THE ANOLES OF SOROA

INTRODUCTION

Among the most intriguing aspects of the evolution of the anoline lizards in the West Indies is the evidence that there have been independent within-island adaptive radiations on each of the Greater Antilles that, have produced, between-island, astonishingly similar, but only distantly related, endpoint species that Williams (1972, 1983) has called "ecomorphs." This paper introduces some revisions in the concept of "ecomorph", in part based on our joint observations in 1983 in Cuba, but also based on reinterpretation of our older observations on the other islands. It will put our revisions in perrspective if we first describe how the concept of ecomorph arose.

History of the ecomorph concept:

One of the first generalizations made about the array of species known from the Greater Antilles was that each of the major islands had its own unique set of species (Stejneger 1904 [Puerto Rico], Barbour and Ramsden 1919 [Cuba], Grant 1940 [Jamaica], Cochran 1941 [Hispaniola).

Since 1941 investigation has increased the number of species on all of the Greater Antilles, There are now seven anole species on Jamaica, about 46 described for Cuba, more than 40, some undescribed, on Hispaniola, 10 on the main island of Puerto Rico, with two more known from the Virgin Islands, which are on the Puerto Rican bank. This phenomenal increase in species number has only made this first generalization stronger still. Only three species are known to occur on

more than one of the large islands: Anolis sagrei is native to Cuba and now occupies between half and two thirds of lowland Jamaica,; it may have been introduced to Jamaica during historical time.. A. cristatellus occurs in small pocket around a sugar mill in Hispaniola; it was introduced there in the 19...s from Puerto Rico. A. porcatus, a native of Cuba, was introduced into Santo Domingo City during one of the international expositions and is now spreading out from that city.

A second generalization was that on each island there were two abundant species common around houses and in parks. One was a medium-sized brown species, changing in color only from lighter to darker, with a more or less distinctive pattern, a stocky build, long legs and moderately wide toe pads with a moderate number of subdigital lamellae. The other was also medium-sized, but green with the power to change to a uniform brown or black, a relatively slender body, short legs and wide toe pads with a higher number of lamellae. The first was abundant on tree trunks and fence posts and commonly came to the ground to feed. The second was also seen on tree trunks but also often in the crown and even on foliage, and fed more often on higher perches than the first.

Initially we ourselves interpreted these two types as representing two separate stocks that had spread among the islands, each giving rise to a different species on the four islands. This can be diagrammed in the following way:

Table 1:

Jamaica	Cuba	Hispaniola	Puerto Rico

lineatopus - - - sagrei - - - cybotes - - - cristatellus

grahami - - - porcatus - - - chlorocyanus - - - evermanni

More sophisticated phylogenetic studies, among them a study of skeletal morphology using X- rays (Etheridge 1960), others of karyotypes (Gorman, especially 1973), of immunology using albumin (Gorman, Buth and Wyles 1980; Schochat and Dessauer 1981; Wyles and Gorman 1980), and most recently Burnell and Hedges (1990) using electrophoresis of slow alleles have contradicted this hypothesis of relationship. There is still no consensus on the relationships of West Indian anoles (Williams 1976, 1989; Gorman, Buth and Wyles,1980; Gorman, Lieb, and Harwood; Wyles and Gorman 1980; Guyer and Savage 1986; Burnell and Hedges 1990), but, whatever the differences of opinion, it now appearsto be a third generalization that species within one island, even of very different appearance, are as often more closely related to one another than to species of very similar appearance on different islands:

Table 2:

Jamaica		Cuba		Hispaniola		Puerto Rico
lineatopus	[- - -]	sagrei		cybotes	[- ? -]	cristatellus
|						|
grahami		porcatus	[- - -]	chlorocyanus		evermanni

At a maximum the between island relationships are at the species group level, implied above by the symbol [- - -] above, and in each

of the two cases the relationship may be more distant than species group might imply. In two of the cases, indicated by the vertical I the two very distinctive ecomorphs in each island are unquestionably close relatives, products of an intra-island radiation.

There thus have clearly been independent adaptive radiations in the several islands resulting in distantly related species occupying not merely similar but substantively identical niches., i. e. the resemblances among these species occupying identical niches must be due to very strong convergence, not to relationship.

