

Papéis Avulsos de Zoologia

SOUTH AMERICAN ANOLES: THE SPECIES GROUPS

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I begin here a summary of the species groups of *Anolis* at present known from South America plus allocations of all published names that are currently assignable. I intend to provide illustrations and tabulations of scale counts for all the species recognized. I leave aside for the moment a few names represented by types that I have been unable to associate with any recently collected populations and also a few new forms that I am reluctant to describe because they are available to me only as old and poorly preserved single specimens or very small series belonging to difficult species complexes.

I am thus providing a work that is less than a revision but much more than a list. As such this work can at least dispel the unwarranted confusion that now surrounds even many of the commonest species of South American anoles. I hope to reduce the areas of difficulty and obscurity to dimensions that will permit local workers to make contributions that will still further reduce the difficult areas.

The only previous lists of all South American anoles are those of Boulenger (1885), Burt & Burt (1933), Barbour (1934) and Peters & Donoso-Barros (1970). Boulenger's volume, despite its antiquity, still has its utility since it alone describes the species it records. It is, of course, woefully incomplete. The lists by Burt & Burt and by Donoso-Barros are lists only, the synonymies often incorrect and the distributions often too extensive or too restrictive. Their primary value lies in their report of the state of the literature at the time of their writing.

Barbour's 1934 paper is a more peculiar and personal statement. Barbour had the assistance of both E. R. Dunn and K. P. Schmidt, but much of the good and the bad in his list and the comments he provided for each species is chargeable only to Barbour himself. His mistakes were sometimes egregious. The synonymizing of *steinbachi* Griffin with *punctatus* Daudin is an example. He did this from the figure without seeing the type or, it would appear, reading the text. Griffin's species is a synonym of *meridionalis*, a form very different from *punctatus* (cf. Vanzolini & Williams, 1970). Again the synonymy of *laevis*, one of the proboscis anoles and of moderate size and from Peru, with *tigrinus*, a dwarf species from Venezuela, and of both with *transversalis*, a large boldly-banded species occurring in Peru, Ecuador and Brasil, was done without checking specimens and clearly without careful comparisons of the descriptions. Regrettably, the only way in which Barbour's paper

is especially useful is in recording the references after Boulenger's catalogue and to the date of publication. Even in this it is not complete.

It is a reflection of the confusion that has existed in *Anolis* literature that, of the 80 names in *Anolis* reported by Burt & Burt, I regard only 42 as valid as used. Some names are erroneously applied; others are synonyms or represent specimens with erroneous locality or are still of doubtful application. Barbour was no better; of the 64 South American names he lists, no more than 36 represent recognizable species. Both Burt and Barbour contributed significantly to confusion and error.

Peters and Donoso-Barros did not attempt more than a literature report. Because of some published correct synonymies, however, their list is somewhat better than the earlier ones. Of 79 names, 59 are correctly employed and represent good species or subspecies.

Peters & Donoso-Barros themselves give their compilation "one star" for low reliability on a scale that rises to "four stars" for high reliability. It is a further indication of their lack of confidence in their *Anolis* listing that it is the only one of the Neotropical lizard genera for which they do not furnish a key but only a random entry matrix of characters. Clearly the present situation requires correction.

I have been working on *Anolis*, including the South American forms, for more than 10 years; my interest in the genus extends back more than 20 years. I have had the good fortune to begin with the excellent base of collections assembled at the Museum of Comparative Zoology by Thomas Barbour. Additions have been made by exchange, purchase and personal collections and the collections and gifts of friends and students. I have seen almost all the extant types and those I have not seen (e.g. *Anolis latifrons* Berthold pose no problems). I alone (1963, 1965, 1966, 1970, 1974 a and b, 1975 a and b) or with others (Williams & Vanzolini 1966, Vanzolini & Williams 1970, Williams & Duellman 1967, Williams, Reig & Rivero-Blanco 1970), have already described or redescribed 17 South American species.

