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WEST INDIAN ANOLES: A TAXONOMIC AND EVOLUTIONARY SUMMARY
1. INTRODUCTION AND A SPECIES LIST

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ABSTRACT. Accumulation of morphological, karyological and ecological data on West Indian anoline lizards permits and requires a taxonomic analysis more elaborate than usual and employing both formal and informal taxonomic categories. The categories are defined in this, the first paper of a series, and a species list of West Indian anolines displays the new arrangement.

INTRODUCTION

Since the pioneer study by Etheridge (1960) there has been a remarkable growth both in our factual knowledge and in the sophistication of our knowledge of one group of lizards — the anolines. This has been especially true in the islands of the West Indies. The mainland members have at the same time received less attention and have proved more refractory. (Certainly the latter fact has influenced the first.)

There is, however, nowhere any gathering together of the new knowledge. Partly this results from the continuing activity. Not even species lists have remained constant. A statement that Cuba or Hispaniola has x species is outdated before it is published. In the same way ecological information, ideas and theory have expanded far past the published record. It is not easy to keep on top of the field.

Just because of this it is necessary that beginnings of a summary be made. Both for old hands and for newcomers an exposition of how far we've come, where we are, and where

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we might go will be a useful thing. I propose as a first step a taxonomic-evolutionary summary. The summary is inevitably provisional and, more than that, intended to promote research, provoke criticism and encourage the search for further evidence and the endeavor for greater understanding.

My objective has been to illuminate ecology and evolution. The taxonomic study I will here provide is one means to that end. The West Indian anoles are a group of enormous diversity, but the interest of this diversity is not in its bare existence but in its structure and origin — its balance, the interlocking of its parts and the historical paths by which this was achieved.

This is no simple radiation — not just the checkerboard subdivision of some original widespread unit. Here the severed units have doubled back upon one another and are completely layered, juxtaposed and interdigitated. The fitting together of so many species is the problem.

Such complexity involves several levels. One such level is generic. In the West Indies I recognize three very distinct genera, two genera autochthonous and old, species-poor and obviously relict, one genus species-rich beyond ordinary imagining, a colonizing and expanding group, a newer invader from the mainlands that adjoin the West Indies to the west and south. The latter is, of course, the group, as full of problems as of interest, that must receive the maximal attention it deserves.

In point of fact, there are few problems for the two old species-poor genera, but also little information.

One of these two genera, *Chamaeleolis,* is represented by two giant casque-headed arboreal species on Cuba which much resemble the tree-crown giants of the *Anolis equestris* group with which they share the island (Garrido and Schwartz, 1968). The species of *Chamaeleolis,* however, are more primitive osteologically, more chameleon-like in movement and appearance and apparently rarer than giant *Anolis.*

The other of the genera, *Chamaelinorops,* initially erroneously reported from the tiny mile-square island of Navassa, west of southwestern Hispaniola, is, in fact, from the south island of Hispaniola, dwarf, ground-dwelling and extremely peculiar osteologically. Richard Thomas (1966) recognizes only a single species.

Chamaeleolis and *Chamaelinorops,* except that they are true anoles sharing the characteristic adhesive pads of *Anolis* and the typical *Anolis* dewlap, are not close to each other nor to

Anolis. Their greatest interest lies in the possibility that they may represent an early (pre-Miocene ?) invasion of the Greater Antilles and may be relicts of an earlier island radiation of which we otherwise know nothing.