Williams (I972, I983), drawing simultaneously upon the ecological studies of Collette (I961), Rand (1964, 1967), Rand and Williams (1969), Schoener and Schoener (1971a and b), Moermond (1979 a and b) and the growing body of data on relationships within anoles coined the term "ecomorph" (in a footnote!) to describe the members of series of anoles similar in morphology and structural niche independent of their phylogenetic relationships. The two first discovered ecomorphs - those described above- were named for their structural niche - trunk-ground and trunk-crown ecomorphs.

. Six West Indian anole ecomorphs were formally named in "The Anoles of La Palma"(Rand and Williams 1969) : crown anoles, twig anoles, trunk-crown anoles, trunk anoles, trunk-ground anoles, grass-bush anoles, but without use of the term "ecomorph." Williams (I983) formally defined and characterized the term, subdivided two of the ecomorphs- twig and trunk-crown- by size, and listed these "ecomorphs" of Jamaica, Puerto Rico, and Hispaniol as "standard ecomorphs" or "standard sequence" ecomorphs". . He explicitly omitted consideration of the anole fauna of Cuba, on the ground of his inadequate personal experience in that island.

He characterized the ecological aspects of the ecomorphs primarily in terms of perch characteristics,,secondarily in terms of anole size.

Perch characteristics have been classically described since Rand (1964) in terms of perch type and diameter and perch height above the ground. Size is conventionally snout vent length.. Each standard ecomorph has associated with it characteristic locomotion patterns (Moermond 1979) and defensive behaviors, as well as colors, proportions, including tail length, and some scale characters. Ecomorphs are essentially defined (TABLES 1 and 2) in terms of the modal behavior and appearance of adult males. Sexual dimorphism, difference in perch and behavior of juveniles, and individual variability are important but explicitly excluded in the interest of didactic clarity.

The Rand census, the methodology invented by Rand in Puerto Rico (Rand 1964), was the breakthrough that permitted the definition of first perch types and then ecomorphs. Other descriptions of the ecology of anoles (e.g. Schwartz and Henderson 1991) tend to be both anectdotal and inadequate. The Rand census permits discovery of the perch mode for each species. It is to be emphasized that anoles are always opportunists, and anoles without other anole species to compete with them are especially so. Within the limits of their functioning anatomy and their physiology (Losos, several papers) they tend to occupy all the space avbailable them. The modalities of each perch type appear genuinely to indicate the habitats the anoles with these perch types are best fitted for. The ontogeny of these modalities again indicates the habitat most appropriate for juveniles, females and adult males.

The paper, Williams (1983), that formally defined and characterized the ecomorphs of three of the Greater Antillean Islands was in many respects both an incomplete and a broad stroke depiction of ecomorphic radiation. Not only did it omit Cuba, the largest of the Greater Antilles, it had to admit many addenda and scolia to the simple concept that was, in fact, based on the trunk-ground and trunk-crown ecomorphs of Tables 1 and 2.

Here we will attempt to update and and complete the West Indian picture. We will be using the anoles of Cuba as part of this effort. and in so doing we will need to make more realistic our definition of ecomorphic categories. We reserve our new scheme until the discussion and, in fact, after detailed comparison of the Cuban data with the picture derived from the three other islands.

CUBA: A Test of the Ecomorph Concept.

As mentioned in the introduction, the purpose of this paper is to present data on the anoles of Cuba. We will ask if the Cuban anoles fit into the standard ecomorphs that we have derived from our field and museum acquaintance with the anoles of the other three Greater Antilles. Because Cuban species are not closely related to those on other islands (Williams 1976) and because they were never used to define standard ecomorphs originally, this will be a test- at least for the Greater Antilles- of the generality of the ecomorph hypothesis.

Our own data for Cuba- which enables us to interpret reports by others- comes from personal experience in several specific localities: Soroa (ASR & EEW), Soledad (ASR), Habana (ASR & EEW), Camaguey (EEW) and more limited experience of localities in Oriente (ASR).

Ecological relationships among anoles are most easily seen when comparing species co-occurring at a single locality. Sometimes when one species is missing, another species will appear to expand its structural niche and be found on perches characteristic of the missing species.(Jenssen I9); Collette (1961-Cuba); Oliver (1940- Bimini), Rand (1964-Puerto Rico; 1967- Jamaica), Schoener and Schoener (1971a- Jamaica, 1971b- Puerto Rico), Rand and Williams (1969- Hispaniola).

We extend this approach to the anoles of Cuba. The locality we have chosen as a focus for this paper is Soroa in Pinar del Rio Province, a spot with a diverse anole fauna that both of us have visited and at which we have jointly collected data.