I, like many others, have made much of the difficulties of this species-rich genus. While there are many startlingly distinct species, there are also, as I shall show in succeeding papers, many small radiations within the genus that have produced confusingly similar species. This is, of course, characteristic of all species-rich genera; the confusing sections are complexes that are only recently and barely differentiated; the distinct species are usually isolated relicts of older radiations.

I admit that convergence and parallelism are very prevalent. I by no means guarantee that the species that I group together on the grounds of similar morphology are necessarily closely related. This again is no novelty in a species-rich genus. I do not, in fact, find *Anolis* to be more difficult or difficult in different ways than other difficult genera. What has defeated analysis far too long, particularly for South American *Anolis*, has been paucity of material — absence of series, insufficient geographic coverage, ignorance of ecology etc. This, of course, makes even recognition of species difficult and uncertain, and taxonomy above the alpha level genuinely hazardous.

Such basic inadequacies and difficulties are now rarely true in the West Indies; this is still not so in South America of some species and in some places, some very substantial local collections have now been made, but it is a bare beginning. South America is too large an area and the range of *Anolis* in it too extensive, the workers too few, and in

most places the density of the genus too low for even massive effort to produce very good results except over a long period of time.

In commenting on South American anoles, I shall constantly be making use of randomly collected museum material. This is clearly not a method of choice. It stands in contrast to the methods that are now in use for anoles of the West Indies. In the latter area collecting is now problem-oriented and is, indeed, in many cases replaced as the major aspect of the study by ecological-ethological observation. This level of study is permitted by the greater clarity of our understanding of West Indian species, a clarity that has itself been permitted by the abundance of the animals and their accessibility. However, the general primitiveness of our knowledge in South America and the intrinsic difficulty in collecting many or most of the species by no means prevents local studies of greater sophistication. (There are areas in South America where anoles are moderately common, at least by mainland standards.) We shall indeed only improve our knowledge of South America anole species by combining wideranging studies of geographic variation and species differentiation with studies of the day to day ecology and social structure of local faunas. It is my hope to encourage studies that will rise to the level already achieved in West Indian work.

The species groups of South American *Anolis* will be described in a standardized fashion. The name of the oldest included species is given to the group, whether or not that species is South American. I do not, however, describe or give synonymies for the extralimital species of any group. They are mentioned only.

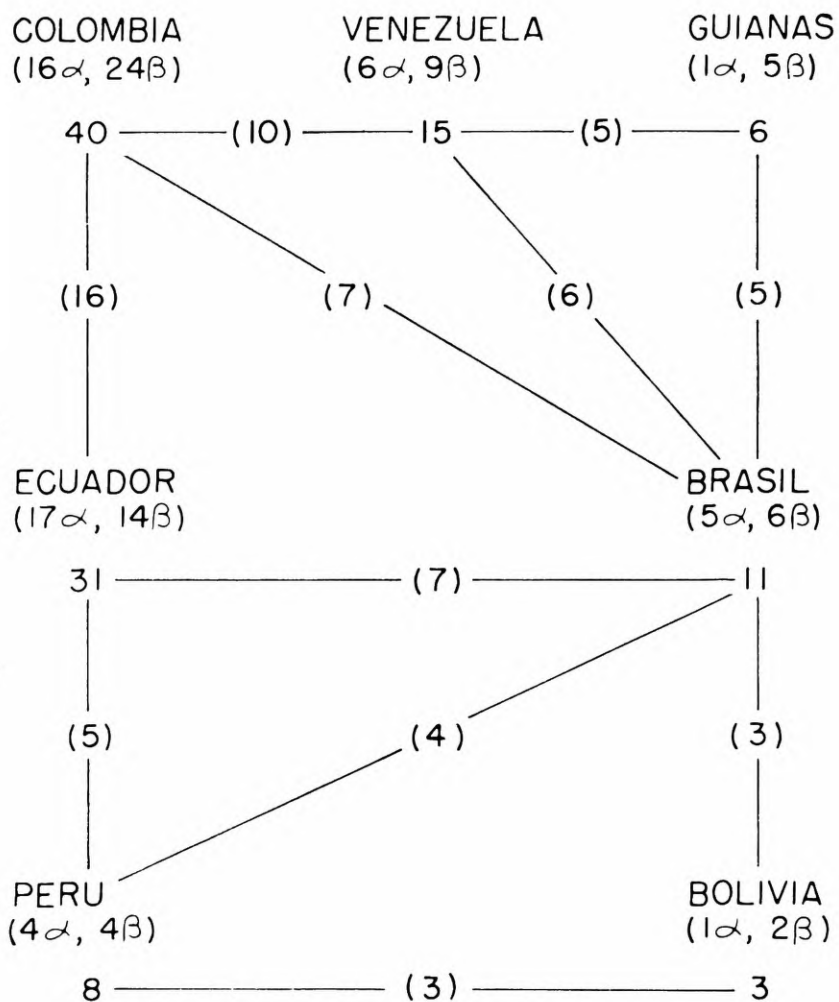
The definitions of groups are brief and admittedly imperfect. We are still well short of a comprehension of phylogenies within mainland *Anolis*. The groups reflect, therefore, as much convenience as relationship. I have not hesitated to place species together if they *might* be related, even if I lack assurance that they are.