The three species just mentioned apart, the remaining anolines of the West Indies are here regarded as belonging to the genus *Anolis*. Fortunately this overlarge taxon divides naturally, as Etheridge showed in 1960, into two sections called by Etheridge alpha and beta. Though this is a dichotomy based on an apparently trivial character, it makes excellent geographic sense. Savage (1973) has suggested that, instead of two sections, two genera be recognized — *Anolis* Daudin (type *Anolis carolinensis* Voigt) and *Norops* Wagler (type *Anolis auratus* Daudin). This would substitute formal designations for the currently informal ones but it would leave no formal (or informal) term for the two sections (or genera) taken together. Savage's action is well taken if alpha *Anolis* are closer to *Chamaeleolis* and *Phenacosaurus* than to beta *Anolis* or the betas are closer to *Chamaelinorops* than to the alphas. This is a point I regard as at least doubtful, preferring to leave it in decent obscurity until there is more and better evidence. My own suggested phylogeny for anolines would have the alpha anoles the more primitive (as they certainly are in many respects), and the beta type of caudal transverse process (which does not resemble those of other iguanids or of other lizard groups) arising secondarily, but only once, from the alpha condition in which the transverse process is absent. The transverse processes of *Chamaelinorops* have only a verbal similarity to those of beta anoles; I question the closeness of the relationship. Richard Etheridge would disagree with this scheme fundamentally. Very recent immunological data (Dessauer et al.) reported at the 1974 meetings of the American Society of Ichthyologists and Herpetologists question the fundamental distinction. I remain convinced of the reality of the two groups but, while so much remains controversial, I do not see the value of the formal designation; it is not even useful mnemonically.

Means to Analysis of a Radiation: The Group Terms Utilized

The two sections of *Anolis* have, according to my interpretation, provided three and only three invasions of the West

Indies — one by *betas* into Jamaica, one by *alphas* into Hispaniola, and a third by *alphas* into St. Lucia. (But see Yang, Soulé and Gorman [1974] for the evidence for a landfall for the third invasion in Grenada instead.) All the extraordinary proliferation, diversity and complexity of *Anolis* in the West Indies has arisen out of these three stocks by intra-island radiation and inter-island interchange. There is therefore a formidable problem in analysis.

Fortunately, part of the basic information is already available. A just published checklist of West Indian Amphibians and Reptiles by Schwartz and Thomas (1975) provides an informed and very careful list of Antillean taxa (including *Anolis*) with original citations and synonymies, as well as the distributions as known to the date of publication. The species are, however, listed alphabetically; no taxonomic arrangement or indication of relationship is attempted. The taxonomic ordering presented below, in remedying this, endeavors to synthesize a great deal of biological information.

I have myself seen 72 species or members of superspecies of West Indian anoles in the field, six additional alive in captivity, and 33 more as preserved specimens. Only three species, all very recently described from Cuba, are known to me only from descriptions (*A. pygmaequestris, A. juangundlachi* and *A. fugitivus*). I have collected and studied anoles on all four of the Greater Antilles, on several of the Lesser Antilles and on one island in the Bahamas. This field knowledge I regard as basic to an undestanding of the group. I have also participated in, encouraged or aided studies at many other levels — osteology, karyotypes, electrophoresis, aut- and synecological studies. All of this information is utilized in the classification below.

No classification can mirror perfectly the complexity of the evolutionary events that have produced the more than 100 species of West Indian *Anolis*. Nor, indeed, are the minuter details of relationship and evolutionary sequence so well understood (or likely to be) that we should attempt so perfect a system. Nonetheless the wealth of species to be allocated and the amount and variety of detail known about these same species seem to me to afford at once the possibility and the justification for an arrangement elaborate much beyond the usual. I therefore utilize a number of informal terms, partly based on those employed by Etheridge in 1960, but descending into greater detail. I define these below.

Formal and Informal Categories Used

Section. The primary dichotomy, a group osteologically defined at the highest level below the genus. Proposed by Etheridge (1960) for his alpha-beta division with *Anolis* osteologically defined on presence or absence of transverse processes on posterior caudal vertebrae.

Subsection. A division setting off a major portion of a section, again osteologically defined. This term, not used by Etheridge, distinguishes *punctetus* and *carolinensis* subunits within the alpha section, basing them on the relationship of interclavicle and clavicle. In the shorthand terms used below, the relationship is described in terms of an arrow-shaped or T-shaped interclavicle.

Series. A phyletic unit under the subsection definable on multiple characters. Osteological, chromosomal and even scale characters are utilized. Ordinarily this includes more than one species group and displays substantial morphological and even chromosomal diversity, i.e., products of a complex radiation that inferentially included several intermediate or annectent forms now extinct.

I have found series to be the unit in terms of which evolution is most conveniently discussed. I shall, therefore, in succeeding papers mention more characters under this unit than under taxa at a higher or lower level. This permits higher comparability between series and puts on display also many of the features and conditions the evolution of which I will later trace.