We have deliberately patterned the heart of this paper on our previous "The Anoles of La Palma" (Rand and Williams I969),which was described as "preliminary to a study comparing the patterns of ecological

adaptations shown by anoles in differing areas and discussing their evolutionary significance."

SOROA DESCRIBED

Soroa is a resort area, Centro Turistico Soroa, about 100 km west of Havana in the Sierra del Rosario, Pinar del Rio, Cuba at about 700-800 meters elevation. A portion of the area is very much developed, with cabins, restaurants, a swimming pool, a picnic area and an orchidarium. Adjoining areas are wilder, with woods and thickets that afford varying degrees of sunlight. In particular a ridge on one side of the Río Manantial has a path that leads through a dark forest to a waterfall. The canopy is broken at various points along the path and there are limestone cliffs at various points.

One of us- Rand- spent 2 days at this area studying the species vermiculatus and making casual observations on other species during October 17-18, 1981. He had the assistance of Lourdes Rodriguez and Julio Novo. Both of us -Rand and Williams-spent five days here - from June 23 to 27- in 1983. We had the company and assistance again of Lourdes Rodriguez and Julio Novo but also of Dale Marcellini, Noel Gonzalez and Coy Otero. In 1983 our joint observations on vermiculatus were somwhat restricted, that species being left to Marcellini and Gonzalez, but with Lourdes Rodriguez and Julio Novo we explored the forest and cliffs along the path leading to the waterfall, and independently or with Julio Novo investigated the picnic area and orchidarium and the woods and thickets on the opposite side of the Rio Manantial. Although the time was short and the area not extensive we had the opportunity to examine a remarkable variety of habitats, ranging from quite open to very dark, and from cultivated

areas with gardens and buildings to closed canopy forest and limestone cliffs.

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Eight species were seen in the Soroa area. All species are Cuban endemics and two - A. vermiculatus and A. mestrei- are restricted to the Province of Pinar del Rio. The others are island wide. All are well known species. We collected data on structural and climatic niches on 220 individuals of these species in 1983. Table 4 reports our observations on structural niche for the 8 species seen. Four additional species are known from near Soroa and were expected there. Our data from Soroa are supplemented by notes by Lourdes Rodriguez on previous visits to Soroa, generously made available to us.

TABLE 4

In 1983 we also jointly took data (Table 4)in the Bosque de la Habana, a city park, where Collette (1961) was the first to examine microhabitat differences among sympatric anoles , We have also over a number of years visited other parts of Cuba. In all,we have field knowledge of 20 of the 43 species recognized on Cuba. These observations are also extended by answers by Schwartz and Gorman to a questionaire in 1965 from EEW on Cuban anole ecology as well as by a review of published data on Cuba, especially the papers by Barbour and Ramsden (1919), Collette 1961, Ruibal and Williams (l961a,b), Ruibal 1961,1964, Peters 1970 and, most recently, by an active group of Cuban herpetologists that includes Garrido, Estrada, Rodriguez, Novo, Gonzalez, and Perez-Beato.

TABLE 5

ECOMORPH CHARACTERISTICS AT SOROA/HAVANA

x = agrees with standard ecomorph (see TABLE 2); differences from standard are spelled out.

	ECOLOGY			MORPHOLOGY			
	PERCH	LOCO-MOTION	DEFENCE	SIZE	COLOR	SHAPE	DORSAL SCALES
CROWN-GIANT							
luteogularis	X	X	X	X	X	X	X
TWIG-GIANT							
C. barbatus	X	X	X	BIG >100 mm	X	HEAD MASSIVE	CREST
TRUNK-CROWN							
porcatus	X	X	X	X	X	X	X
TRUNK-CROWN							
DWARF							
angusticeps	X	X	X	X	X	X	X
TRUNK							
loysiana	X	CRAWLS	CRYPSIS	X	X	X	SOFT

							SPINES
TRUNK-GROUND							
sagrei	X	X	X	X	X	X	X
homolechis	X	X	X	X	X	X	X
allogus	X	X	X	X	X	X	X
GRASS-BUSH							
alutaceus	X	X	X	X	X	X	X

Nine of the twelve species on the Soroa list seem to fit the ecological (but not necessarily the morphological or behavioral) characteristics of our ecomorph categories. Differences from the ecomorph categories as understood on other Greater Antillean islands are recorded in Table 5.

