

STUDIES ON THE FAUNA OF CURAÇAO AND OTHER
CARIBBEAN ISLANDS: No. 134.

THE LIZARDS OF THE ANOLIS EQUESTRIS COMPLEX
IN CUBA

by

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	Pages	Figures
INTRODUCTION	1	
SPECIES ACCOUNTS	8	
<i>Anolis luteogularis</i> Noble & Hassler	8	
— <i>luteogularis luteogularis</i> Noble & Hassler	8	1, 5A
— <i>luteogularis nivevultus</i> new subsp.	11	1, 5B
— <i>luteogularis hassleri</i> Barbour & Shreve.	14	1, 5C
— <i>luteogularis delacruzii</i> new subsp.	16	1, 5D
— <i>luteogularis sectilis</i> new subsp.	19	1, 5E
— <i>luteogularis coctilis</i> new subsp.	22	1, 5F
— <i>luteogularis calceus</i> new subsp.	25	1, 5G
— <i>luteogularis jaumei</i> new subsp.	27	1, 5H
<i>Anolis equestris</i> Merrem	30	
— <i>equestris equestris</i> Merrem	31	2, 6A
— <i>equestris buidei</i> new subsp.	34	2, 6B
— <i>equestris persparsus</i> new subsp.	36	2, 6C
— <i>equestris juraguensis</i> new subsp.	39	2, 6D
— <i>equestris thomasi</i> Schwartz	42	2, 6E
— <i>equestris verreonensis</i> new subsp.	44	2, 6F
The Oriente situation	48	
<i>Anolis noblei</i> Barbour & Shreve.	51	
— <i>noblei noblei</i> Barbour & Shreve	52	3, 7A
— <i>noblei galeifer</i> Schwartz	53	3, 7B
<i>Anolis smallwoodi</i> Schwartz	56	
— <i>smallwoodi smallwoodi</i> Schwartz	56	4, 8A
— <i>smallwoodi palardis</i> Schwartz.	59	4, 8B
— <i>smallwoodi saxuliceps</i> Schwartz	63	4, 8C
<i>Anolis baracoae</i> Schwartz	66	4, 8D
DISCUSSION	69	
Extracto.	77	
REFERENCES	78	

Anolis equestris Merrem, the Cuban giant anole, was described in 1820. The formal description is based upon an account of the lizard by CUVIER ("le grand *Anolis* à crête") in 1817. MERREM's description is very brief but sufficiently detailed to assign the name to the Cuban species rather than to any other Antillean giant anole. The lizard was redescribed by BELL (1827) as *Anolius* [sic] *rhodolaemus*, based upon material collected by W. S. MACLEAY. NOBLE & HASSLER (1935) named *Anolis luteogularis* from a long series from western Cuba. This species was relegated to subspecific status under *A. equestris* by BARBOUR & SHREVE (1935), who also named *A. e. hassleri* from the Isla de Pinos (based upon two specimens) and *A. e. noblei* from eastern Cuba (based upon three specimens). SCHWARTZ (1958) named *A. e. thomasi* from Camagüey Province and later (1964) reviewed the status of the species in Oriente Province, naming *A. e. smallwoodi*, *A. e. palardis*, *A. e. baracoae*, *A. e. galeifer*, and *A. e. saxuliceps*. As presently understood, there are ten subspecies of *A. equestris* throughout Cuba and the Isla de Pinos. Comments by SCHWARTZ (1964) indicated that there were several Oriente specimens which did not agree with the concepts of the subspecies defined by him and suggested that there was still a great deal to be learned about the distribution and variation in *A. equestris* at least in Oriente, the physiographically and ecologically most diverse of the Cuban provinces.

The junior author became interested in *A. equestris* when he encountered lizards from various Cuban localities which did not agree in detail with taxa already named. In addition, the discovery of two "subspecies" (*equestris* and *luteogularis*) occurring syntopically in the same wooded area suggested that perhaps the entire complex needed serious restudy and revision. Accordingly, GARRIDO made extensive collections of *A. equestris* from much of Cuba and the Isla de Pinos (whence previously only very few specimens have been available) as well as on Cayo Cantiles in the Archipiélago de los Canarreos. In addition, GARRIDO succeeded in securing large series of some populations which had previously been known from single individuals or very small samples.

Material collected by the senior author, under National Science Foundation grants G-3865 and G-6252, is deposited in the American Museum of Natural History (AMNH) and that collected by the junior author in the Instituto de Biología, Academia de Ciencias (IB). In addition to examination of our own material, much of which is carefully documented as far as coloration and pattern in life are concerned, we have examined specimens in the collection of Brigham Young University (BYU), Museum of Comparative Zoology (MCZ), Museo Felipe Poey (MFP), Natur-Museum und Forschungs-Institut Senckenberg (SMF), Museum of Zoology, University of Michigan (UMMZ) and the United States National Museum (USNM). For the courtesy extended to us in the loan of material we wish to thank WILMER W. TANNER, ERNEST E. WILLIAMS, MIGUEL L. JAUME, ROBERT MERTENS, CHARLES F. WALKER, ARNOLD G. KLUGE, the late DORIS M. COCHRAN, and JAMES A. PETERS. Our collaboration has been made possible through the efforts of Ing. HÉCTOR SAGUÉ D. and Ing. ISRAEL GARCÍA. In the field the senior author has had the cooperation of JOHN R. FEICK, WILLIAM H. GEHRMANN, Jr., RONALD F. KLINIKOWSKI, DAVID C. LEBER, LARRY H. OGREN, JAMES D. SMALLWOOD, BARTON L. SMITH, RICHARD THOMAS, PETER J. TOLSON, JAMES A. RODGERS, Jr., and GEORGE R. ZUG. MESSRS. KLINIKOWSKI and LEBER were recipients of National Science Foundation Undergraduate Research Participation grants under the direction of the senior author. The black-and-white drawings of the heads of the various taxa are the work of DAVID PARROTT. We are greatly in his debt for his efforts on our behalf - efforts which add to the visualization of these lizards and of the characteristics which we regard as taxonomically important. Finally, ANDREW SPIELMAN donated specimens of giant anoles which he had collected while stationed at the United States Naval Base at the Bahía de Guantánamo in 1958.

We have been especially fortunate not only in being able to assemble a total of 583 *Anolis equestris* from American, Cuban, and foreign collections, but also in that we have had access to the excellent collections made by CHARLES T. RAMSDEN in the vicinity of the city of Guantánamo, Oriente Province. These lizards, previously housed at the Universidad de Oriente in Santiago de Cuba, have now been placed in the Museo Felipe Poey. The Guantánamo area is particularly critical as far as Oriente *equestris* is concerned and the importance of the RAMSDEN material can hardly be minimized. In addition to specimens in the collections noted above, we have studied specimens in the Museo y Biblioteca de Zoología de la Habana (MBZH), under the direction of Sr. JAUME, as well as other specimens, more recently collected, in Sr. JAUME's collection (MLJ), plus material in the collections of the senior author (AS and ASFS).

The senior author, through the efforts of PETER J. TOLSON and the United States Marine Corps, was able to spend two weeks on the United States Naval Base at the Bahía de Guantánamo in 1969. Mr. TOLSON had previously secured a specimen of giant anole on the Naval Base prior to the visit, and JAMES A. RODGERS, Jr., secured two more individuals during the time of our visit. These specimens, along with paratypes of new subspecies, are deposited in the Albert Schwartz Field Series (ASFS). Paratypes of many new taxa have been deposited in the Harvard (MCZ) and United States National Museum (USNM) collections, and also in the collection of the National Museum of Canada (NMC).

We have no illusions that our conclusions concerning the *Anolis equestris* complex are final. First, there are too many areas in Cuba whence there is still no available material, despite the fact that we now have abundant specimens from some regions. There are still isolated lizards from various places about whose taxonomic position we are uncertain. Secondly, and perhaps more important, our systematic arrangement is partially inductive. We have certain evidence for sympatry and syntopy for two forms (*equestris* and *luteogularis*, *galeifer* and *smallwoodi*, *noblei* and *saxuliceps*) in only three areas. In two of these instances, GARRIDO has collected both *equestris* and *luteogularis*, and *noblei* and *saxuliceps* in the same immediate area, without evident intergradation. The two forms in each case are quite distinctive in both scutellation and color and pattern. Additional material, in the United States National Museum, indicates that sympatry between *equestris* and *luteogularis* occurs elsewhere but has gone unrecognized until now. There are specimens of *galeifer* and *smallwoodi* with identical locality data, but in this case the material was collected by persons other than ourselves and thus is subject to some (albeit possibly very slight) doubt. In addition, there is an old specimen of *thomasi* from "Santiago de Cuba" (presumably within the range of *smallwoodi*) which presents an added problem insofar as nomenclaturally arranging the forms *galeifer*, *smallwoodi*, and *thomasi* in some reasonable manner. All in all, we have attempted to adhere to a conservative course and have let the specimens determine the number of species involved.