This is not to say that the greater number of characters makes the definition of series sharper or more rigorous. On the contrary, precisely because series are the units within which evolution is most readily seen, recognition of series is a matter of some subtlety — as Tables 1–4 show. Morphological and karyological characters may broadly overlap (Table 1). Ecology and geography are major clues, but convergence in ecological adaptations is rampant (Table 2), and geography must be used with discretion.

A balancing of all the evidence — not all of which is on record in Tables 1–4 — is the basis for the recognition of series.

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subseries: a category utilized when a series has several recognizable subunits, ordinarily including more than one species group.

species group: the products of a simple radiation but often including species now widely sympatric (they may exhibit chromosomal diversity). I have sometimes used species group for a single species when that species is very distinct and may well be the last remnant of a radiation.

species subgroup: employed when readily definable and sympatric subgroups can be determined.

superspecies: the products of a radiation, the representatives of which are still completely or mostly allopatric and usually chromosomally uniform. Species status often uncertain. (See below.)

species: the most recent evidence indicates that the recognition of valid species is much harder than was formally assumed. It cannot be routinely assumed that allopatry or parapatry imply subspecific status. As I indicate above, I have used the superspecies category for a number of equivocal or doubtful cases.

subspecies: intraspecies differentiation differs so much in different species that this unit is of very different value from one case to another. I do not report currently recognized subspecies in the species list below. I will do so in the detailed species group and species definitions to come, but I will do so without passing judgment on their validity. I imply only that the differentiation so indicated — in contrast with that implied by the use of superspecies — is clearly intraspecific.

THE ANOLINES OF THE WEST INDIES:[1]

Taxon		Island or Bank[2]
Genus	*Chamaeleolis* COCTEAU	
species	*chamaeleonides* DUMERIL AND BIBRON 1837	Cuba
	porcus COPE 1864	Cuba
Genus	*Chamaelinorops* SCHMIDT	
species	*barbouri* SCHMIDT 1919	Hispaniola
Genus	*Anolis* DAUDIN	
	Alpha section	
	punctatus subsection	
	roquet series	
	luciae species group	
	luciae superspecies	
	luciae Garman 1887	St. Lucia
	blanquillanus Hummelinck 1940	Blanquilla
	bonairensis Ruthven 1923	Bonaire
	richardi superspecies	
	richardi Dumeril and Bibron 1837	Grenada, Tobago
	griseus Garman 1887	St. Vincent

[1]My definition of the West Indies is, like most definitions of the West Indies, idiosyncratic. I omit from this list the anoles of Providencia and San Andres (*pinchoti* and *concolor* respectively) although other reptiles on these islands have West Indian affinities, because the anoles themselves have no Caribbean relatives. I include the anoles of Bonaire and Blanquilla (*bonairensis* and *blanquillanus*) because they are obvious members of the *roquet* species group of the southern Lesser Antilles.

[2]Non-West Indian ranges are not cited here but will be given in the fuller discussion in succeeding papers in this series.

Taxon	Island or Bank
trinitatis REINHARDT AND LUTKEN[3]	St. Vincent, introduced on Trinidad
roquet species group	
roquet superspecies	
aeneus Gray	Grenada, introduced on Trinidad, Guyana
extremus Garman 1840	Barbados, introduced on Bermuda
roquet Lacepede 1788	Martinique
cuvieri series	
ricordii species group	
roosevelti GRANT 1931	Culebra
ricordii superspecies	
ricordii Dumeril and Bibron 1837	Hispaniola
barahonae Williams 1962	Hispaniola
baleatus Cope 1864	Hispaniola
cuvieri species group	
cuvieri MERREM 1820	Puerto Rico
bimaculatus series	

[3]The device of using capitals for the names of species describers except in the case of the members of superspecies is entirely for the purpose of making the sharply distinct sympatric species contrast with those *closely related* allopatric or mostly allopatric species about which questions of species status have often arisen. The emphasis on this difference does *not* imply that many or most of the members of superspecies are not biological species. Many are known to be in contact without interbreeding or with only a small zone of infertile hybrids. It calls attention solely to the demonstrable fact that the differentiation of members of a superspecies has not achieved the grade of *ecological* differentiation that permits them to be widely sympatric.