TABLE 6

ECOMORPHS IN CUBA

	OBSERVED OR EXPECTED AT SOROA	KNOWN ELSEWHERE IN CUBA	TOTAL
CROWN GIANT	luteogularis RW	equestris RW, noblei, smallwoodi, baracoae, pigmaequestris	6
TWIG GIANT	C. barbatus	C. chamaeleonides W, C. porcus, C. guamuhaya	4
TWIG DWARF 2		isolepis, guazuma, pumilis	
TRUNK-CROWN	porcatus RW	allisoni RW	2
TRUNK-CROWN DWARF	angusticeps RW	paternus W	2
TRUNK	loysiana RW	centralis R, argillaceus	3
TRUNK-GROUND	sagrei RW, homolechis RW, allogus RW	bremeri W, jubar RW, imias, quadriocellifer, ahli W, delafuentei, rubribarbus, birama	10

GRASS-BUSH	alutaceus RW	anfilioquioi, clivicola, cupeyalensis,cyanopleurus, fugitivus, juangundlachi, mimus R, spectrum, vanidicus **inexpectata**	11
NON-STANDARD			
STREAMSIDE	vermiculatus RW		1
ROCKWALL	mestrei RW	bartschi R, lucius RW, argenteolus	4
GROUND	ophiolepis		1

R = seen by Rand

W = seen by Williams

Three species do not fit the Standard ecomorphs and are assigned to Non-Standard categories

The species at Soroa and what is known about their relatives elsewhere in Cuba are described below: Assignment to ecomorph categories is given in Table 6.

Anolis luteogularis morphologically completely fits the Crown Giant stereotype. Size reaches a known maximum of 191 mm SVL. It is green spotted with yellow and with yellow axillary streaks.

At Soroa this species must be considered scarce, and, as well, unpredictable as to locality, occurring in forest or along forest edge on large trees in low to moderate shade. It sometimes comes to the ground The perch of the two observed in 1983 was in the canopy, well above two meters..

All members of the equestris superspecies (**equestris**, **noblei**, smallwoodi, **baracoae**, **pigmaequestris**) that have been observed in the field (we have ourselves seen equestris itself elsewhere) conform extremely well to the Crown Giant concept.

No Twig Giant was seen. Possibly Chamaeolis barbatus, known from nearby localities, fills this niche. It is a cryptic, slow moving, crown species and thus fills parts of the ecomorph definition. We have called it a Twig Giant, with, however, reservations because it is quite large, larger than any other Greater Antillean candidate for the category Twig Giant, and has a middorsal crest and a very massive head. In these characters it is sharply different from the type species of Twig Giant, Jamaican valencienni. All members of the endemic Cuban genus Chamaeolis (the

other described species are C. **chamaeleonides**, C. **porcus**, C. **guamuhaya**)are quite similar and are equally like (and unlike) valencienni.

No Twig Dwarf is known from Soroa, or, indeed, from Pinar del Rio. Twig Dwarfs are known elsewhere in Cuba (isolepis and guazuma). No explanation is known for the absence of this ecomorph from Pinar del Rio.

Missing also in 1983 were the Trunk-Crown and the Trunk-Crown Dwarf. The quite typical Trunk-Crown species- A. porcatus- **has been recorded at Soroa on other visits (Lourdes Rodriguez, peronal communication) as well as in nearby lowland localities,** and we ourselves found it in 1983 quite common in the Bosque de la Habana (n = 68). The Pinar del Rio population of A. porcatus belongs to the western of the three types described by Ruibal and Williams (1961a). which are currently regarded as belonging to a single island-wide species. The quite distinctive central population is sympatric with a larger related species, A. allisoni. All members of this complex conform well to the classic image of the Trunk-Crown ecomorph, differing among themselves in details of ear shape, frontal and canthal ridges, and the amount of blue on head and body.

Although we did not ourselves find it at Soroa, the Trunk-Crown Dwarf ecomorph appears to be represented there by angusticeps, We found angusticeps to be well represented in the Bosque de la Habana (n = 16), where Collette (1961) has already reported it. It was always perched on bushes and small trees, not on grass or herbs one two meters above ground.

Angusticeps has an allospecies relationship with paternus.. angusticeps occupies most of Cuba, while. paternus has a limited range in southwest Pinar del Rio near the Isle of Pines and on that island itself.

