evermanni, cuvieri* and are seen in the trio today:

(1) Giant species such as *cuvieri* cannot, as adults, utilize the finer twigs and branches of the crown; they are necessarily confined to the more central area of the crown, the heavier branches, and they do use the trunks of their trees and do descend not infrequently to the ground. We unfortunately know extremely little about the habitat of smaller individuals and hatchlings.[5] However, hatchling *cuvieri* are already larger than adult *occultus*. The species may therefore always be confined to larger perches than those characteristic of *occultus*. Neither adults nor juveniles of *cuvieri* have even been found sleeping on low perches readily accessible to the human eye.

(2) Dwarf species such as *occultus* do use very small twigs, vines and stems. We have the advantage for *occultus* of the detailed observations of T. P. Webster (1969), who provides the following summary: "*Anolis occultus* appears to be an inhabitant of the peripheral vegetation. Branches and bushes along trails have characterized all the productive collection localities discovered to date; these somewhat artificial conditions give the collector access to vegetation continuous with the more or less high canopy characteristic of Puerto Rico's montane forest." *Occultus* has most frequently been collected sleeping, again on twigs and branches and at or a little above eye height. (It may also sleep high in the canopy but this has not been observed.)

In essence then, *cuvieri* occupies the central, and *occultus* the peripheral, parts of the tree crown. Their habitats then are contiguous but not broadly overlapping.

The situation appears to be different with *evermanni*. *Anolis evermanni* belongs to the group of anoles that Rand and Williams (1969) have called "trunk-crown" anoles. These are often seen high on the trunk and also use the

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[5] We do know for *cuvieri* that very young specimens have a radically different (banded = cryptic?) pattern from that of the uniform green adults.

crown, and sometimes emerge into the sun at the top of the crown. The young are found occasionally on twigs and small branches. They thus appear to broadly overlap both *occultus* and *cuvieri* and, as we have suggested, the size of all three seems to have been adapted to alleviate resource competition.

Interaction between the three species has not been seen, but there may be some behavioral adaptation also. Thus (1) Webster (1969) reports that, despite the occasional use of small perches already mentioned, juvenile *evermanni* seem to prefer perches of large diameter, a preference tending to minimize overlap with *occultus*. (2) If *cuvieri*, like *equestris* and *richardi*, is partially frugivorous (Schoener and Gorman, 1968; Schoener, personal communication: Lazell, 1971), competition with the other two species is further reduced. (3) *Anolis occultus* may differ behaviorally also in its more frequently slow mode of locomotion, capable though it is of quick jumps and leaps. It may in correlation with this stealthy habit be more of a searcher than a pursuer than the other two to some degree are, at least.

All three species live in shaded forest. *Anolis occultus* may be the most restricted by shade and humidity; *evermanni*, which is by far the commonest, may be the most versatile and require shade least; *cuvieri* is intermediate. Even museum data on distribution demonstrate this; it is not tied at all strictly to montane or wet habitats. The three are certainly not different enough to be categorized as occurring in different climatic niches. Whether they are said to use different structural niches is a matter of definition. All use the tree crown. If we choose to subdivide the crown niche, we might usefully speak of a twig or dwarf niche, a giant niche and a trunk-crown niche.

But with these three the primitive crown niche—the higher level of vegetation of the shaded forest—however broadly conceived, is full. An additional species no longer adapts primarily to size. It uses some additional ecological parameter—structural or climatic or both.

The statement that the crown niche of the shaded forest is full is empirical, not theoretical. There appear to be three and only three subniches to the crown. This is true not only for Puerto Rico but for the two larger islands—Cuba and Hispaniola—as well. There are indeed on Puerto Rico and on each of the larger islands more than three crown species, but the additional species are allopatric or allotopic over most or all of their ranges; there may be overlap but there is never regular and total syntopy. On each island the situation is, in fact, complex, but its complexity may reflect the difficulty of achieving stable syntopy for even three species (Table 6). Note that in Jamaica there is *not* syntopy of three crown species. There is a giant (*garmani*) and a near-dwarf in the forest but a third (*grahami*) is a species of more open country. There is even a fourth crown species (*valencienni*), partly syntopic with *grahami* but differing in foraging behavior from all other Jamaican species. Except for *valencienni*, the Lesser Antillean relationship roughly holds in all cases between adjacent sizes *within the same climate.*

Table 6. Differentiation of *Anolis* spp. With in the Three Subniches of the Crown Niche in the Greater Antilles[a]

F = Forest; O = Open Situations. Numbers = Maximum Male Size.