stratulus subseries	
evermanni species group	
evermanni STEJNEGER 1904	Puerto Rico
stratulus species group	
stratulus subgroup	
stratulus COPE 1861	Puerto Rico
distichus subgroup	
distichus superspecies	
distichus Cope 1861	Bahamas, introduced in Florida
dominicensis Reinhardt and Lütken 1862	Hispaniola, introduced in Florida
brevirostris superspecies	
brevirostris Bocourt 1870	Hispaniola
caudalis Cochran 1932	Gonave, Hispaniola
Species A Webster and Burns[1]	Hispaniola
altavelensis NOBLE AND HASSLER	Alto Velo
bimaculatus subseries	
acutus species group	
acutus HALLOWELL 1856	St. Croix
bimaculatus species group	
bimaculatus subgroup	
gingivinus COPE 1864	Anguilla Bank
sabanus GARMAN 1887	Saba
bimaculatus superspecies	
bimaculatus Sparrmann 1784	Statia Bank

[1]Webster and Burns (1974) demonstrated the distinctness of this taxon, but did not name it.

Taxon	Island or Bank
leachii Dumeril and Bibron 1837	Antigua Bank
marmoratus superspecies	
nubilus Garman 1887	Redonda
lividus Garman 1887	Montserrat
marmoratus Dumeril and Bibron 1837	Guadeloupe Bank
ferreus Cope 1864	Marie Galante
oculatus subgroup	
oculatus COPE 1880	Dominica
wattsi species group	
wattsi superspecies	
wattsi Boulenger 1894	Antigua
forresti Barbour 1923	Barbuda
schwartzi Lazell 1972	Statia Bank
pogus Lazell 1972	Anguilla Bank
cristatellus series	
cybotes subseries	
cybotes species group	
cybotes superspecies	
cybotes Cope 1862	Hispaniola
haetianus Garman 1887	Hispaniola
armouri Cochran 1934	Hispaniola
shrevei Cochran 1939	Hispaniola
longitibialis Noble 1923	Hispaniola
whitemani Williams 1963	Hispaniola

marcanoi Williams 1975	Hispaniola
cristatellus subseries	
pulchellus species group	
gundlachi subgroup	
gundlachi PETERS 1876	Puerto Rico
pulchellus subgroup	
krugi PETERS 1876	Puerto Rico
pulchellus DUMERIL AND BIBRON 1837	Puerto Rico
poncensis STEJNEGER 1904	Puerto Rico
cristatellus species group	
cristatellus superspecies	
cristatellus Dumeril and Bibron 1837	Puerto Rico
scriptus Garman 1887	Inagua, Caicos Bank, Mariguana
monensis superspecies	
monensis Stejneger 1904	Mona
cooki Grant 1931	Puerto Rico
carolinensis subsection	
occultus series	
sheplani subseries	
sheplani SCHWARTZ 1974	Hispaniola
occultus subseries	
occultus WILLIAMS AND RIVERO 1965	Puerto Rico
darlingtoni series	
darlingtoni species group	
darlingtoni COCHRAN 1935	Hispaniola

Taxon	Island or Bank
insolitus WILLIAMS AND RAND 1969	Hispaniola
monticola series	
fowleri species group	
fowleri SCHWARTZ 1973	Hispaniola
christophei species group	
christophei WILLIAMS 1960	Hispaniola
monticola species group	
etheridgei subgroup	
etheridgei WILLIAMS 1962	Hispaniola
rimarum THOMAS AND SCHWARTZ 1967	Hispaniola
monticola subgroup	
monticola SHREVE 1936	Hispaniola
rupinae WILLIAMS AND WEBSTER 1974	Hispaniola
koopmani RAND 1961	Hispaniola
carolinensis series	
equestris species group	
equestris superspecies	
equestris Merrem 1820	Cuba
luteogularis Noble and Hassler 1935	Cuba
noblei Barbour and Shreve 1935	Cuba
smallwoodi Schwartz 1964	Cuba
baracoae Schwartz 1964	Cuba
pigmaequestris GARRIDO 1975	Cuba
chlorocyanus species group	