In some ways, the situation in the *equestris* complex resembles that of the species *Leiocephalus cubensis* and *L. stictigaster*: there are no meristic data which will absolutely separate the entities which we are regarding as full species. This is quite in contrast to the status of the two species of *Chamaeleolis* (GARRIDO & SCHWARTZ, 1968) wherein we were able to differentiate two species on the basis of both structural and meristic characters. Also, in the *equestris* complex, when data from all populations which we assign to a particular species are combined, our species diagnoses themselves become weakened. For instance, *equestris* and *luteogularis* (which we regard as full species because of the sympatry without character

dilution as noted above) are eminently distinct entities both through their currently known ranges and in the area of geographic overlap; no one should experience difficulty in distinguishing these species in Pinar del Río and Habana provinces. Nominate *luteogularis* is a small-scaled form with 14 to 27 vertical dorsal scales in the snout-eye distance (see below for techniques for counting scales) and nominate *equestris* is a much larger-scaled form with 10 to 18 vertical dorsal scales. There are also very characteristic pigmental and pattern differences between the nominate forms of these two species. However, when we combine the vertical dorsal counts, for instance, of all populations which we regard as subspecies of *equestris* or *luteogularis*, the count in the former is 9 to 19, in the latter 11 to 27. Here, even though *luteogularis* has consistently higher counts, the amount of overlap is greater (and thus scale size *per se* is variable) and one criterion for species differentiation is somewhat weakened.

We have taken the following measurements and counts on all specimens: 1) snout-vent length in millimeters; 2) number of vertical dorsal scales included in the distance between the tip of the snout and the anterior border of the orbit; 3) number of horizontal dorsal scales included in the distance between the tip of the snout and the anterior border of the orbit; 4) number of vertical caudal scales, taken near the base of the tail, in the snout-eye distance; 5) number of supralabials to the center of the eye; 6) number of lamellae on phalanges II and III of the fourth toe. As one of us (SCHWARTZ, 1960: 408) previously stated, the taking of the snout-eye counts is subject to the vagaries of preservation of any particular specimen. Lizards which have been injected and laid out to harden neatly in trays give reliable counts of dorsal scales, whereas those which have been curled in jars, have not been injected, or have been haphazardly preserved give counts which are less (often very much less) reliable. This is especially true of counts of horizontal dorsals; when the snout-eye distance is placed upon the side of an uninjected lizard, this count is invariably higher than that on an injected or well preserved specimen since some of the much smaller ventral scales are included in the count. We have avoided this pitfall by

not including data from such specimens. The number of fourth toe lamellae likewise is unreliable. It is a rare lizard indeed in which there are complete lamellae extending the entire lengths of phalanges II and III. For varying distances (especially on phalanx III) the lamellae are most often interrupted by a series of divided or irregularly arranged scales which appear to be aberrant lamellae. There is no way to avoid including such scales in a lamellar count, and our counts include those from many lizards with such a condition. As far as supralabials to eye center are concerned, although this feature is variable and there seem to be some trends toward more or less supralabials in several populations, the variability is such that we do not use this count to diagnose species or subspecies. When everything is considered, we have placed most emphasis on snout-vent length and vertical dorsal and caudal counts, since these are the most reliable and lack or minimize the error inherent in horizontal counts and fourth toe lamellar counts.

In *Anolis*, color and pattern play a vital part in species and subspecies definitions. We are fortunate in that many of the lizards collected by ourselves are well documented as far as color and pattern are concerned. Although *A. equestris* and its relatives often demonstrate metachrosis, with hues varying between greens and browns, there are fortunately stable pattern differences between populations which remain, despite changes in hues of the lizards themselves. In addition, the precise shade of green, for instance, which most forms demonstrate, varies by population. The stability of pattern elements and the shades involved in the body color are fortunate adjuncts to the study of *A. equestris*. But, as in all instances where the investigator must use undocumented material collected by others, we are much less certain of our assignments of lizards not collected by ourselves. In some cases, of course, we have no doubts, but in others we are not so certain as we might wish to be; we have had no hesitancy in stating the situation when it arises.

Dewlap color, often a very strikingly differentiating character in species and subspecies of *Anolis* (see SCHWARTZ, 1968, in *Anolis distichus*) is annoyingly stable in the *equestris* complex. Most populations have the dewlap some shade of pink, but one population

has a white dewlap, another an orange dewlap, and a third may have a blue-green dewlap. The orange-dewlapped lizards, nominate *luteogularis*, are distinctive in dewlap color from all other populations; but if we correctly associate other populations with *A. luteogularis*, the dewlap color in the species (by population) varies from orange to pink and whitish yellow. Since other populations (of *A. equestris*) regularly have pink to white dewlaps, dewlap color is not a character which is species-constant.

Our division of "*Anolis equestris*" into five species is virtually without precedent. However, when NOBLE & HASSLER described *luteogularis*, that taxon was named as a species distinct from *A. equestris*; apparently they were convinced that *luteogularis* and *equestris* were two separate entities, not subspecies of the same species. The junior author proposed, at the outset of the present study, a series of three hypotheses; these hypotheses demonstrate our reasoning and the courses of action open to us.

1) There is but one variable species, *Anolis equestris*. We reject this hypothesis on the basis of certain sympatry between *luteogularis* and *equestris*, and *noblei* and *saxuliceps* and virtually certain sympatry between *galeifer* and *smallwoodi*.

2) There are two species, *A. luteogularis* and *A. equestris*, each of which is variable in its own right, with several subspecies. This would be the simplest course of action and would minimally multiply the species involved. But the evidence of near sympatry without intergradation between pairs of "subspecies" in Oriente Province deters us from using this as a basis for further elaboration.

3) There are five species (*equestris*, *luteogularis*, *thomasi*, *baracoeae*, and a small form on Cayo Cantiles). This arrangement has much to recommend it, but we arrange *thomasi* as a subspecies of *equestris*. As far as the Cayo Cantiles lizards are concerned, we now regard them as a dwarf representative of *A. luteogularis*; perhaps they would be better considered a separate species, but such a course is not deemed advisable for the present.

Our final arrangement, which fits the facts as presently demonstrated, is that "*Anolis equestris*" is a composite of five species: *A. luteogularis*, *A. equestris*, *A. noblei*, *A. smallwoodi*, and *A. baracoeae*

The rationale for this division will be discussed in detail in the present paper. The species are discussed from west to east.

SPECIES ACCOUNTS

Anolis luteogularis Noble & Hassler

Anolis luteogularis NOBLE & HASSLER, 1935, Copeia 3: 113.

TYPE LOCALITY: San Diego de los Baños, Pinar del Río Province, Cuba.

DEFINITION: A giant species of the genus *Anolis* characterized by a combination of 1) moderate to high number of vertical dorsal scales, 2) moderate number of caudal scales, 3) size variable from very large to very small by population, 4) dewlap variable, from orange to pink or whitish yellow, 5) axillary stripe white or dull yellow, at times with a yellow to mustard "tongue" included in the stripe over the forelimb insertion, 6) upper and lower jaws white or pale yellow and often with a bold dark (brown) streak or elongate subangular blotch on the gular region below the angle of the jaws, and 7) tail with broad transverse bands.

DISTRIBUTION: Western Cuba, including Pinar del Río and western Habana provinces; the Península de Zapata in Las Villas Province; Isla de Pinos, and Cayo Cantiles in the Archipiélago de los Canarreos (Fig. 1).

Anolis luteogularis luteogularis Noble & Hassler

DEFINITION: A subspecies of *Anolis luteogularis* characterized by a combination of 1) large size (males to 191 mm, females to 176 mm snout-vent length), 2) high number of vertical dorsal scales (14–27), 3) high number of caudal scales (19–28), 4) body yellow-green, heavily flecked with yellow on individual scales giving in general a finely dotted aspect, 5) dewlap pale orange, rarely peach, pink, or yellow, 6) axillary stripe dull yellow, fairly conspicuous, 7) jaws white or yellow (Fig. 5A), 8) subangular blotch absent or very much reduced, and 9) tail banded gray and brownish.

DISCUSSION: *Anolis luteogularis luteogularis* occurs throughout

much of Pinar del Río Province, from the vicinity of Isabel Rubio on the west, east to Habana Province (Bosque de la Habana, Laguna de Ariguanabo, San Antonio de los Baños, Central Providencia). The nominate form is replaced in extreme western Pinar del Río by a different subspecies on the Península de Guanahacabibes. Throughout its relatively broad range, *A. l. luteogularis* remains remarkably constant in its color and pattern features. *A. l. luteogularis* occurs sympatrically with *A. e. equestris* in Habana Province and details of this sympatry will be discussed under the latter form.

Anolis luteogularis luteogularis is basically a greenish yellow lizard flecked with yellow dots which encompass one (or two at times) small dorsal scale, thereby giving an overall flecked-with-yellow appearance. The throat, lower and upper jaws are white to yellow, unmarked or without pattern, and the pale upper jaw color extends upward to invade at least part of the loreal region. Often the canthal scales and the snout are also concolor with the pale throat and upper jaw scales. The white or yellow gular color regularly sends a branch dorsad just posterior to the auricular opening onto the posttemporal region. The subangular dark marking is always much reduced or absent, and never reaches the intensity of the mark in some other *luteogularis* subspecies. The top of the head (= casque) is flecked with yellow in the same fashion as the remainder of the body; the scales on the upper surfaces of both the fore- and hindlimbs likewise are flecked with yellow. The axillary stripe is pale yellow, usually not extensive (restricted to the anterior third or quarter of the flank) and is fairly conspicuous. The tail is transversely banded with broad bands of gray and brownish, although some individuals show this feature to a lesser degree than others. The venter is pale yellowish to pale greenish.