The intention is heuristic. I do not intend to provide final answers but only to provide a means to further study — systematic, ecological, evolutionary. I expect numbers of new species to be found. However, better data on those already named will be more important. For more than half of the *Anolis* already described we need information beyond the fact of their existence. For still others (including some I will tentatively recognize) even their existence requires confirmation.

I adopt a listing of species names and synonyms that is deliberately somewhat repetitive but with the intention that maximal nomenclatural information be transmitted in each citation without the need for checking elsewhere. I omit citation of erroneous use of names and of erroneous identifications. Nomenclatural discussions are provided when required.

For each species group or section of a species group, a section is provided reporting the distinguishing characters of the species. I am here stressing differences. I nowhere provide a formal or complete description of any species, but *only* of those features which I have found useful in their discrimination. It will be obvious that I have seen few of these species alive, almost never all of any species group. The characters that I provide may therefore not be those most useful in the field. I intend, however, to provide figures of every species that I recognize — dorsal and lateral views of the head, lateral view of the body, and, where necessary, additional sketches of significant characters.

I also report for each species the range as determined by specimens seen by me and ecological information also when this is possible. For crucial or peripheral place names, coordinates are given, whenever possible, which will permit finding the localities on the 1:1000,000 maps of Hispanic America (*). For common widespread species *only* peripheral localities are cited.



Numbers in parentheses are species held in common.

Numbers for the several countries include some undescribed species, but are more probably minimum than maximum numbers.

(*) Since this citation will include degrees of latitude and longitude, the larger and better known localities will be findable on most readily available maps. It is also a fact of our knowledge of the distribution of most South America species that a statement of general locality or region will often be as useful as any precise demarcation. Most species are far more widespread than we know.

Ecological information from whatever source and no matter how limited is provided when possible. Its usual inadequacy is well highlighted by this procedure.

THE PRIMARY DIVISION: ALPHA AND BETA ANOLES

All taxonomic study of *Anolis* now necessarily begins with the recognition of the Etheridgean division of the genus into alpha and beta sections (Etheridge, 1960). Both sections are well-developed in South America and are in a broad sense coterminous in range.

This crucially important taxonomic division is described in Etheridge's thesis which was never published formally. It has, however, since 1960, been available from University Microfilms, Ann Arbor, Michigan (order number: 60-2529) as microfilm or bound xeroxed copy (the latter, at least in recent copies, bearing the inscription "published on demand"). I have repeatedly treated the Etheridge thesis as published and, whether or not the University Microfilms service is publication under the International Rules, there is no greater difficulty in obtaining a copy of this important work than there is in obtaining any book from its publisher. I think it inappropriate in these circumstances to disregard an original source of information, e.g. C. W. Myers, 1971: "an unpublished doctoral thesis [not seen]", and cite, as some have done, only my secondhand mentions of the allocations of species.