Giant Niche	172-191 *equestris* complex (several, probably 5 allopatric species) (F)	175 *ricordii* complex (possibly 3-4 allopatric species) (F)	137 *cuvieri* (F) 157 *roosevelti* (F?) (allopatric)	124 *garmani* (F)
Trunk-Crown Niche	78 *porcatus* (FO) 91 *allisoni* (O) (mostly allopatric but differing in climatic niche where sympatric)	80 *chlorocyanus* (F) 84 *coelestinus* (F) (=a parapatric lowland pair) 60 *aliniger* (O) 52 *singularis* (F) (= allopatric montane pair)	78 *evernanni* (F) 50 *stratulus* (O) (differing in climatic niche)	57 *opalinus* (F) 72 *grahami* (O) (differing in climate and hence usually allotopic to *garmani* and *opalinus*) 86 *valencienni* (O) (differing in foraging behavior from all other Jamaican species)
Dwarf Niche	46 *isolepis* (F) *angusticeps* (O) (these differ in climatic niche)	40 *insolitus* (F)	40 *occulus* (F)	

[a]Classification into these categories is primarily by size but also partly by habitat, e.g., *opalinus*, *stratulus*, and *singularis* are nearly of dwarf size but are not twig anoles. *Anolis singularis* (recently collected specimens) appears to be larger than here recorded when allopatric to *coelestinus*.

How does it happen that the crown niche becomes full? A possible explanation is the following: Recall again the size relationships between the three crown species: they differ in size according to a relationship by which the largest is almost twice the size of the second, and the second approximately twice the size of the third. This spread of sizes is that which we saw in most Lesser Antillean species pairs, and the Lesser Antillean ratio is that which *ex hypothese* we expect whenever species are coadapted by size. Let us now try to insert into the crown another species. Wherever we try to insert it, if the size ratio of nearly 2X for adjacent species is maintained, the spread of extremes becomes improbably great: if the new species is nearest the small end of the series, by spread of extremes, the smallest would pass the floor, which we have seen empirically limits size change in this direction: the smallest species would be impossibly small. If the new species is inserted nearer the large end of the series, the largest species would by the same phenomenon far exceed the largest anole known: the largest species would be implausibly large (perhaps more on biochemical than on bioenergetic grounds). Clearly a definite floor prohibits size change in one direction, and evident resistance impedes size change in the other. Within the crown, therefore, we should see a maximum of three size classes.

Once the crown is full, whatever the reason, it follows that when *gundlachi* is added to the faunal complex as its fourth species, it inserts itself *below* the high arboreal niches of the three previous species. It takes its place in the lower levels of vegetation, the males on the lower tree trunk, the females and juveniles on adjacent bushes and shrubs and saplings. This is a change of structural niche. Climatically, *gundlachi* is. like the other three species, an animal of the shaded wet forest. Indeed, as Schoener and also Webster have emphasized, *gundlachi* is in deeper shade than the other species because its habitat under the closed canopy is so far from the crown's access to the sun.

The station of male *gundlachi* is, as we have said, on the lower tree trunk and, more important still, its attention is focused downward; its foraging area is on the ground.[6] It is probably for this reason that, though male *gundlachi* abuts in the higher parts of its territory on the lower (trunk) parts of the range of *evermanni*, there is effectively little competition between the two species and hence no requirement at all for size adaptation: *gundlachi* is as large as or a little larger than *evermanni*.

It is necessary to note here that empirically—from the evidence of Recent *gundlachi* and of its analogues on other island—the adaptations to the lower trunk and ground are not as simple as statement of the change in behavioral terms only would seem to imply. Trunk-ground are morphologically as well as behaviorally different from crown species; there is a difference in length of limbs, in general habitus. a reduction in number of adhesive lamellae under the toes. There is in fact a complex assortment of morphological changes, which it is

[6] Hence the term "trunk-ground" for its niche (Rand and Williams, 1969).

plausible to assume were more difficult to accumulate genetically and therefore took longer to attain than the adjustments empirically seen as minor in size change, the change seen in the crown species. Here is another reason to believe, quite aside from our model, that *gundlachi* was not, as the dendrogram might suggest, contemporaneous in origin with *evermanni*.