Meristic data (means and extremes) for 105 *A. l. luteogularis* are: vertical dorsals 14–27 (18.9), horizontal dorsals 15–26 (19.8), caudals 19–28 (23.4); largest male 191 mm, largest female 176 mm snout-vent length. Supralabials to eye center vary between 7/7 and 10/10; the mode is 8/9. Fourth toe lamellar counts vary between 28 and 43 (mean 36.2).

Dewlap colors are generally some shade of orange (MAERZ &

PAUL, 1950, designations include Pls. 3A9, 2A9, 9C6, 11B6) although a few specimens have been recorded as "pale pink" (AMNH 78078-81), "pink" (AMNH 78082) and "pale yellow" (AMNH 78150). Of these aberrant individuals, AMNH 78078-82 are from San Vicente, whence many orthodoxly colored specimens are available, and AMNH 78150 is from the same general region (Cabezas).

The juvenile pattern consists of four fine yellow crossbands between the neck and the sacrum on a green ground (AMNH 82864, IB 1163); the two small lizards with this pattern have snout-vent lengths of 70 mm and 73 mm. However, another juvenile (AMNH 83030) lacks indications of the crossbands and has a snout-vent length of 67 mm. A somewhat larger lizard (MCZ 7939, snout-vent length 96 mm) still shows remnants of the pale crossbands. All other subadult *A. l. luteogularis* lack pale crossbands. Additionally, young lizards are not so clearly flecked with yellow as are adults, although incipient dotting occurs in lizards with snout-vent lengths of 112 mm.

In addition to the specimens listed below, we have casually examined a long series (AMNH 46134-73, 57751-52) of *A. l. luteogularis* purportedly collected in "Havana" by JACOBO EZRA in July 1931. Although, as we have noted previously, *A. l. luteogularis* occurs in Habana Province and even within the city limits of La Habana itself, it seems hardly likely that this entire lot of lizards originated in La Habana or even in the province; in all other collections from Habana Province *A. equestris* greatly outnumbers *A. luteogularis*, and the former appears to be the dominant member of the species pair in that region. Accordingly, we have not included these specimens in our calculations and suspect that in reality they were collected somewhere in Pinar del Río Province, were shipped from La Habana, and were subsequently mislabeled as to locality.

SPECIMENS EXAMINED: *Pinar del Río Province*. 7.6 mi. (12.2 km) E Isabel Rubio, 2 (AMNH 78086-87); San Vicente, 44 (MCZ 38411, AMNH 78076-82, AMNH 78084-85, AMNH 78088-114, AMNH 78150, AMNH 76547, AMNH 82862, AMNH 82864-66, AMNH 83030); Baños San Vicente (not mapped), 4 (MCZ 38407-10); mountains near (= NW) San Vicente, 1 (AMNH 78075); Viñales, 1 (AMNH 78083); cave 1, near Viñales (not mapped), 2 (MCZ 55576-77); Valle de Pío Domingo, Pica Pica (not mapped), 1 (IB 1163); Valle de Pica Pica, Sumidero, 1 (ASFS V22306); 8.4 mi. (13.4 km) W San Vicente, 1 (AMNH 82863); "Mt. Mogota" (not mapped),

1 (AMNH 7762); Pinar del Río, 1 (MCZ 11978); El Guamá, 1 (USNM 27334); Herradura, 1 (MCZ 7905); San Diego de los Baños, 22 (MCZ 7939, USNM 27504, USNM 75811, USNM 75813-15, AMNH 58764-72 + 6 untagged specimens, AMNH 63088); Soroa, 3 (IB 348-49, ASFS V22305); Candelaria, 6 (IB 350-52, IB 354-55, IB 361); Guanajay, 1 (USNM 27675); swamps south of Artemisa, 5 (AMNH 49046-49, AMNH 57961); Finca la Selva, Artemisa, 1 (IB 347); Vuelta Abajo (not mapped), 4 (IB 343-46); Cabañas, 1 (USNM 51842); La Ortigosa, 1 (IB 366). - *Habana Province*. Paredones, Ceiba del Agua, 6 (IB 353, IB 358-60, ASFS V22320-21); Laguna de Ariguanabo, 1 (IB 489); El Husillo, Puentes Grandes, 3 (IB 367-68, IB 448); Bosque de la Habana, 1 (IB 408); San Antonio de los Baños, 1 (MCZ 10917); Central Providencia, S of Güines, 1 (USNM 164275).

***Anolis luteogularis nivevultus*, new subspecies**

Anolis equestris guanahacabibensis G. PETERS, 1970, Mitt. Zool. Mus. Berlin 46: 203.
[nomen nudum]

HOLOTYPE: IB 339, an adult male, from El Veral, Península de Guanahacabibes, *Pinar del Río Province, Cuba*, taken 11 November 1965 by I. García and R. G. Broche.

PARATYPES: All from Pinar del Río Province, USNM 51841, Cabo de San Antonio, J. B. Henderson and P. Bartsch, 26 May 1914; MCZ 119384, La Tumba, O. H. Garrido, 18 January 1966; ASFS V22307, NMC 12273, La Jaula, native for O. H. Garrido, 20 January 1966; MCZ 119383, La Jaula, native for O. H. Garrido, 11 April 1966; NMC 12272, María la Gorda, M. O. Facciolo, 16 January 1966; ASFS V22308, María la Gorda, native for O. H. Garrido, 1 May 1966; IB, El Veral, L. Moreno and O. H. Garrido, 1 December 1967; IB, El Veral, L. Moreno, 28 November 1967; IB, Caravelita, L. Moreno, 6 December 1967; IB (2 specimens), Limón Chico (La Jaula), L. Moreno, 14 December 1967.

Name from Latin "niveus" (snowy, white as snow) and "vultus" (countenance) in allusion to the extensively white face.

DEFINITION: A subspecies of *Anolis luteogularis* characterized by a combination of 1) moderate size (males to 176 mm, females to 167 mm snout-vent length), 2) low number of vertical dorsal scales (12-19), 3) low number of caudal scales (17-23), 4) body grayish yellow or greenish yellow with many darker scales greenish brown to blackish and without yellow dots or flecks as in the nominate subspecies, 5) dewlap pure pink, 6) axillary stripe not conspicuous in life, white to whitish with some yellow anteriorly above forelimb insertion, 7) jaws marble-white with a post-temporal and nuchal whitish to white diffuse spot or figure (Fig. 5B), 8) subangular blotch usually long, prominent and dark brown and 9) tail banded with grayish brown.

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 162 mm and tail length of 292 mm; horizontal, vertical, caudal, and supralabial counts not taken since head is somewhat crushed; 41 fourth toe lamellae.

Color (as preserved) pale brown without paler dotting or flecking; casque slightly darker brown, without dotting or flecking but suffused posteriorly with whitish; canthal scales white; circumorbital skin brown, the brown extending posteriorly as a rather poorly defined postocular spot; throat, lower lips and upper lips white, the white extending dorsad to encompass almost all of the loreal region, the lower portion of the temples (below the darker postocular spot), and including the auricular opening; occiput white, with a pair of brown spots on the neck, the white occipital area extending onto the neck as a rather diffuse and large whitish figure; axillary stripe white, broad and fairly extensive, its anterior end sharply delimited by an irregular dark brown lateronuchal blotch which extends, with a slight interruption, as a dark brown subangular stripe on the sides of the otherwise immaculate throat; limbs concolor above with dorsum, the forelimbs irregularly marked with grayish, the hindlimbs with a pair of gray transverse lines on the thigh and three lines on the crus, and two lines on the pes; tail conspicuously banded with about 14 broad brown bands alternating with narrower gray bands; venter dull grayish tan.

VARIATION: The series of 13 *Anolis luteogularis nivevultus* has the following counts: vertical dorsals 12–19 (16.1), horizontal dorsals 13–17 (14.1), caudals 17–23 (19.8). Supralabials are either 8/8 or 8/9; the mode is 8/9. Fourth toe lamellae range from 35 to 42 (mean 38.1). The largest male has a snout-vent length of 176 mm, the largest female 167 mm. Color notes made by the junior author indicate that the body color varies between greenish yellow and grayish yellow with many darker scales which are greenish brown to blackish. The dewlap is pure pink in life, and the axillary stripe, although broad and fairly extensive, is inconspicuous in the living animals; the stripe is white to white with some yellow above the forelimb insertion at the beginning of the stripe. The head is grayish, often with some bluish in the parietal and temporal regions. The throat and lips are marble-white and the venter is lemon yellow or

greenish, and at times the uppersides of the limbs and tail are also greenish.

As preserved, the paratypic series agrees very well with the description of the holotype. Most striking features are the extensive upward extension of the white supralabial markings to include the ear opening and the posterior temporal region, the inclusion of at least the lower half of the loreal region in the white supralabial pigmentation, and the usually extensive dark brown subangular marking which may in some specimens extend more than half way the length of the mandible. The axillary stripe is usually very bold, but in the only subadult specimen (MCZ 119384, snout-vent length 127) it is not obvious against the paler dorsolateral ground. There is always some white marking on the occiput and anterior neck, and often on the snout and canthals, but none of the paratypes has these white areas so extensive as does the holotype.