Table 1. Character range in South American anoles

	α anoles	β anoles
Number of lamellae	14-30	10-27
Scales across snout	4-25	7-20
Scales between semicircles	0-7	0-4
Dorsal scale rows enlarged	0-2	0-12

In any event, Etheridge (1967: 699-721) has provided descriptions and figures of the two conditions of the tail vertebrae that distinguish the alpha and beta sections of *Anolis*. As C. W. Myers (1971:11) has most recently demonstrated, it is quite possible, given appropriate X-ray equipment, to verify the alpha or beta status of any species or specimen.

There is unfortunately no external character by which the two sections can be separated. As Table 1 (modified from Williams, 1965) records, there are differences of range and average between the two groups but no external differences that are always reliable.

THE DISTRIBUTION OF THE SOUTH AMERICAN SPECIES GROUPS

Table 2 gives separately for alpha and beta anoles a list of the species groups I recognize in South America. Distribution for each group is indicated under areal categories that seem to be useful for *Anolis*; I make no claim that all of these would be appropriate for many or most other groups. The species listed under each group may be all of those known for a group, but if a "+" occurs in any column, I

already know of additional species, described or undescribed, that seem referable to the particular group and are found in the region indicated by the plus mark.

I do not at this time want to define or discuss the several species groups. This will be done in detail in succeeding papers where documentation can be given and the hesitations made necessary by imperfect evidence can also be made plain. The list in Table 2 is provided at this time because the species cited are those that, in fact, are best known in the areas for which they are specified and thus, even without the further papers in this series at hand, those with access to prior literature can get some perspective on the story that I will attempt

Table 2. Distribution of South American *Anolis* Species Groups

	TRANS-ANDEAN	CIS-ANDEAN			
		Northern Tier (NE Colombia, NW Venezuela)	Amazonia, the Orinoco and Guianas	Central Brasil and adjacent Paraguay	Brasilian Coastal Forest
I. α anoles					
Groups					
<i>laevis</i>	<i>proboscis</i>	-	<i>laevis</i> <i>phyllorhinus</i>	-	-
<i>tigrinus</i>	-	<i>tigrinus</i> <i>solitarius</i>	-	-	<i>nasofrontalis</i> <i>pseudotigrinus</i>
<i>latifrons</i>	<i>latifrons</i> <i>frenatus</i> <i>fraseri</i>	<i>squamulatus</i>	-	-	-
<i>aequatorialis</i>	<i>aequatorialis</i> <i>eulaemus</i> <i>mirus</i> <i>parilis</i>	-	+	-	-
<i>punctatus</i>	<i>chocorum</i> <i>chloris</i> <i>fasciatus</i> <i>peraccae</i> <i>festae</i> <i>boettgeri</i> <i>gemmosus</i> <i>nigrolineatus</i> +	<i>jacare</i> <i>nigropunctatus</i>	<i>punctatus</i> <i>transversalis</i> <i>dissimilis</i> <i>caquetae</i> <i>detae</i> +	-	<i>punctatus</i>
II. β anoles					
Groups					
<i>meridionalis</i>	-	-	-	<i>meridionalis</i>	-
<i>petersi</i>	<i>biporcatus</i> <i>apollinaris</i> <i>sulcifrons</i> <i>ibague</i>	-	-	-	-
<i>pentaprion</i>	<i>pentaprion</i>	-	-	-	-
<i>lemurinus</i>	<i>vittigerus</i> +	-	-	-	-
<i>lionotus</i>	<i>poecilopus</i> <i>macrolepis</i>	-	-	-	-
<i>humilis</i>	<i>notopholis</i>	-	-	-	-
<i>fuscoauratus</i>	<i>maculiventris</i> <i>antonii</i> +	<i>fuscoauratus</i>	<i>fuscoauratus</i> <i>ortoni</i> <i>trachyderma</i>	-	<i>fuscoauratus</i> <i>ortoni</i>
<i>auratus</i>	<i>auratus</i> <i>tropidogaster</i> <i>bitectus</i> <i>granuliceps</i> <i>gracilipes</i>	<i>auratus</i> <i>tropidogaster</i>	<i>auratus</i> <i>chrysolepis</i> <i>bombiceps</i>	<i>chrysolepis</i>	-
<i>onca</i>	-	<i>onca</i> <i>annectens</i>	-	-	-