The only Trunk ecomorph recognized at Soroa Anolis loysiana (n = 3) does not fit does not that category as well as might be wished. Loysiana is unlike the Hispaniolan type species A. distichus in being much slower moving and in having curious scale projections making it particularly cryptic against the moss- and lichen-covered bark of the forest trees on which it lives. At Soroa it is reportedly scarce and localized, with one or two indiduals found in the same part of the forest on each trip (Rodriguez, personal communication). The species is, however, so cryptic on trunks with lichens that it is obviously easy to underestimate both its distribution and abundance. We saw two between one and two meters high in dark forest, but it may well range higher and out among branches and twigs, since the third specimen that we saw was on on a twig of an isolated tree extending out over the waterfall.

The related centralis and argillaceus lack the soft scalely projections and in this respect are more like distichus, but both argillaceus and centralis are described as slow-moving which is certainly not true of distichus.

There are three representatives of the Trunk-Ground ecomorph at Soroa-sagrei, homolechis, allogus, which differ especially in microclimate Sagrei (n = 3) occurred in 1983 only in one very sunny situation, a small open patch with grass and bushes, surrounded by second growth forest, always below 2 meters. It is reported as scarce at Soroa, found on previous visits (Rodriguez) in open sunny areas in the park-like area of the resort, always on bushes.

Though rare at Soroa, sagrei is widespread and very abundant in the lowlands of Cuba, perhaps the commonest lowland anole in Cuba, particularly around human habitations, always in sunny situations, often on

the lower trunks of trees, almost always below porcatus where the two co-occur. It was the commonest species in the Bosque de la Habana (n = 78).

Homolechis in Soroa (n = 112), as elsewhere in Cuba, is seen in areas of partial shade. It was abundant in the forest and on its edges, usually under a thin to moderate canopy, never in the darkest and most heavily shaded parts of the forest, perhaps avoiding also extremely damp microhabitats. It was on bushes or trees, usually on the main stem or trunk. Usually below 2 meters, it was rarely on rocks, boulders or cliff faces.

Allogus (n = 51) was in the most heavily shaded parts inside the Soroa forest, abundant in the darkest and dampest parts, particularly along the stream. It occurs on trunks and sometimes on bushes but also on rocks and boulders and prefers high humidity, avoiding the dryer, warmer microhabitats.

The same set of three Trunk-Ground species impressed one of us (EEW) as an especially clear case of climatic replacement (Sierra de Cubitas, reported in Ruibal and Williams 1961b). These three species are islandwide. Other members of the same species group occur in Cuba and are Trunk-Ground ecomorphs (ahli, Sierra de Trinidad, central Cuba; birama, known only from the type locality in Holguin Province in eastern Cuba, bremeri, southern Pinar del Rio Province and the Isle of Pines, delafuentei, Sierra de Trinidad in central Cuba, imias, known with certainty only from the male type and female paratype from Imias, Guantanamo Province in eastern Cuba, jubar, widespread in eastern and central Cuba, quadriocellifer, Peninsula de Guanahacabibes in extreme western Cuba, and rubribarbus, northeast coast in eastern Holguin Province and the interior in

northern Guantanamo Province), but these are local and do not sort as neatly as the three found at Soroa in terms of microclimate (Ruibal and Williams 1969b).

At Soroa only one Grass-Bush animal was observed- A. alutaceus (n = 1). Although this species has been described (and is known to us from other localities) as primarily an animal of shaded forest, the one specimen seen by us was on a low bush in a relatively open area, where homolechis was also seen. Lourdes Rodriguez reports the species as scarce and localized at Soroa, one or two individuals found on each visit at one small area in the forest. occurring in moderate shade, on the twigs and stems of grass and small shrubs, and perching very low, usually at less than 1 meter high. At the Bosque de la Habana the same species was seen (n = 8) in typical habitat.