COMPARISONS: *Anolis luteogularis nivevultus* differs very strikingly from the nominate subspecies. The much larger dorsal scales in *nivevultus* (verticals 12–19) contrast with the much smaller dorsals in *luteogularis* (verticals 14–27); although the amount of overlap is great, mere observation of scale size between the two subspecies convinces the observer that the eye is a more efficient tool than the vernier. Other features of differentiation between the two forms include the absence of individual scale flecking in *nivevultus* and the inclusion of the auricular opening in the dorsad extension of the white labial pigment. In *luteogularis*, this white dorsal extension occurs only behind the opening, not before it. The well developed subangular marking in *nivevultus* contrasts with its usual absence (or at best very reduced condition) in *luteogularis*.

Anolis luteogularis luteogularis and *A. l. nivevultus* are known from localities separated by about 48 kilometers (*nivevultus* from La Jaula, *luteogularis* from Isabel Rubio). Part of the intervening area is the Plains of Remates, which separate the forested Península de Guanahacabibes (which is inhabited by *nivevultus*) from the more eastern forests, both in the uplands and lowlands, which are the home of *luteogularis*. We do not know which subspecies, if any, occurs in the Plains of Remates, but suspect that this region is inhabited by *luteogularis*. Several subspecies of other reptiles

(*Dromicus andreae*, *Leiocephalus carinatus*, *L. macropus*, *L. stictigaster*, *Ameiva auberi*) are limited to the Península de Guanahacabibes and are separated from their relatives on the mainland by the Plains of Remates, or intergrade with mainland subspecies in that region. In addition, *Anolis quadriocellifer* is a species restricted to the Peninsula and *Leiocephalus raviceps* has an isolated outlier subspecies in this general region. It is therefore not surprising that *A. l. niveovultus* has also diverged from its parent stock in Pinar del Río Province.

***Anolis luteogularis hassleri* Barbour & Shreve**

Anolis equestris hassleri BARBOUR & SHREVE, 1935, Occ. Papers Boston Soc. Nat. Hist. 8: 251.

TYPE LOCALITY: Los Indios, Isla de Pinos, Habana Province, Cuba.

DEFINITION: A subspecies of *Anolis luteogularis* characterized by a combination of 1) moderate size (males to 180 mm, females to 171 mm snout-vent length), 2) moderate number of vertical dorsal scales (13–20), 3) moderate number of caudal scales (19–24), 4) body green to bottle green or brown, with four clear blue to pale blue-gray transverse bands and without a dotted aspect, 5) dewlap pink basally, spotted with white distally, 6) axillary stripe white in brown phase, absent or inconspicuous in green phase (Fig. 5C), 7) jaws white, subangular brown blotch usually absent or very small and restricted, and 9) tail prominently banded in same colors as body.

DISCUSSION: *Anolis luteogularis hassleri* was described from two adult females from Los Indios on the northern portion of the Isla de Pinos. The Isla de Pinos is composed of two parts, of which the northern two thirds are separated from the southern third by the Ciénaga de Lanier; effectively, then, the Isla de Pinos is two islands, divided by an extensive swamp, across which there is little means for genetic exchange for terrestrial animals except at such localities as Paso de Piedras, a forested corridor between the two "islands". Giant anoles have regularly been difficult to secure on the Isla, but

the junior author and his companions have succeeded in securing good series from both the northern and southern portions of the Isla de Pinos. As in the case of *Leiocephalus stictigaster* (SCHWARTZ, 1959), the *A. luteogularis* from the two parts of the Isla are distinctly different; even more remarkably, the northern section of the Isla de Pinos has two subspecies of *A. luteogularis*, one of which (*hassleri*) is widespread and the other (to be named below) has an apparently limited distribution at Santa Isabel in the southeastern portion of the northern section of the Isla de Pinos. Rationale for this peculiarity will be discussed beyond.

Meristic data on the series of 16 *A. l. hassleri* are: vertical dorsals 13–20 (17.8), horizontal dorsals 16–28 (20.1), caudals 19–24 (21.1); largest male 180 mm, largest female 171 mm snout-vent length. Supralabials to eye center vary between 7/7 and 9/9; the mode is 8/9. Fourth toe lamellar counts vary between 32 and 42 (mean 36.4).

Anolis luteogularis hassleri is a relatively small-scaled subspecies like *A. l. luteogularis*, but its style of coloration and pattern are completely different from those of the nominate subspecies, *A. l. hassleri* is basically a green (tending toward deep bottle green) lizard with four clear blue to blue-gray crossbands on the dorsum; the lizards are capable of assuming a brown phase and the crossbands persist when this metachrosis takes place. The tail, in either phase, is also prominently crossbanded in the same colors as the body itself. The venter is lemon yellow to greenish in the green phase. The axillary stripe is white but not especially conspicuous in the green phase because of the disruptive effect of the first two pale body crossbands. The gular region and upper and lower lips are white, but the white pigment seldom invades the loreal region. The brown subangular blotches are usually small to absent, but in one lizard (ASFS V22310) they are long and conspicuous, and in another specimen (ASFS V22309) the entire posterior two-thirds of the throat are dark (almost black) in the preserved lizard. There is a dorsad extension of the pale lip color onto the temporal region in many specimens. This extension crosses the temples and extends toward the dorsal midline, and the auricular opening lies within it. The casque is mottled with green (or brown) and cream, and

usually there are more dark than light areas on the casque. A pale (cream) occipital figure is variably expressed; in some specimens (IB 378) it is large and extensive, and in others it is much smaller and restricted by the darker dorsal color (ASFS V22310). There is often a darker brown parietal spot present in the brown phase.

The dewlap is basically pink above and pink-and-white blotched or spotted below.

The single juvenile (IB 1306), with a snout-vent length of 67 mm, shows no pale transverse body lines and is solid green; this is all the more remarkable since juvenile *A. l. luteogularis* show this pattern element and adults lack it, whereas in the *A. l. hassleri* juvenile, the body lines are absent. Two subadults (IB 375-76) with snout-vent lengths of 95 and 121 mm likewise show little or no indication of body banding although this may be an artifact of preservation.

Anolis luteogularis hassleri resembles *niveovultus* in basic cephalic coloration and pattern, but the latter subspecies is never cross-banded; in scutellation, *hassleri* is small-scaled and thus like *A. l. luteogularis*, but the latter is flecked and dotted rather than cross-banded as is *hassleri*. In addition, *luteogularis* rarely has the dewlap pink, whereas this is the basic color in *hassleri*.

SPECIMENS EXAMINED: *Isla de Pinos, Habana Province*. Finca Jaime Playa (not mapped), 1 (ASFS V22309); Sierra de Casas, Nueva Gerona, 1 (MBZH 183); Río Santa Fé, 7 (IB 377-81, IB 383, ASFS V22310); El Respiro, Santa Fé, 2 (IB 1285, IB 1292); Finca la Jungla, 1 (IB 372); La Vega, 3 (IB 374-76); Los Indios, 1 (IB 1306).

***Anolis luteogularis delacruz*, new subspecies**

HOLOTYPE: IB 1277, an adult male, from Santa Isabel, southeastern portion of the northern two-thirds of the Isla de Pinos, north of the Ciénaga de Lanier, *Isla de Pinos, Habana Province, Cuba*, taken by Gilberto Silva Taboada and Jorge de la Cruz on 20 March 1967.

PARATYPES: USNM 167301, NMC 12274, ASFS V22311-12, MCZ 119385, IB 1284, IB 1287, all with same data as holotype; IB 1283, same locality as holotype, G. Silva Taboada, J. de la Cruz, 23 March 1967.

Named in honor of one of the collectors, JORGE DE LA CRUZ.

DEFINITION: A subspecies of *Anolis luteogularis* characterized by a combination of 1) large size (males to 187 mm, females to 176

mm snout-vent length), 2) high number of vertical dorsal scales (15–21), 3) high number of caudal scales (20–26), 4) body distinctly bicolor (pale green to almost olive below, more brownish above, and with either longitudinal or transverse bands whitish) and apparently without a distinct green phase, 5) dewlap uniform pale pink with scales yellowish green and brown, 6) axillary stripe whitish, inconspicuous, with yellowish or greenish tints anteriorly, 7) throat and jaws white, often flecked with brown or green (Fig. 5D), 8) subangular blotches large and conspicuous in males, present but reduced in females, and 9) tail prominently banded whitish and chocolate-brown.

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 178 mm and tail length of 310 mm, almost complete; vertical dorsal scales 18, horizontal dorsal scales not countable, caudal scales 22, supralabials to eye center 8/9, 37 fourth toe lamellae.