to unfold. I have annotated some of the papers cited below to indicate their utility or to point out possible sources of error. I provide also a provisional key to species groups. I am acutely aware of its inadequacy; it is precisely the more difficult groups (e.g. the *punctatus* and *fuscoauratus* groups) that are separated by the characters least easy to use. I am unable to do better at this time, but I feel the need to provide as much help as I can in this first paper. For more the reader must wait for the succeeding papers in the series.

A PROVISIONAL KEY TO THE SPECIES GROUPS OF SOUTH AMERICAN *Anolis*
(NO EXTRALIMITAL SPECIES ARE CITED)

1. Toes with smooth lamellae under phalanges two *and* three ... 2
Lamellae absent or under phalanx two only *annectens* group
(Two species, *onca* and *annectens*, in northern Venezuela and adjacent Colombia).
2. A protuberance *above* the rostral scale (proboscis) present
..... *laevis* group
(Three species, one, *phyllothinus*, in middle Amazonia, one, *proboscis*, in trans-Andean Ecuador, one, *laevis*, in Amazonian Peru).
No proboscis 3
3. Axillary pockets present *humilis* group
(One species, *notopholis*, in trans-Andean Colombia).
No axillary pockets 4
4. A zone of enlarged *flat* smooth or slightly keeled dorsal scales
..... *lionotus* group
(Two species, *poecilopus* and *macrolepis*, both in trans-Andean Colombia).
Middorsals, if enlarged, not flat 5
5. Ventrals smooth and/or dorsal squamation quite uniform 6
Ventrals keeled, middorsals noticeably larger than flank cells
..... 11
6. Small anoles (ca 50 mm snout-vent length) with large, flat
head scales 7
Anoles large or small but not with large head scales 8
7. Tail compressed, caudal vertebrae with transverse process
..... *pentaprion* group
(Trans-Andean and inter-Andean Colombia).
Tail round, caudal vertebrae without transverse processes
..... *tigrinus* group
(A disjunct distribution, NE Colombia, northern Venezuela and Espírito Santo in eastern Brasil).
8. Toe lamellae narrow in species of moderate to large size
..... *eulaemus* group
Toe lamellae wide 9

9. Giant anoles (over 100 mm snout-vent length) ... *latifrons* group
(Trans-Andean and inter-Andean Colombia, trans-Andean Ecuador and northern Venezuela).
Anoles under 100 mm snout-vent length 10
10. Caudal vertebrae with transverse processes .. *fuscoauratus* group
(Widespread on both sides of the Andes).
Caudal vertebrae without transverse processes. .. *punctatus* group
(Widespread on both sides of the Andes).
11. Fourth toe lamellae 21 or more *biporcatus* group
(Trans-Andean and inter-Andean Colombia, trans-Andean Ecuador).
Fourth toe lamellae 20 or less 12
12. Adhesive digital pads projecting at least slightly beyond insertion
of first phalanx *chrysolepis* group
(Widespread on both sides of the Andes).
Adhesive digital pads joined to first phalanx without a projecting
edge *meridionalis* group
(One species in central Brasil).

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No. 60-2529. [Map 2, which has been copied more than
once, is in error on the distribution of the alpha section of
Anolis in South America; it is as widespread to the east as
the beta section.]
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1966. Studies on South American anoles: *Anolis transversalis* A. Duméril. *Pap. Avuls. Dept. Zool.*, S. Paulo, 19: 197-204. [The figure is of a female, not a male.]