chlorocyanus superspecies[1]	
chlorocyanus Dumeril and Bibron 1837	Hispaniola
coelestinus Cope 1862	Hispaniola
aliniger superspecies	
aliniger Mertens 1939	Hispaniola
singularis Williams 1965[2]	Hispaniola
hendersoni species group	
hendersoni superspecies	
hendersoni Cochran 1923	Hispaniola
bahorucoensis Noble and Hassler 1933	Hispaniola
dolichocephalus Williams 1963	Hispaniola
carolinensis species group	
carolinensis subgroup	
carolinensis superspecies	
[*carolinensis* Voigt 1832][3]	
porcatus Gray 1840	Cuba
smaragdinus Barbour and Shreve 1935	Great Bahama Bank
fairchildi Barbour and Shreve 1935	Cay Sal
maynardi Garman 1888	Little Cayman
longiceps Schmidt 1919	Navassa

[1]These may be only ecological equivalents, *not* closest relatives. Were this demonstrated, the superspecies grouping should be dropped.

[2]There is an undescribed blue-dewlapped form resembling *A. singularis* in the Sierra Martin Garcia of the Dominican Republic.

[3]Cited as the type species of the group only.

Taxon	Island or Bank
brunneus Cope 1894	Acklins
allisoni BARBOUR 1928	Cuba, Bay Islands, Half Moon Cay
isolepis COPE 1861	Cuba
angusticeps subgroup	
angusticeps superspecies	
angusticeps HALLOWELL 1856	
paternus Hardy 1966	
argillaceus species group	
argillaceus COPE 1862	Cuba
centralis PETERS 1970	Cuba
loysiana DUMERIL AND BIBRON 1837	Cuba
lucius series	
lucius species group	
lucius superspecies	
lucius Dumeril and Bibron 1837	Cuba
argenteolus Cope 1861	Cuba
vermiculatus species group	
bartschi COCHRAN 1928	Cuba
vermiculatus DUMERIL AND BIBRON 1837	Cuba
alutaceus series	
alutaceus species group	
alutaceus superspecies	
clivicola Barbour and Shreve 1935	Cuba
alutaceus Cope 1861	Cuba

cyanopleurus COPE 1861	Cuba
cupeyalensis PETERS 1970	Cuba
fugitivus GARRIDO 1975	Cuba
juangundlachi GARRIDO 1975	Cuba
mimus SCHWARTZ AND THOMAS 1975	Cuba
spectrum superspecies	
spectrum Peters	Cuba
vanidicus Garrido and Schwartz 1972	Cuba
semilineatus species group	
semilineatus COPE 1864	Hispaniola
olssoni SCHMIDT 1919	Hispaniola
new species[1]	Hispaniola
Beta section	
grahami series	
grahami species group	
garmani STEJNEGER 1899	Jamaica
grahami superspecies	
grahami Gray 1845	Jamaica, introduced into Bermuda
conspersus Garman 1887	Grand Cayman
opalinus GOSSE 1850	Jamaica
lineatopus GRAY 1840	Jamaica
reconditus UNDERWOOD & WILLIAMS 1959	Jamaica

[1]An undescribed species from the Barahona Peninsula (Hertz, in preparation). The third species previously recognized, *A. cochranae* Williams, has been demonstrated to merge clinally into *semilineatus*.

Taxon	Island or Bank
sagrei series	
valencienni species group	
valencienni DUMERIL AND BIBRON 1837	Jamaica
sagrei species group	
sagrei superspecies	
sagrei Dumeril and Bibron 1837	Cuba, Bahamas, Little Cayman, costal areas of Mexico, Belize, introduced into Florida
luteosignifer Garman 1888	Cayman Brac
bremeri Barbour 1914	Cuba
nelsoni Barbour 1914	Swan Island
homolechis superspecies	
homolechis Cope 1864	Cuba
quadriocellifer Barbour and Ramsden 1919	Cuba
jubar Schwartz 1968	Cuba
mestrei BARBOUR AND RAMSDEN 1916	Cuba
allogus superspecies	
ahli Barbour 1925	Cuba
allogus Barbour and Ramsden 1919	Cuba
rubribarbus BARBOUR AND RAMSDEN 1919	Cuba
imias RUIBAL AND WILLIAMS 1961	Cuba
ophiolepis COPE 1861	Cuba