Color (as preserved) rich dark brown above without indications of dorsal crossbands; tail brown above and with about ten pale (gray) crossbands indicated; venter pale grayish white, including upper and lower labials and chin, with a prominent pair of dark brown subangular blotches extending as far anteriorly as the posterior margin of the eye; lores white, the color confluent with that of the supralabials; casque brown, somewhat paler on the snout and occiput but no definite or well defined pale or dark areas delimited; supralabial white pigment extending dorsally to form a poorly defined auricular white patch; upper surfaces of limbs brown and grayish, with vaguely defined alternating rows of gray, brown and red-brown rows of scales to give a finely barred aspect; axillary stripe white but very vaguely defined.

VARIATION: The series of nine *Anolis luteogularis delacruzi* has the following counts: vertical dorsals 15–21 (18.3), horizontal dorsals 23–24 – four specimens only – (23.5), caudals 20–26 (22.6), supralabials 7/7 to 9/9 (mode 8/9), fourth toe lamellae 31–42 (36.1). *A. l. delacruzi* is generally a bicolor lizard which lacks a distinct green phase. The body coloration is brownish green or brown above with either longitudinal or transverse whitish body lines or bands, and the venter is pale green to almost olive. The tail is banded with

narrow whitish and broad chocolate-brown bands. The limbs and sides of the tail are yellowish green like the venter, the limbs with a profusion of whitish scales which become reddish brown as the lizard assumes the brown phase. In life, the anterior portion of the casque and the neck are flesh, whereas the supraocular area and the center of the casque is brownish; the supra- and infralabials are white, spotted with brown. The axillary stripe is indistinct and whitish, with at times some yellowish or greenish pigment anteriorly. The dewlap is uniform pale pink with the rows of scales yellowish green and brown. Males have large and conspicuous subangular brown markings. These markings are also present in females, but they may be somewhat reduced (or at least less well defined) in that sex than in males. As preserved, the casque may be entirely brown as described for the holotype, with limited and diffuse paler regions, or (as in NMC 12274) it may be entirely pale, or (as in USNM 167301) there may be extensive pale areas on the snout with less well defined pale areas on the occiput and parietal regions. The axillary stripe is regularly poorly defined and in many individuals it can be determined only with difficulty. The lores are regularly pale and concolor with the supra- and infralabial white coloration, and there is often a dorsad extension of the supralabial white pigment in the lower temporal region to include the auricular opening. Several specimens (ASFS V22311, ASFS V22312, USNM 167301) have a white nuchal "collar" which involves remnants of a first body crossband plus a pale occipital area. There are no juveniles in the short series.

COMPARISONS: Although it has high scale counts (and thus small scales), *Anolis luteogularis delacruzi* is easily distinguished from nominate *luteogularis* in that the latter is dotted whereas the former is not; the basic color in *A. l. luteogularis* is green, whereas the basic color of *delacruzi* is brown to brownish green above and with either transverse or longitudinal whitish bars or lines. From *nivevultus*, *delacruzi* differs in smaller scales and in an entirely different scheme of body and casque pattern and color. Obviously, *delacruzi* is most closely related to (and is presumably a derivative of) *A. l. hassleri*. These two subspecies can be distinguished by the bottle green to brown dorsal color of *hassleri* with four transverse clear blue body bands; the dorsum in *delacruzi* is brownish green to brown and

the body bands are whitish and not so prominent as in *hassleri*. *A. l. delacruzi* likewise has the subangular blotches well developed in males and at least indicated in females, whereas even male *hassleri* do not regularly have the blotches present, and rarely are they so well expressed as they are in male *delacruzi*. *A. l. delacruzi* averages greater in all scale counts and apparently reaches a slightly larger size in both sexes than does *hassleri*.

The occurrence of a distinctive subspecies of *A. luteogularis* in the southeastern portion of the northern section of the Isla de Pinos (which is elsewhere occupied by *A. l. hassleri*) is peculiar. *A. l. hassleri* inhabits both lowland and montane (Sierra de Casas) broadleaf forest but is absent from the pinelands which cover much of the Isla de Pinos. At Santa Isabel, the lizards were found exclusively in broadleaf forest on two isolated hills which are surrounded by the swampy lowlands of the Ciénaga de Lanier and by the bleak Isla de Pinos pinelands. Thus the Santa Isabel region consists of a broadleaf forest isolate, suitable for inhabitation by *A. luteogularis*, completely cut off from connections with *A. l. hassleri* to the north and from the southern Isla de Pinos subspecies (named below) to the south by the intervening swamp. The junior author was very impressed with the differences between *hassleri* and *delacruzi* when he saw the first specimens of the latter subspecies; many of the very distinctive features of *delacruzi* are obscured by preservation, and it was with some reluctance that the senior author was finally convinced of the distinctness and name-worthiness of this isolated population. But the very special situation which pertains at Santa Isabel tends to enforce the distinctness of *delacruzi* from *hassleri*. To group all these specimens together under one name obscures the characteristics of the Santa Isabel population.

***Anolis luteogularis sectilis*, new subspecies**

HOLOTYPE: IB 388, an adult male, from Pedernales, *Isla de Pinos, Habana Province, Cuba*, taken December 1965 by O. H. Garrido.

PARATYPES: All from Isla de Pinos, Habana Province. IB 387, IB 389, same data as holotype; IB 385–86, Carapachibey, O. H. Garrido, 11 October 1965; IB 384, Carapachibey, O. H. Garrido, 19 April 1965; MLJ 64, lighthouse at Carapachibey, P. Borro, February 1952; IB 392, USNM 167302–03, NMC 12275, El Jorobado,

native for O. H. Garrido, December 1965: MCZ 46233, Jacksonville, J. P. Heath, August 1941; ASFS V22313-14, "south of Isla de Pinos", R. Carvajal, no date; NMC 12276, "south of Isla de Pinos?", native for O. H. Garrido, December 1965.

ASSOCIATED SPECIMENS: Isla de Pinos, Habana Province. Cayo Piedras, 4 (IB 394-97).

Name from Latin "sectilis" (cut, cloven) in reference to the separation of the subspecies from northern *hassleri* and *delacruzi*.

DEFINITION: A subspecies of *Anolis luteocularis* characterized by a combination of 1) moderate size (males to 181 mm, females to 151 mm snout-vent length), 2) moderate number of vertical dorsal scales (13-22), 3) moderate number of caudal scales (16-27), 4) body lichen-green, sides whitish gray, or greenish brown dorsally, 5) dewlap pale faded pink or whitish yellow, 6) axillary stripe white with an anterior included yellow tongue above the forelimb insertion (Fig. 5E), 7) throat and jaws white, 8) subangular blotches restricted or absent, and 9) tail prominently banded gray to white and lichen-green.

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 170 mm and tail length of 200 mm, slightly incomplete; vertical dorsal scales 17, horizontal dorsal scales 18, caudal scales 23, supralabials to eye center 9/9, 36 fourth toe lamellae.

Color (as preserved) dull green above without crossbanding, dotting, or flecking; head dark brown (almost black) above, canthals somewhat paler, the dorsal head color extending behind each eye onto the temporal region as a diffuse postocular patch; axillary stripe white, bold, bordered above by a broad dark brown area; upper surfaces of fore- and hindlimbs concolor with dorsum, without transverse bands; tail prominently banded with alternating bands of greenish black and brown; venter, throat, dewlap scales, upper and lower lips white, with a very small dark brown subangular spot on each side; upper lip white pigment extends dorsad to include about half of loreal region and posteriorly to surround the auricular opening; eyeskin dark brown with a pale spot anteriorly and a second and larger pale spot posteriorly.

VARIATION: The series of 18 *Anolis luteocularis sectilis* has the following counts: vertical dorsals 13-22 (17.4), horizontal dorsals 15-19 (17.0), caudals 16-27 (20.8), supralabials 7/7 to 9/9 (mode 8/8), fourth toe lamellae 31 to 40 (36.3). *A. l. sectilis* is generally a

dull green (lichen colored) lizard without transverse banding, pale dotting, or flecking. The sides are whitish gray and the axillary stripe is white, usually with an included tongue of yellow pigment in the stripe above the forelimb insertion. The dewlap color varies from pale faded pink to whitish yellow. The venter, throat, and lips are regularly immaculate white and the subangular spots are either extremely reduced or absent entirely. A white occipital figure is often present, but it is small and restricted; some specimens had the anterior portion of the casque sulfur yellow in life. The white upper jaw pigment extends dorsad posteriorly and includes the auricular opening. Remarkably, the two pale spots on the eyeskin are regular features in the series; color slides show that these spots are white in life. Some individuals (USNM 167302) have the dorsum much marbled with white, and there is an irregularly edged white nuchal crossbar.