A. alutaceus is slender and small in typical Grass-Bush fashion but instead of the lateral stripe so prominent in the type of Grass-Bush ecomorph, A. olssoni, there is a more or less well-defined dorsal stripe. Other species of the same species group are anfilioquioi (known with certainty only from Guantanamo Province in eastern Cuba), clivicola (Sierra Maestra and Sierra Cobre in eastern Cuba from 4400 to 6600 ft, cupeyalensis (Sierra de Nipe and Sierra del Cristal and also Jatibonico in eastern Cuba), cyanopleurus (most of Guantanamo Province and extreme eastern Holguín Province), fugitivus (Guanatanamo Province) , inexpectata (known only from the type locality in Holguín Province), juangundlachi (vicinity of the type locality, Matanzas Province, central Cuba), mimus (western Sierra Maestra. Sierra de la Gran Piedra, and adjacent lowlands) spectrum (Matanzas Province in central Cuba) , and vanidicus (Sierra de Trinidad and adjacent lowlands in central Cuba and near Santiago de Cuba

in easstern Cuba). All are Grass-Bush ecomorphs, inhabitants of forested areas, and all have a dorsal rather than lateral stripe.

The three species at Soroa that do not fit our standard ecomorphs are very different from one another:

Restricted entirely to Pinar del Rio, mestrei's primary association is with rock faces. At Soroa (n =21) it is abundant in the forest where rock cliffs and boulders were present, not, however, on every apparently suitable outcrop. It was sometimes on the trees associated with big rocks and boulders and cliff faces but was much more frequently on the latter types of surfaces It was often well above ground on a vertical surface. It did not go far back into caves or crevices. It ranged from deep to moderate shade, in this respect, distinctly overlapping allogus and homolechis.

The nearest relatives of mestrei are in the Trunk-Ground series that includes sagrei, homolechis and allogus, and in all its morphology it is very similar to these (Ruibal and Williams 1961b). These close relatives often use rock faces as well as tree trunks for their sit-and-wait foraging strategy, but mestrei is unusual in being nearly restricted to rock faces.

Another Cuban anole- bartschi-, like mestrei restricted to western Cuba, is even more severely restricted to rock faces.. It is considered a close relative of the one other Cuban anole that lacks a dewlap- vermiculatus -with which it was grouped as the genus Deiroptyx. Its other close relatives- lucius of central Cuba .and argenteolus of eastern Cuba- share bartschi's preference for perches on wide vertical surfaces but have large dewlaps and are more often on large complex tree trunks than on rock-faces

Vermiculatus has no close parallels elsewhere in Cuba and is, like bartschi, restricted to western Cuba. At Soroa this large anole is abundant along streams, even very small ones, in forest and at its edge, and is found in moderate to heavy shade and, occasionally, in very open sunny spots. Never more than a couple of meters from a stream, vermiculatus perches on trunks and on the branches of trees, often over water, and occasionally on rocks that may be in stream. The perch is below 3 m, but commonly 1-2 m up, particularly for males; females and juveniles tend to perch lower (Marcellini & Rodriguez?).

The ground anole of Cuba is ophiolepis. It was reported to us as occurring at Soroa, but we did not observe it there and have not observed it elsewhere. To our knowledge there are four published reports on its ecology (Gundlach 1880; Barbour and Ramsden 1919; Ruibal 1964; Schwartz and Henderson 1991), all of which are in full agreement. Ruibal's observations are the most succint and useful: p. 489: "This is not a rare species; it is merely rarely caught. This is the only truly terrestrial species of the Cuban anoline lizards. The species is found in pastures and savannas, on the ground and runs to take refuge in grass tussocks. I have observed the species sleeping on the leaves of small bushes."

DISCUSSION

It is to be expected that the selective forces that impose convergent characters on ecologically equivalent lizards never quite identical. Variation in one detail or another from ideal ecomorphic assemblages is to be expected.. The information we have just summarized goes beyond reinforcing that unsurprising conclusion. It requires a revision of the ecomorph concept.

The ecomorph concept was devised to accomodate the two empirical generalizations that we cited at the beginning of this paper: (1) the observation that on each island there were species phenetically so similar that it seemed unimaginable that similarity did not mean very close relationship; (2) the evidence that in no two of the islands did the these extraordinarily similar native species belong to the same species group. Such was the strong impact we ourselves felt from these two contradictory results that it impelled us (Rand and Williams 1969)first to categorize recognizable structural and climatic habitats and the distinctive anoles that perched in them by naming the latter by their perch types and then later (Williams 1972, 1983) emphasize the importance that we attached to the phenomenon by coining the word "ecomorph."