Add now a fifth species. Where will it go? We have shown that it is not likely to be added to the crown. Can it be added in the basic niche of *gundlachi*? An accurate answer here requires more careful scrutiny of the *gundlachi* niche. It includes the lower tree trunk but also the peripheral grasses and bushes. There is obvious here a possible coadjustment analogous to that which resulted in *occultus* and *cuvieri*—one species specializing on the center, the other on the periphery of the niche. In Puerto Rico the fifth species—*krugi*—does stand in relation to *gundlachi* much as *occultus* does to *cuvieri*. It is in the same level of vegetation as *gundlachi*, but it occurs peripherally in grasses and bushes and on these extends a bit beyond the shaded forest into the sunnier edges. It has begun to emerge from the forest.

Anolis krugi is smaller than *gundlachi* but the ratio between the two is 1.3, not 2. Why is *krugi* not smaller? Very probably because it has begun to emerge from the forest. It is so far peripheral to *gundlachi* that it has begun to emerge into a different climatic zone: it is spatially *and* climatically distinct from *gundlachi*; unlike *occultus-cuvieri-evermanni* the overlap is not intimate and extensive. Size reduction there may be, but it need not be of the maximal kind seen in most Lesser Antillean pairs. One can instead see in *krugi-gundlachi* a parallel to the relation of *wattsi* and *gingivinus*, where also there is a strong spatial and climatic displacement compensating for or allowing a less than maximal size displacement.

With *krugi* the shaded forest (and its edge) appears to have been filled in Puerto Rico. All further evolution of Puerto Rican anoles is the evolution of climatic vicariants[7] of anole types already represented in the shaded forest:

(1) *Anolis stratulus* is the dry country trunk-crown vicariant of *evermanni*. It finds its place in more open situations, more isolated or sunnier trees. Schoener and Schoener (1971b) have shown, however, that it does overlap peripherally with *evermanni*—sometimes extensively—and hence they have suggested that its small size (ratio *evermanni* 78:*stratulus* 50 = 1.5) is an adaptation to alleviate competition between the two species. Here Schoener and Schoener (1971b) consider the size adaptation secondary to the climatic, and I agree. I assume that *stratulus* achieved its climatic adaptation in dry and open forests (perhaps in southwest Puerto Rico) but acquired its small size after contact with *evermanni*.

(2) *Anolis cristatellus* and *cooki* are respectively the dry adapted and the dryer adapted trunk-ground vicariants of *gundlachi*. Schoener and Schoener (1971b) have shown there is minimal overlap between *cristatellus* and *gundlachi*. It is not

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[7]Vicariant: an ecological analogue (=ecologue) of a species, characteristically allotopic or allopatric.

surprising then that they are of equivalent sizes. *Anolis cooki*, on the contrary, though its range is small (in portions of southwest Puerto Rico only), does overlap with *cristatellus* over a significant part of its very limited range, and it is in fact smaller. The ratio, however, is not as high as is usual in anole size adaptations (*cristatellus:cooki* = 1.2) and this accords with a suspicion that the contact and overlap of the two species are relatively recent.

(3) *Anolis pulchellus* and *poncensis*—dry country grass-bush anoles—are strict parallels to *cristatellus* and *cooki* and ecologues of *krugi*. Again, *poncensis* is slightly smaller than *pulchellus*. Again, there is known to be overlap. The size ratio is again low. Does this mean recent contact or does it mean only minimal overlap? Or has it some physiological reason quite apart from competition?

These two climatic vicariants, it is obvious, parallel in a much more radical way the thermal difference which Schoener and Gorman demonstrated for the two anoles of Grenada. They again reinforce our proposition that size adaptations have severe limits as means of coadaptation and at some point must be supplemented or replaced by other ecological shifts.

A LOOK BACK FROM THE NEW VANTAGE POINT

We have now completed our review of the Puerto Rican radiation. How well does it fit our theoretical expectations? Astonishingly well. Recall that we have insisted on size change as primary and, following Schoener, as a consequence only of the need for partitioning of food resources. We have resisted all other explanations until they have been forced upon us. Such requirements are, we must confess, unrealistically stringent. That they have not defeated us is testimony that size divergence may really have been a major *initial* factor in the radiation of West Indian anoles.