COMPARISONS: *Anolis luteogularis sectilis* differs from *A. l. hassleri* in that the former is gray-green in basic color, is not transversely banded on the body, and has reduced (or absent) subangular blotches; the dewlap colors of the two subspecies also appear to be different, with that of *hassleri* pink and white, and that of *sectilis* pale faded pink or whitish yellow. In scutellation the two subspecies are comparable, with *hassleri* having slightly higher means of both vertical dorsals and caudals. *A. l. luteogularis* differs from *sectilis* in that the latter is paler green in life, lacks dorsal dotting, and lacks a pale orange dewlap. From *A. l. delacruzi*, *A. l. sectilis* differs especially in lacking the large and conspicuous subangular markings of *delacruzi*. The dorsal scales are slightly larger in *sectilis* (mean 17.4) than in *delacruzi* (18.3), as counted in vertical distance. In addition, *sectilis* has white throat and jaws, and, although *delacruzi* has a similar condition, the jaws and throat are regularly flecked with brown or green and lack the bold and clear white aspect of *sectilis*. Compared with *A. l. nivevultus*, *sectilis* averages higher in vertical and horizontal dorsals, often has a yellow tongue in the axillary stripe which is white in both subspecies, has a grayish green rather than greenish yellow or grayish yellow dorsum, has a paler pink dewlap, and has the subangular blotches reduced or absent in contrast to their prominence in *nivevultus*. *A. l. sectilis*

and *A. l. nivevultus* appear to reach about the same size, but both dorsal counts average higher in *sectilis* (17.4 vertical, 17.0 horizontal) than in *nivevultus* (16.1 vertical, 14.4 horizontal).

We have included four specimens from Cayo Piedras, the wooded pass between the two portions of the Isla de Pinos with *sectilis* rather than *hassleri*. The series includes two adult males, one adult female and a juvenile lizard. We regard these lizards as being closer to *sectilis* on the basis of the clear white throats, but the adults regularly have extremely long subangular blotches and were apparently weakly crossbanded dorsally in life (although none shows any evidence of crossbanding at present). Considering their intermediate geographic position, these lizards are almost ideal intermediates between *hassleri* and *sectilis*, since they combine some color and pattern characteristics of both subspecies, but in total we consider them closer to *sectilis* than to *hassleri*.

Two juveniles (IB 397, MLJ 64) with snout-vent lengths of 84 mm, show no indication of dorsal transverse lines.

Two other reptiles (*Leiocephalus stictigaster*, *Ameiva auberi*) are known to have different subspecies on the north and south portions of the Isla de Pinos. Doubtless, considering the low-lying Ciénaga de Lanier which is interposed between these two sections of the Isla, the island itself has at various times been completely separated and populations of animals have differentiated on both the north and south islands under these circumstances. Even today, there is but limited access for one portion of the Isla to the other, and northern and southern populations are effectively isolated from each other. *A. l. hassleri* and *A. l. sectilis* are a pair of subspecies which can be added to those reptiles which follow this pattern of differentiation.

***Anolis luteogularis coctilis*, new subspecies**

HOLOTYPE: IB 402, an adult male, from Punta del Inglés, *Cayo Cantiles*, Archipiélago de los Canarreos, *Habana Province, Cuba*, taken 2 May 1966 by O. H. Garrido.

PARATYPES: All from Cayo Cantiles. ASFS V22317, MCZ 119386, same data as holotype; IB 401, IB 403-05, O. H. Garrido, 1 May 1966; IB 1324, El Cocal de Rafael, M. L. Jaume, 12 April 1967; IB 1337, La Aguada de la Laguna del Inglés, O. H. Garrido, 15 April 1967; MCZ 119387, USNM 167304, NMC 12277, Punta del Negrito, O. H. Garrido, 12 April 1967; ASFS V22315-16, Punta del Negrito, O. H. Garrido, 29 April 1966. 1

Name from Latin "coctilis" (baked) in allusion to hot Cayo Cantiles.

DEFINITION: A subspecies of *Anolis luteogularis* characterized by a combination of 1) small size (males to 148 mm, females to 137 mm snout-vent length), 2) low number of vertical dorsal scales (13–18), 3) low number of caudal scales (15–21), 4) body clear green with scattered sky blue scales and without crossbands, pale dotting, or flecking, 5) dewlap pale pink, 6) axillary stripe white with a mustard tongue included in the stripe above the forelimb insertion, or yellow posteriorly and white anteriorly (Fig. 5F), 7) throat and jaws white, 8) subangular blotches absent, 9) tail obscurely banded with green of brown alternating with paler scales, and 10) lores, eyeskin and postocular region sooty black to very dark brown, a large black nuchal blotch preceded by a pale occipital blotch and followed by a pale diagonal bar which joins the pale upper jaw color in the temporal region.

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 147 mm and a tail length of 276 mm; vertical dorsal scales 13, horizontal dorsal scales 12, caudal scales 18, supralabials to eye center 9/–, 30 fourth toe lamellae.

Color (as preserved) grayish above, irregularly blotched and marbled with dull yellow; axillary stripe dull yellow, bordered above and below by very dark gray; uppersides of fore- and hindlimbs marbled gray and yellow; casque dull brown with an irregular pale area in depression between canthal ridges; throat, and upper and lower jaws white, vaguely marked with very pale gray, the white pigment barely extending onto the loreal region and continuous posteriorly across the auricular opening and thence dorsally to the midline of the back, thereby forming a complete pale horseshoe on the neck; lores, eyeskin, and temporals very dark brown; a very dark brown nuchal blotch, almost continuous with the dark postocular blotch, but cut off from the latter by a fine vertical pale line; a large pale occipital spot bordering the postocular and nuchal blotches dorsally and anteriorly; venter pale grayish; tail vaguely banded with broad dark brown bands and narrow pale bands.

VARIATION: The series of 14 *Anolis luteogularis coctilis* has the following counts: vertical dorsals 13–18 (15.0), horizontal dorsals 10–16 (13.3), caudals 15–21 (17.5), supralabials 8/8 to 9/9 (mode 9/9), fourth toe lamellae 27 to 36 (31.3). The dorsal ground color of *A. l.*

coctilis was described as clear green with some scattered sky blue scales, or yellow-green in life. The nuchal fold is at times black and orange. The anterior portion of the casque and the sides of the neck may be sulfur yellow, with an orange band behind a black one on the neck. The occipital blotch or spots are also orange. The axillary stripe is either white with a mustard tongue above the forelimb insertion, or white anteriorly and yellow posteriorly; the stripe is broad and short, and outlined above and below by darker. The dark brown to black loreal-postocular-nuchal "mask" is a constant feature, although, rather than the nuchal area being separated from the postocular region by a fine vertical line as in the holotype, more often the postocular and nuchal blotches are continuous. The throat and jaws are basically white, but they may be vaguely mottled or marbled with gray; the pale upper jaw pigment may extend to the dorsal midline (including the auricular opening in its passage dorsally), but in other lizards the pale nuchal band is not clear dorsally and is restricted to the lower temporal region. In many lizards, the rostral and mental regions are dark, thereby giving a darkly tipped effect to the entire head. In the greenish phase, the limbs and tail are aquamarine, and the tail is only vaguely banded; in the dark phase, when the lizard is brown, the tail is banded with yellowish and brownish. The venter is greenish and the dewlap is pale pink in life.

COMPARISONS: No other subspecies of *Anolis luteogularis* combines the characteristics which exemplify *coctilis*. The distinctive head and nuchal pattern of the latter form differentiates it from all other subspecies. In size, *A. l. coctilis* is the smallest of the subspecies and is considerably smaller than *nivevultus*, the next smallest race. *A. l. coctilis* also has the largest scales of any subspecies of *A. luteogularis*, but it is closely approximated by *nivevultus*.

As stated in the introduction, the junior author suggested in his third hypothesis that the Cayo Cantiles form might best be regarded as a species distinct from all others of the *equestris* complex. We have decided at least provisionally to include it in *A. luteogularis*, despite its smaller size and rather large dorsal scales. We feel that *coctilis* combines, in some ways, the characteristics of the subspecies *sectilis* and *nivevultus*, and if these are to be considered subspecies

of *A. luteogularis*, we are forced into also so considering *coctilis*. We admit the distinctness of the head and neck patterns of *coctilis*, but in some features (such as the details of axillary stripe in *coctilis* and *sectilis*, for instance) it seems preferable to regard this entire complex as one species. See also the discussion of the following subspecies.

Another reason for associating *sectilis* with *coctilis* is the fact that the reptilian fauna of the Archipiélago de los Canarreos is one which has been derived directly, as far as known, from the south island of the Isla de Pinos. The subspecies of *Ameiva auberi* in the Archipiélago is quite obviously a derivative of that on the southern portion of the Isla de Pinos, for instance, and *Leiocephalus cubensis pambasileus* has been derived from the Isla de Pinos *L. c. gigas*. It seems more than likely that *coctilis* and *sectilis* are sequentially related to each other in the same fashion as the above examples. Details of the herpetofauna of Cayo Cantiles are to be found in GARRIDO & SCHWARTZ (1969).

***Anolis luteogularis calceus*, new subspecies**

HOLOTYPE: IB 1295, an adult male, from Santo Tomás, *Ciénaga de Zapata, Las Villas Province, Cuba*, taken 26 February 1967 by O. H. Garrido.

PARATYPES: ASFS V22318-19, same locality as holotype, J. de la Cruz, 6 August 1966; IB 1291, same locality as holotype, O. H. Garrido, 25 January 1967; MFP (7 specimens), same locality as holotype, R. Carvajal, 5 May 1967.

Name from Latin "calceus" (shoe) in reference to the Ciénaga de Zapata.