TABLE 1[1]

Selected characters of West Indian *Anolis* series

SERIES	Autotomy planes open	Splenial present	Inscriptional ribs[2]	Karyotype (2n)	Vertebral crest	Caudal crest	Dewlap	Presacrals	Lumbars (mode)	Aseptate caudals
[α — arrow interclavicle = *punctatus* subsection]										
(*roquet*)[3]	+	+	4:0	36/34	—	—	♂	24	3/4	7/8
cuvieri	+	±	3:2/3:1	36	+	+	♂ ♀	24	3 (2)	7/8
bimaculatus	+	±	3:1	26-33	—	±	♂	24	3/4	5/6
cristatellus	+	±	2:2	36/27-29	—	±	♂	24/23	3/4	2-7
[α — T — interclavicle = *carolinensis* subsection]										
occultus	±	?	6:0/5:1	36	(+)	—	♂ ♀	24	3	all/8
darlingtoni	—	?	4:0/3:1	?/44	(+)	—	♂ ♀	24	3	all
monticola	+	?	3:1	36/40-48	—	—	♂ ♀/♂	24	5	7/8
equestris	+	+	3:1	36	+	+	♂ ♀	24	3	9/10
carolinensis	+	(−)	3:1/2:2	36	—	—	♂	24	3/4	6-8
lucius	+	—	3:1	36/34	—	—	♂ or none	24	4	6
alutaceus	+	—	3:1	36	—	—	♂	24	5	7
β										
grahami	+	—	3:1	30/30-37	—	—	♂	24	3/4	7
sagrei	+	—	2:2	30/28	—	±	♂ ♀/♂	24	3/4	5

[1]Osteological data are from the notes and tables for his thesis, which were generously provided by Richard Etheridge. Karyotype information is from George Gorman.

[2]Inscriptional ribs are calcified cartilage elements embedded in the myocommata in iguanid lizards (Etheridge, 1965). They are either attached to the corresponding dorsal ribs or float free in the myocommata. The number of fixed or floating inscriptional ribs is a taxonomic character reported by a numerical formula (as in the present table), which gives first the number of fixed ribs, second the number of free ribs.

[3]In my listing this is a sub-series, but as the only West Indian representative of mainland series that are poorly understood, they deserve a place here.

TABLE 2

ECOMORPHS[1]

SERIES	generalist	crown giant	twig giant	twig dwarf	trunk crown	trunk crown dwarf	trunk ground	grass bush	trunk	rock and other
α — arrow interclavicle										
(roquet)	+									
cuvieri		+								
bimaculatus	+				+	+			+	
cristatellus							+	+		
α — T interclavicle										
occultus				+						
darlingtoni			+	+						
monticola								+	+	+
equestris		+								
carolinensis				+	+	+			+	
lucius										+
alutaceus								+		
β										
grahami		+			+	+	+			+
sagrei			+				+	+		

[1]In the sense of Rand and Williams (1969) and Williams (1972) adaptive types distinctive in size, shape and color and in other aspects of their morphology and with characteristic stations in trees or on the ground, as suggested by their names. Different ecomorphs are often syntopic, but members of the same ecomorph are usually allotopic (climatically separated) or allopatric (geographically separated).

TABLE 3

Distribution of series

SERIES	Cuba	Jamaica	Hispaniola	Puerto Rico	Lesser Antilles
[α — arrow interclavicle = *latifrons* subsection]					
(*roquet*)					+
cuvieri			+	+	
bimaculatus			+	+	+
cristatellus			+	+	
[α — T — interclavicle = *carolinensis* subsection]					
occultus			+	+	
darlingtoni			+		
monticola			+		
equestris	+		+		
carolinensis	+				
lucius	+				
alutaceus	+		[+]		
β					
grahami		[+]			
sagrei	+	+			