It is first necessary, however, to be quite clear about what we have done. We have *not* demonstrated a *phylogeny* of size change; we have only demonstrated the theoretical predictability of certain *sequences* of changes in size and in other aspects of ecology. The distinction is an important one: the size/ecology sequence does not require that the relation of the members of the sequence be ancestor-descendant. In this case we believe them to be so, because the probable sequence of sizes as derived from a simple ecological model is in agreement with a probable phylogeny as derived from other evidence. But the sequence originates in the exigencies of an ecological situation quite apart from the origin or phylogeny—whether by radiation *or perhaps by invasion*—of the species that are *fitted together* in the size sequence.

In point of fact, on the two larger islands the phyletic evidence requires that the same sequence which we have constructed here be built from phyletically diverse components: thus on Cuba the crown anoles are alpha anoles in the sense of Etheridge (1960) and have come into Cuba from Hispaniola, while the trunk-ground anoles are betas in the sense of Etheridge and have arrived from

Jamaica. The bush-grass anoles of Cuba have come from both sources. In Hispaniola the same ecomorphs[8] are the results of three different invasions.

Thus, though we have here on Puerto Rico compared a hypothetical size sequence with a putative phylogeny, we were never in fact interested in the genetic ancestor-descendant aspect of that phylogeny; we were only interested in the fact that the phylogeny affirmed a certain sequence of species, which we could then compare with our postulated sequence of the *fitting together* of species ecologically. For the size/ecology sequence we did not care how—or where—the species were produced which were and *had to be* fitted together in a certain way: so long as the actors in the drama were somehow available, the drama could proceed.

Indeed, from a conventional point of view, there have been two notable omissions in our discussion of the history of Puerto Rico. I have, first of all, nowhere attempted a chronology. I have not done so because no evidence permits even a tentative and imperfect chronology. A sequence appears to imply some sort of chronology, but even as to this I will not agree to any postulation of a given time interval between events; any appearance of accuracy implied by such a statement would be false.

Again I have here nowhere discussed the topic of the geography of species origin on the Puerto Rico bank. I have, in fact, attempted this analysis but without results that satisfy me. As we have seen, it has not been essential to the portion of the story that has concerned us. We know that the whole Puerto Rican bank, including the present Virgin Islands, was available for species origins; we infer from the localization of certain species in southwest mainland Puerto Rico that some area here promoted species differentiation. We have, therefore, sufficient complexity to generate the required species, and we need not for our present purpose look behind this fact of sufficient complexity to the actual geography of history.

The limited story that I have attempted here is an ecological history told strictly in ecological terms: given certain ecological facts, certain consequences should have taken place and should have done so sequentially. In this limited history there has been no need for geography to intrude.

In the real world of Puerto Rico, geography does intrude at one point. In all of the previous discussion we have treated one species—*A. roosevelti*—as outside the story, a dangling irrelevancy. It is, in fact, a reminder that not all islands will be as simple as Puerto Rico has *appeared* to be. On all islands the populations that become syntopic species were once geographic isolates. The frequent dual process of isolation and then reunion may sometimes be interrupted, and an isolate may remain allopatric to the close relative from which it has diverged. This is the process by which the climatic series which we have described as the

[8]species with the same structural habitat/niche, similar in morphology and behavior, but not necessarily close phyletically.

climax of the Puerto Rican radiation came into being. On the two largest islands these vicariants (cf. Table 6)—sometimes climatically differentiated and hence able to exist sympatrically but also sometimes not obviously ecologically different and holding extensive parapatric or minimally overlapping distributions—make up a substantial element of the high species diversity of these islands. Even on Puerto Rico the anoles of the arid southwest—*A. cooki* and *A. poncensis*—were certainly at some not too distant time allo- or parapatric to the widespread species *A. cristatellus* and *A. pulchellus*. *A. roosevelti*—perhaps already extinct—seems clearly to be such a residual population. perhaps a Culebra autochthon, but perhaps only a relict there. On the Puerto Rican bank *A. roosevelti*, however, is only a detail that complicates the story without disturbing its flow.

For other islands, not only the two larger Greater Antilles but also for Jamaica, relictual populations may be essential elements both in history and in the present. For all the islands it is probably essential to the full story that isolation and reunion of populations results *each time* in the extinction of some local populations that do not coadjust and that at a maximum are able only to achieve a brief stand-off with their newly-met ecological equivalents. The largest islands have permitted survival of numbers of local isolates as well as many coadjusted species.