DEFINITION: A subspecies of *Anolis luteogularis* characterized by a combination of 1) moderate size (males to 180 mm, females to 163 mm snout-vent length), 2) very low number of vertical dorsal scales (11-18), 3) very low number of caudal scales (15-19), 4) body color green without dotting or flecking but with a dark (brown) phase with two vague pale body crossbands, 5) dewlap pink, 6) axillary stripe yellow or greenish yellow, 7) throat and jaws not white or yellow, jaws spotted with brown, 8) subangular blotches absent, 9) tail not banded, and 10) lores, eyeskin, and postocular region dark brown (Fig. 5G), a large black nuchal blotch preceded by an extensive white occipital figure and without a pale diagonal

bar behind the nuchal dark blotch, and with a black postocular patch.

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 180 mm and a tail length of 235 mm, distal half regenerated; vertical dorsal scales 13, horizontal dorsal scales -, caudal scales 19, supralabials to eye center 9/10, 33 fourth toe lamellae.

Color (as preserved) pale tan with some admixture of grayish green scales, especially posteriorly; upper sides of fore- and hindlimbs brownish gray, vaguely reticulated or finely crossbanded; upper and lower jaws pale grayish yellow with the supra- and infralabials each with a darker grayish central smudge, the pale pigment extending over the lower half of the loreal region and posteriorly onto the side of the neck to include the auricular opening; upper half of lores, eyeskin, and postorbital region very dark brown, forming a conspicuous mask; a large dark brown nuchal blotch, triangular in outline with its apex pointed posteriorly on the dorsal midline; throat grayish yellow; dewlap pink; casque pattern consisting of cream (yellow in life?) and brown pigments, with a quinquepartite figure radiating from the interocular region, and intruding upon a large pale occipital figure which bounds the postocular dark blotch dorsally; canthal scales pale; axillary stripe white, broad and fairly long, bordered below by a dark brown to black line; tail not banded but with tan and greenish gray scales randomly arranged; venter grayish yellow.

VARIATION: The series of 16 *Anolis luteogularis calceus* has the following counts: vertical dorsals 11-18 (13.3), horizontal dorsals 12-18 (15.0), caudals 15-19 (16.8), supralabials 8/8 to 9/10 (mode 8/9), fourth toe lamellae 27 to 34 (31.4). *A. l. calceus* is a very large scaled subspecies and thus has the lowest means of vertical and caudal scales of the subspecies (represented by adequate series) of *A. luteogularis*. The preserved specimens agree well with the description of the holotype in pattern. The major area of variation is the amount of pale color on the casque and whether the postocular and nuchal blotches are in contact or separated as they are in the holotype. The most extreme condition as far as pale casque pigment is concerned occurs in ASFS V22319, where the entire casque is pale except for a few scattered darker areas, the most

extensive of which is in the interorbital region. The quinquepartite central dark blotch is a fairly constant feature; even if the anterior median line is absent, the posterior two lines are usually present and thereby aid in the formation of a large pale W-shaped occipital figure. As far as a postocular-nuchal blotch juncture is concerned, more often these two figures are joined, not separated. Two specimens (MFP) show vague indications of one pale crossband on the neck and two on the body. The jaws may be pale with only some brown smudging on each labial, or they may be very dark brown. The axillary stripe is always bold, long, and usually bordered either above or below (or on both sides) by a dark brown line. There is never an indication of the pale upper jaw pigment extending dorsally posterior to the nuchal blotch. The only juvenile (MFP, snout-vent length 75 mm) has no pale crossbands.

COMPARISONS: *Anolis luteogularis calceus* most closely resembles *coctilis* in details of color and pattern; the two subspecies are quite different in size (with *coctilis* much the smaller) and in that *calceus* lacks a pale nuchal band posterior to the dark nuchal blotch. In vertical dorsals and caudals, *calceus* has lower extremes and means than does *coctilis*. The Zapata subspecies differs from nominate *luteogularis* in smaller size and much larger scales; these two forms can be separated on the number of caudal scales (19–28 in *luteogularis*, 15–19 in *calceus*). By virtue of its head pattern and lack or reduction of tail and/or body banding, *calceus* is readily differentiable from all other subspecies of *A. luteogularis*.

***Anolis luteogularis jaumei*, new subspecies**

HOLOTYPE: IB 369, an adult (?) male from Playa Larga, *Ciénaga de Zapata, Las Villas Province, Cuba*, taken 27 April 1965 by O. H. Garrido.

PARATYPE: MFP, same locality as holotype, M. L. Jaume, 20 January 1967.

Name in honor of MIGUEL JAUME, director of the Museo Felipe Poey, long-time friend of both authors, and outstanding Cuban malacologist.

DEFINITION: A subspecies of *Anolis luteogularis* characterized by a combination of 1) apparently small size (male 147 mm, female 144 mm snout-vent length), 2) very low number of vertical dorsal scales (12 in both specimens), 4) body color green but head and

lores sky-blue, and without dotting or flecking, 5) dewlap pink, 6) axillary stripe white and long with a yolk-colored "tongue" above the forelimb insertion (Fig. 5H), 7) throat and jaws not white or yellow, jaws spotted with green or brown, 8) subangular blotches absent, 9) tail not banded, and 10) without a pale casque and black postorbital blotch, or black nuchal collar.

DESCRIPTION OF HOLOTYPE: A presumably subadult male with a snout-vent length of 147 mm and a tail length of 99 mm, almost completely regenerated; vertical dorsal scales 12, horizontal scales –, caudal scales –, supralabials to eye center 8/9, 30 fourth toe lamellae.

Color in life: Dorsum green with the casque and sides of the head (= lores) sky-blue; upper and lower jaws mottled with brownish; axillary stripe wide and long, whitish, with a yolk-colored "tongue" above the forelimb insertion; dewlap pink. Color as preserved: dorsum drab brown, with a broad and long white axillary stripe and a conspicuous white supralabial stripe which extends posteriorly to include the auricular opening; casque brownish with the canthal scales, portions of the supraoculars, and a W-shaped occipito-parietal figure pale; a few scattered irregular pale markings on the neck, including a few dorsal crest scales; throat dull grayish, dewlap pale pink, venter dull grayish brown.

VARIATION: The MFP female paratype has a snout-vent length of 144 mm, 12 vertical dorsal scales, 15 horizontal dorsal scales, 18 caudal scales, 8/9 supralabials to eye center, and 31 fourth toe lamellae. As preserved, it resembles the holotypic male except that the casque has more dark than pale areas and the occipito-parietal W is composed of a series of five pale spots, roughly arranged as portions of a W. The anteriormost dorsal crest scales are pale, and there seem to have been about four narrow pale body bands present in life.

COMPARISONS: *Anolis luteogularis jaumei* is distinctive from all other subspecies of *A. luteogularis* in having a blue head and lores and an axillary stripe with an included yolk-colored "tongue" (although a mustard "tongue" occurs in some *coctilis*). In addition, it appears to have larger scales (and thus lower counts) on both the body and the tail, although the series is very small. Direct comparison of specimens of *jaumei* and *calceus*, whose known ranges are

separated by a distance of only 55 kilometers, shows that these two subspecies are very distinctive in both color and pattern, although they both are very large scaled subspecies of *A. luteogularis*. Aside from the blue head in *jaumei*, the extensive pale casque and black nuchal blotch of *calceus* will at once distinguish this taxon from *jaumei*. The extensive swampy lowlands of the Ciénaga de Zapata presumably separate these two subspecies. Santo Tomás, the type locality of *calceus*, lies on a small area of dry wooded ground in the Ciénaga itself, whereas the type locality of *jaumei* is in an area of extensive and relatively high, moderately mesic, coastal hardwood forest.

The subspecies *coctilis*, *calceus*, and *jaumei* are obviously related; of them, *jaumei* is the most divergent. We have suggested that *coctilis* is a Canarreos derivative of *sectilis* from the southern Isla de Pinos. If this is the case, then *calceus* can only be interpreted as either a derivative of *sectilis* which has re-invaded the mainland from the southern Isla de Pinos or Cayo Cantiles; the latter possibility seems more likely geographically, since Cayo Cantiles lies 60 km south of the Península de Zapata, whereas the range of *sectilis* lies much further to the southwest. However, the postulation of derivation of *calceus* from *coctilis* implies that a moderately sized subspecies has been derived from a dwarf subspecies; perhaps both forms have been independently derived from *sectilis*, rather than in a *sectilis-coctilis-calceus* sequential series. *A. l. jaumei* appears to be small like *coctilis*, but its style of coloration and pattern bears little resemblance to the Isla de Pinos and Ciénaga de Zapata members of the species. The relationships of *jaumei* are discussed in more detail below.

We had at first considered regarding *calceus* as a Zapata representative of *A. equestris*; surely the differences between *A. l. luteogularis* and *A. l. calceus* are such that, without the intervening subspecies, one would hardly consider them subspecifically related. The very small scales of *luteogularis* versus the very large scales of *calceus* (as well as *jaumei*) and the very different styles of head and body coloration and pattern, would seem to militate against a direct relationship between these taxa. *A. l. jaumei* even more violates our basic concepts of *A. luteogularis* as a specific entity. It

is of course possible that we have oversimplified this entire complex of forms; perhaps a more accurate and realistic assessment would be *A. luteogularis*, *A. hassleri*, and *A. nivevultus* with *sectilis*, *coctilis*, *delacruzii* and *calceus* as its subspecies, and *jaumei* as a subspecies of *A. equestris*. But apparent intergradation between *hassleri* and *sectilis* suggests that this arrangement is not correct, and that those subspecies associated above with *nivevultus* might more properly be considered *hassleri* subspecies. Still another possibility is that *hassleri* is a subspecies of *A. equestris*; but, as we understand *hassleri*, that subspecies has variably present subangular blotches (although admittedly these blotches may be absent and if present, are usually small and restricted) – a feature which is never found in *A. equestris*. All in all, we have adhered to a conservative course; there is no question about the distinctness of the populations named here as subspecies of *A. luteogularis*; what is doubtful is that we have correctly arranged them all as subspecies of *A. luteogularis*.