However, even "The Anoles of La Palma" in which we introduced the classic terms and the classic definitions of anole ecomorphs (although not the term itself) did not deal with a classic ecomorphic anole assemblage. La Palma was a montane locality. The "standard sequence" of ecomorphs of Williams I983- are a lowland set, and in Cuba, as in Hispaniola, are regularly present in the lowlands, though there may be additional anole species with ecologies or morphologies different from

those of the "standard sequence. Montane localities, as we discovered at La Palma (800m) in 1969, tend to be anomalous to a greater or less degree when compared with those of the lowlands

However, even in the lowlands of Hispaniola there is one species, still undiscovered and undescribed in 1969, eugenegrahami, that is equivalent in ecology and behavior but almost not at all in morphology to vermiculatus in Cuba. There is no resemblance morphologically in size, nor in color or pattern or shape but is only the compressed tail important for both species in the aquatic part of their habitat.

It was already clear in 1983 that it was not only in montane habitats that anomalous- i.e. more or less non-standard species. occurred. Williams therefore invented the category OTHER to accomodate the species like eugenegrahami, armouri, shrevei, monticola, rimarum, rupinae and reconditus that he felt were totally outside the ecomorph concept and in his Table 15a,b shoehorned certain others (christophei, etheridgei,koopmani, baharucoensis, dolichocephalus, hendersoni) into standard categories despite his own reservations expressed in the text. He explicitly admitted the problem arising from montane faunas by doubly underlining montane species in his Table 15b but overlooked the disturbing significance of the fact that eugenegrahami was lowland (215 m) i.e. the implication that some factor relating to montane faunas could not be whole explanation of the OTHER category.

The Cuban anoles have made the montane explanation of anoles deviating in one or another respect from the standard sequence quite untenable. Cuba has only a very minor montane anole fauna., all of it clearly derived from lowland groups. Yet it is in the lowlands that anomalies are found the Twig Giant interpretation of the genus Chamaeolis is suspect.

The small Trunk-Crown representatives, angusticeps and paternus, seem to have as their modal perch bushes. The anoles, loysiana, centralis, argillaceus, that may possibly represent the Trunk ecomorph are in all cases behaviorally slow, quite unlike their supposed Hispaniolan equivalent. distichus., and one species, loysiana, is unique morphologically.

It will be useful to resurvey the total sample island by island, emphasizing or adding certain details to the summary in Williams (1983), which is still not outdated for the three islands it covers.

Jamaica. The Jamaican bank is the smallest in the Greater Antilles. There is just one endemic species group which has, however, evolved within the island 5 ecomorphs, Crown Giant, Twig Giant, Trunk Crown I, Trunk Crown II, and Trunk-Crown, belonging to Williams (1983) "standard sequence." and one non-standard montane species, reconditus. It is not easy to visualize the biogeographic separations that might be responsible for such a radiation within a relatively homogeneous island. Williams (I983) suggested climatic islands, and Hedges and Burnell (I990) sea-level changes. Perhaps some combination of these factors will be the solution.

There are no allospecies, unless reconditus can be considered one. Lineatopus and reconditus are allopatric uniquely among Jamaican species. Although reconditus was considered to be related to lineatopus on phenetic grounds by Underwood and Williams (I959), and this has been confirmed by Hedges and Burnell (I990), the differentiation of the species,which includes significantly greater size.(maximum SVL in reconditus 100mm, in lineatopus 73 mm in adult males) exceeds that usually accorded to allospecies.

Climatic vicariants in Jamaica are at best infraspecific. The 2 subspecies of grahami correspond roughly to a wet-dry dichotomy. The climatic aspects of the four subspecies of lineatopus are more complex but essentially are on the same axis.

Non-native sagrei extends from western Jamaica over about 2/3 of the island. It is always more heliophilic than any subspecies of lineatopus. It has been extending its range eastward in recent years (person. observation, G.Mayer person comm.)

Puerto Rico: With its bank Puerto Rico is the second largest of the Greater Antilles. The Virgin Island element of the bank affords a more obvious opportunity/theater for geographic speciation than the simpler island of Jamaica. There are also a larger number of described species on the Puerto Rican bank than on Jamaica-12 rather than 7. All are endemics. One, roosevelti, the second crown giant, may be extinct, and one, ernestwilliamsi, known only from one very small cay in the English Virgin Islands, surrounded by its close relative, cristatellus, may be either an extraordinary relict or a synonym.