I have written about the evolution of Puerto Rico anoles as though the remarkable coadjustment of species we observe was achieved without difficulty and without carnage. Extinction has not been mentioned. This is an artifact permitted by the invisibility of the prior process of competition. No transitional or disappearing species—except *roosevelti* (which may be already gone)—seem exposed to our view. But this may be an erroneous judgment. *Anolis cooki* is even now a species of very limited range (Fig. 12) and at all the terrestrial borders of that range and on the offshore island of Cajo de Muertos (not mapped) it is intimately in contact with *cristatellus*. It is clearly ecologically somewhat different: it clearly survives as of now. But is this a stable situation? It is easy to see climatic change wiping *cooki* out. But even without climatic change is *cooki* holding its own? It is not possible to answer this question on any current evidence, but the existence of *cooki* may already be marginal. It may be the very model of a species about to submerge.

Anolis poncensis may be little better. In its very limited range, *A. cooki* is often abundant. *Anolis poncensis* is nowhere as abundant, though it has a substantially greater total range. Again it is clearly restricted by climate. Climatic oscillation one way might expunge it; in the other direction it would expand its range.

For either of these species it is not possible now to visualize how in the event of extinction they could be replaced. Clearly lizard species diversity in Puerto Rico is a fragile thing. Extinction for certain species has a perhaps low but quite
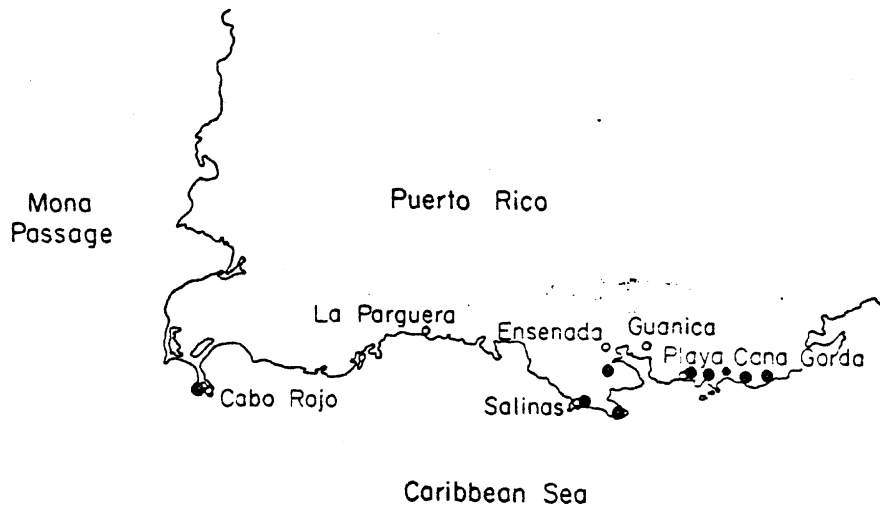
Fig. 12. The present distribution of Anolis cooki.

evident probability: replacement has no probability calculable in terms of human ability to see it happen.

Anolis roosevelti is larger than *cuvieri*. Clearly it is a product of the spread of extremes, and thus, though it is more primitive than *cuvieri*, it is no relict of any very ancient stage: probably it belongs to the stage just before the present. Nothing more can be guessed about it. Such relicts provide us little new information. They are, along with such local species as *A. cooki* and *A. poncensis*, however, very important as reminders of the invisible part of history—of the real but usually unrecorded role of extinction.

FROM THE SPECIAL TO THE GENERAL: THE ORIGIN OF FAUNAS

Puerto Rico is a special case—as I have admitted—an exceptionally favorable case. Dare we generalize from it?

I have already stated that no other island provides at this time as good a case as Puerto Rico that each other of the Greater Antilles has its own special problems and difficulties. Still we may attempt to generalize, to look at the faunas of islands abstractly and generally but with as much realism as abstraction permits.

I have written above about the intraisland radiation in Puerto Rico in terms of "adding" species. This obviously, when we deal with intraisland radiation, is only a device that permits us to ignore for the moment the geography and chronology of speciation. I have used such a device only because, as we have seen above, ignorance does not at the moment permit us to do more.

But realistically, what did happen? At least in general terms can we describe the process we believe to have occurred?

Let us treat intraisland radiation in terms of geographic speciation. Though other modes of speciation may sometimes occur, may have occurred in the Greater Antilles, we know very little about the processes and mechanisms involved. In contrast, enough cases of apparent geographic speciation have been analyzed—including some complex cases—that we may comfortably think of the geographic origin of species in general terms, rather than in terms of some individual, perhaps special case.

If radiation is a result of geographic isolation resulting in species difference, then clearly the formation of faunas is a matter of repeated secondary contacts—first isolation and then reunion. Theoretically at least, this has an interesting consequence. If isolation is continued long enough to permit differentiation to go to species level and this process is continually repeated, then clearly the original number of species held in common between an isolate and its parent population has each time an opportunity to double.

Think of this in its simplest terms (Fig. 13).[9] Imagine an island inhabited by a single species. Let this island be divided by any barrier—a physiographic one for simplicity's sake. Given time enough—and we need not initially define time enough—one species may become two. Theoretically this process could be indefinitely repeated. But clearly, faunas do not increase by N^2 with time.

Two factors must be involved in the limitation on increase: it must be difficult to achieve syntopy (only certain syntopic coadjustments are achieved with ease) and extinction must be a frequent phenomenon. Looking carefully at the phenomenon of faunal build up, we can list the following set of expected events if geographic speciation and then secondary contact occurs:

(1) *Syntopy by coadaptation*: Any species that are able to coadapt syntopically by differences in structural habitat survive. In the Puerto Rico forest five anole species have achieved syntopy: *cuvieri, occultus, evermanni, gundlachi,* and *krugi.* If the arguments previously made have been valid, syntopic coadjustment was achieved sequentially and *in an apparently inevitable sequence.* In the genus *Anolis*, in the absence of the competition of noncongeners and given the ecological adaptations possible to it, the sequence of five syntopic states is, we predict, a preferred sequence, a *main* sequence, readily and almost inevitably attained—given space and time enough. And in fact, on the two larger Greater Antillean islands this sequence of five syntopic states is in fact present—with additions and complications. On the smaller Jamaican bank only four syntopic states of this sequence are achieved. The latest and fifth state, the grass-anoles state, is missing. Since differentiation requires space, we may look

[9]Compare with this Fig. 10 of Bock (1970) or Fig. 4 of Moore (1960) for demonstration of the inevitability of diagrams such as this in the geographic analysis of sequences in speciation.
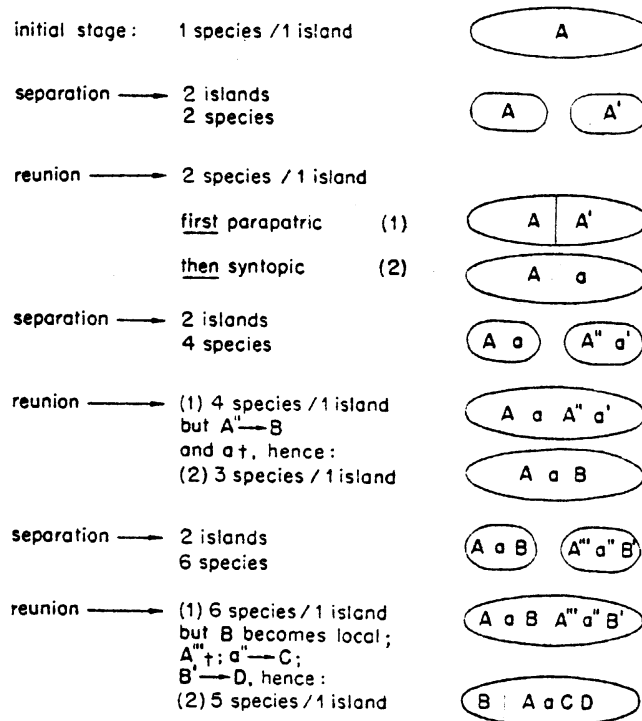
initial stage :   1 species / 1 island

separation ———► 2 islands
                2 species

reunion ————► 2 species / 1 island

first parapatric   (1)

then syntopic   (2)

separation ———► 2 islands
                4 species

reunion ————► (1) 4 species / 1 island
              but A"—►B
              and a †, hence :
              (2) 3 species / 1 island

separation ———► 2 islands
                6 species

reunion ————► (1) 6 species / 1 island
              but B becomes local ;
              A"' †; a"—►C ;
              B'—►D, hence :
              (2) 5 species / 1 island

Fig. 13. A diagram of the possible origin and evolution of a fauna of moderate complexity generated by the subdivision and reunion of an island.

first to Jamaica's smaller area as an explanation. (But the Jamaican phenomenon requires careful analysis on its own in a paper consecreated to it.)