On islands of the Virgin bank there are only 5 species of the total of 12 , cristatellus, a Trunk Ground species, most often

Eugenegrahami known from just one locality in Haiti is the Hispaniolan parallel to vermiculatus). Elsewhere aquatic anoles are known only from the mainlands. Barkeri is a representative of this set in Mexico. Aquaticus occurs in the Pacific versant of southern Costa Rica and western Panama, and there are one or two geographically replacing forms very close to aquaticus north of that species in the same Pacific versant of Costa Rica. More impressive is the lionotus series, a set of geographically replacing species extending from Nicaragua to Colombia, oxylophus in Nicaragua, Costa Rica and western Panama. lionotus in central Panama, poecilopus in eastern Panama and northern Colombia, macrolepis in western central Colombia, and the recently discovered (Williams 1986)rivalis in southwestern Colombia, the last sympatric with a larger, very distantly related aquatic anole discovered at the same time, maculigula.. Except in the case of very close relatives, these species share very little, certainly not size, only their riparian habitat, the behavioral feature of escape into water, and morphologically a strongly compressed tail without a dorsal crest.

It is the most striking feature of the standard ecomorphs, on the Greater Antilles, that they are as similar as they are found to be. The lowland Crown Giant, Trunk-Crown, Trunk-Ground anoles on all four Greater Antilles are extraordinarily consistent in size, in behavior, and morphology,. What are the features common to these islands that have produced so strong an ecological convergence in the anole radiations that are phylogenetically diverse on each of the four islands?

First, the Greater Antilles are all faunistically impoverished islands compared with the mainlands , except for a few lineages, like anoles , that have radiated dramatically in the islands. These four relatively large islands are similar in topographic relief, climate, vegetation, competitors for food and predators (other lizards, snakes, insectivorous and predatory birds-- all reduced in diversity as compared with the mainlands) These similarities among the islands and the differences from the mainlands may explain both the island convergences and the absence of <u>any</u> strong ecomorphic parallels in the mainlands.

There is, in fact, only one impressive montane anole fauna in the Greater Antilles, the one in Hispaniola.. In Jamaica reconditus is the one distinctive montane anole . Puerto Rico has no anole that is strictly montane. Cuba has only the endemics of Pico Turquino. Hispaniola has both south and north island endemics, none of which fit well into the strong lowland ecomorphs..Most of the endemics are in montane broad leaf forest. The only endemic that occurs in pine forest is shrevei,, a relative of cybotes, which is a Trunk-Ground anole in lowland Hispaniola. The endemics of the broadleaf forest belong to species groups without known close lowland relatives.

1) All Cuban species fit the full set of ecomorphs- strong, moderate, and weak

2) The weak ecomorph Cuban species (rockwall, streamside, ground) have Hispaniolan parallels.

3) There are number of montane species in Cuba. They are all derived from lowland relatives and occupy similar ecomorphs. There has been no montane radiation in Cuba comparable to that seen in Hispaniola.

4) Within Cuban ecomorphs as in Hispaniola there are closely related species with the same standard ecomorph that replace one another along a climatic gradient (climatic vicariants). There are also, as in Hispaniola, closely related species that replace one another geographically (allospecies).

5) The location of the zones of contact between Cuban allospecies do not seem readily explicable on historical grounds.

CONCLUSIONS

From these data we can conclude:

(1) All of the anoles of Cuba fit into ecologically definable categories that are the "eco" aspect of ecomorph. All appear to have at least analogs on the other large island of the Greater Antilles, Hispaniola.. As was previously determined for the other three islands similarity, even strong ecological [and morphological] similarity], in no case implies close relationship with species on the other islands. In every case the between-island phyletic distance is at least that between strongly marked species groups and may even be generic.

(2) Many Cuban species have almost identically the morphological and behavioral specializations seen on the other Greater Antilles. These we have called "strong ecomorphs."

(3)In other cases there are sharp differences in morphological or behavioral aspects. The fit in morphology or behavior is in these cases not merely not perfect; it may be in one or another aspect very different. The cause or causes may be phylogenetic constraints (the non-Anolis genera or even the "sections" of Anolis may have diverged early) or there may be alternative solutions to the same adaptive problem or there may be ecological differences not allowed for in the admittedly crude ecomorph categories used. We are compelled to recognize "weak ecomorphs" and an finely graded spectrum between "weak ecomorphs"

(3) All of the strong ecomorphs are filled on Cuba, as they are on Hispaniola,and on the smaller islands of Puerto Rico and Jamaica. The additions have been made in the "weak ecomorphs".

(4) As in the other Greater Antilles, where distinct species in

Cuba occupy the same ecomorph, they differ from one another in geographic range or in climatic preference.