(2) *Syntopy by special adaptations:* Any species that achieves a radical innovation, not part of such a preferred sequence described above, but adequate to avoid syntopic competition will again survive. The anoline faunas of the two largest Antilles and also Jamaica have species or series of species, not readily compared from one island to another, which locally or over the entire island have achieved syntopy by strategies which take them largely out of the competitive framework which by character displacement has produced the main syntopic sequence. Anole species that appear to fit this category do not exist in Puerto Rico but on Cuba include the *lucius-argenteolus-bartschi-vermiculatus* series, on Hispaniola the *monticola* series, and on Jamaica *valencienni.* In one or another way, distinctive for each set, these have ecologies which set them up alongside the main sequence anoles without competitively disturbing them.

(3) *Sympatry without syntopy:* Species that differ in climatic preference may coexist. In Greater Antillean anoles there thus result syntopic series that are partial analogues of the original syntopic sequence of the forest. Thus in Puerto

Rico, to the five syntopic species of the forest there correspond the three roughly syntopic species of dryer areas—*stratulus, cristatellus,* and *pulchellus,* and in still drier areas the two, again roughly syntopic species *cooki* and *poncensis.* (The climatic borders for the different structural habitats are not the same and hence *cristatellus* is not strictly syntopic with *stratulus* nor *cooki* with *poncensis.*)

(4) *Parapatry*: Species with otherwise similar adaptations may achieve a stand-off if the point of contact is a transition point in climate or ecology permitting one to be *locally* superior in one climate or ecology and the other *locally* superior in the other. No clear case of this exists in Puerto Rico but classic parapatry is seen in such geographically replacing species as *argenteolus, lucius, bartschi* in Cuba, and *coelestinus-chlorocyanus* in Hispaniola.

(5) *Allopatry*: Any species protected by barriers that minimize contact may survive locally. In Puerto Rico the relevant case is *A. roosevelti* isolated on Culebra.

(6) All species unprotected by barriers and not superior in any ecology, even a local one, go extinct. *Anolis cooki* in Puerto Rico is not protected by a barrier and is superior only in and limited to very hot dry areas. Should climatic change eliminate its present climatic zone, the species would also go. More interestingly, there must in the past have been many evanescent species, locally differentiated, but unable to hold their own on secondary contact.

It is in the aspect of extinction after secondary contact that intraisland radiation in lizards compares best with the faunal turnover that ornithologists (e.g. Mayr, 1965) have so much emphasized. Because the process is much slower in lizards, it is not evident in the way that is true of faunal change during colonization in birds (MacArthur and Wilson, 1963) or insects (Simberloff and Wilson, 1969). This aspect of faunal build-up is largely invisible (Williams, 1969). What is obvious is an accumulation of coadapted species with a relatively stable community structure, i.e., a fauna.

CONCLUSIONS

The relevant data for a historical ecology of Puerto Rican anoles has been provided (1) by the phyletic studies of Etheridge, and the zoogeographic data of Gorman and Atkins, and (2) by the work of Schoener, and of Schoener and Gorman on the ecology of solitary anoles and species pairs. On this as a base, with very few subsidiary assumptions, it has been possible to erect a necessary sequence of ecological changes: Primitively and primarily adapted to the tree crown in shaded forest, the anoles of Puerto Rico, as they radiate with the island bank, are first able to utilize size difference as a major means to syntopic coexistence. Beyond the stage of the third species, however, size ceases to have the same importance, and spatial shift, and the use of parts of the tree other than the crown, and climatic shift, and use of open rather than shaded

situations, become essential elements in the adaptations that permit the addition of species to the fauna.

SUMMARY

Historical ecology is possible. In a test case utilizing the anoline lizards of Puerto Rico, it is demonstrated (1) that, given some ecological rules derived from simple cases in living animals, it is possible to reconstruct the historical sequences by which species are fitted together into the coadapted units that are called faunas, and (2) that this postulated ecological sequence can be tested against and receive confirmation from a phyletic sequence erected on quite independent evidence. The case chosen is an exceptionally favorable one in terms of completeness of the evidence. Presumably, however. such sequences, once established, may be extrapolated to cases in which less evidence now exists and at least illuminate the problem and perhaps, in the happiest event. lead on to the solutions.

Historical ecology such as this is independent of the precise geography or chronology of the faunal build up. The only prerequisites for the achievement of any grade of ecological complication are geography complex enough and time long enough to permit the origin (or establishment) and coadjustment of appropriate species. Such a process, however, is not simple and involves much experimentation and extinction.

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