Anolis equestris Merrem

Anolis equestris MERREM, 1820, Syst. Amph.: 45.

Anolius rhodolaemus BELL, 1827, Zool. Jour.: 235.

TYPE LOCALITY: Unknown: here restricted to the vicinity of La Habana, Habana Province, Cuba.

DEFINITION: A giant species of the genus *Anolis* characterized by a combination of 1) low number of vertical dorsal shales, 2) low number of caudal scales, 3) size moderate in almost all populations, never small, rarely very large, 4) dewlap with limited variation from pink to white, 5) axillary stripe brilliant yellow to white, at times with a yellow "tongue" included in the stripe over the forelimb insertion, 6) upper and lower jaws blotched or marbled, never with a subangular dark blotch, and 7) tail without broad transverse bars.

DISTRIBUTION: Central Cuba, from (apparently) San Diego de los Baños, Pinar del Río Province, through Habana, Matanzas, Las Villas, Camagüey and northern and western Oriente provinces (Fig. 2).

Anolis equestris equestris Merrem

DEFINITION: A subspecies of *Anolis equestris* characterized by a combination of 1) moderate size (males to 179 mm, females to 167 mm snout-vent length), 2) high number of vertical dorsal scales (10–18), 3) body green to bottle green, without scattered pale scales posteriorly and without prominent lateral body streaking between the scales, 4) dewlap pink, 5) axillary stripe bright yellow, 6) casque with extensive yellow markings on canthus and occiput (Fig. 6A), and 7) a postlabial yellow bar, not directed dorsad, including the auricular opening.

DISCUSSION: *Anolis equestris equestris* occurs, as far as freshly collected specimens are concerned, from Habana Province east to northwestern Las Villas Province (where it intergrades with the subspecies next to the east). In southern Las Villas Province, south of the range of *A. e. equestris*, occurs *A. l. calceus* and *A. l. jaumei* on the Península de Zapata and at Playa Larga. Throughout its range, the subspecies is remarkably stable in characters. Basically, *A. e. equestris* is a bottle green to green lizard with large dorsal and lateral scales and without additional dorsal or lateral markings. The axillary stripe is sulfur yellow. Dewlap colors for *A. e. equestris* have been recorded in life as pink; MAERZ & PAUL color designation is Pl. 3 D1 (Jaruco). The casque usually has the canthal scales bright yellow and there is a sulfur yellow postlabial stripe onto the temporal region; this stripe is not directed dorsally as it is in those *A. luteogularis* subspecies which have such a feature, but rather its posterior end is rounded behind the auricular opening. The patch of rugose scales in the upper temporal region is likewise often bright yellow and set off from the balance of the head and casque ground color. The tail is not transversely banded but there are often irregularly scattered paler and darker scales so that the tail is not uniformly green as is the body. Of a series of 12 juvenile *A. e. equestris* from Habana Province, none, even the smallest (MFP, snout-vent length 56 mm) shows any indication of pale body bands.

Meristic data (means and extremes) for 49 *A. e. equestris* are: vertical dorsals 10–18 (14.0), horizontal dorsals 11–21 (15.0), caudals 14–21 (17.6); largest male 179 mm, largest female 167 mm snout-

vent length. Supralabials to eye center vary between 7/8 and 10/11 (mode 8/9); fourth toe lamellar counts vary between 27 and 38 (mean 31.8).

We have restricted the type locality of *A. e. equestris* to the vicinity of La Habana; this seems a logical course, since not only did seaports offer the presumed prime source of material in the period of the original description of *A. equestris*, but the description itself, brief as it is, neither violates our concept of *Anolis equestris* nor makes it possible for us to associate the name with any other form. The occurrence of *A. luteogularis* and *A. equestris* in La Habana suggested that possibly the name *equestris* might more correctly be applied to the species now referred to as *luteogularis*; this seems but a slight possibility, and there are no serious grounds for such a nomenclatural change. BELL's (1827) description of *Anolius rhodolaemus*, on the other hand, can clearly be associated with *A. equestris*; the color and pattern on head and body are sufficiently detailed as to associate definitely this name with *A. equestris*. The fact that the original material was collected by W. S. MACLEAY, who resided in Guanabacoa between 1827 and 1836 (CONDE, 1958: 261) also affirms the relegation of *rhodolaemus* to synonymy under *A. equestris*.

Among the specimens studied by us is a series from La Habana (MCZ 35507-09) which do not agree with our concepts of either *A. l. luteogularis* or *A. e. equestris*, the two subspecies which are sympatric in this region. These specimens resemble very closely *A. l. calceus* from the Peninsula de Zapata and have a bold dark brown nuchal band and pale occipital areas as does that subspecies. Dr. WILLIAMS has assured us that the locality data are correct insofar as he knows, but it seems likely that there has been some error concerning these particular lizards. If they are from the environs of La Habana, the complexities of the relationships between *A. l. luteogularis*, *A. e. equestris*, and *A. l. calceus* are multiplied. Until the presence of lizards resembling these three in the La Habana region can be verified, we regard the series as incorrectly labeled as to locality.

We have previously referred to sympatry of *A. luteogularis* and *A. equestris*; in the regions of sympatry, the nominate subspecies of both are involved. The junior author has collected both forms at El Husillo, Puentes Grandes, and Bosque de la Habana, both localities within the city limits of La Habana itself. In the series from Central Providencia in the United States National Museum,

one *A. luteogularis* was discovered among 12 *A. equestris*; in addition, there is an *A. equestris* (USNM 71852) from San Diego de los Baños (the type locality of *A. l. luteogularis*). We cannot of course verify the locality data for these latter two occurrences of sympatry, but we tend to regard at least the Central Providencia record as reliable and the San Diego de los Baños record with some suspicion. It is pertinent that in each of these two instances, there is but a single specimen of one species and many of the other from the same locality, precisely what one might expect in marginal regions of sympatry between two related species.

The two localities which we know intimately (El Husillo; Bosque de la Habana) are remnants of the primal forest of the northern Cuban coast and are not artificial situations. Both are now completely enclosed within the city of La Habana, and there is no direct contact with rural *Anolis* populations. Inspection of preserved material from these two localities leaves little doubt as to the identification of individual lizards; each specimen can be assigned with ease to either *luteogularis* or *equestris*. The junior author noted, however, that in the Bosque de la Habana there are typical *A. luteogularis* and typical *A. equestris*, as well as some individuals which we interpret as hybrids (rather than intergrades) between the two species. The facts that *luteogularis* extends well into the western border of Habana Province, that *equestris* occupies the eastern two-thirds of Habana Province, and that in no case have we seen any *populations* of lizards which are intermediate or intergradient in the orthodox sense of the word, make us certain that these two taxa are distinct specific entities. It is noteworthy that in the Jardín Botánico in the city of La Habana, apparently neither *luteogularis* nor *equestris* occurs. The area now occupied by the Jardín was formerly swampy, and the wooded areas there now are a later development due to the introduction of plants for study. The Jardín Botánico is very near to El Husillo, but apparently neither species has been able to invade these relatively newly created ecologically suitable situations in the Jardín.

SPECIMENS EXAMINED: *Pinar del Río Province*. San Diego de los Baños, 1 (USNM 71852). — *Habana Province*. La Habana, 3 (AMNH 58352–53, SMF 24855); “La Habana”, 3 (MCZ 35507–09); El Husillo, Puentes Grandes, 1 (IB 449); Bosque de la

Habana, Marianao, 2 (IB 450, IB 611); Marianao, 1 (USNM 164265); Loma de Tierra, 1 (IB 602); Finca Plata, Nazareno, 7 (MFP); Campo Florido, 1 (AMNH 57962); 9 km SW San José de las Lajas, 1 (AMNH 78074); 6.8 mi. (10.9 km) W Jaruco, 1 (AMNH 78147); Madruga, 1 (MCZ 7906); Central Providencia, S of Güines, 12 (USNM 164273-74, USNM 164276-85); "southern Habana Province", 6 (USNM 164266-71). - *Matanzas Province*. No other data, 1 (USNM 58856); Cárdenas, 1 (SMF 51645); road entering Agramonte from Perico, 1 (MFP); Carretera Central nr. Perico, 3 (MFP).

***Anolis equestris buidei*, new subspecies**

HOLOTYPE: IB 1294, an adult male, from ca. 0.5 km from Rincón Francés, *Península de Hicacos, Matanzas Province, Cuba*, taken 27 February 1967 by Orlando H. Garrido, George C. Gorman, and Miguel L. Jaume.

PARATYPES: All from the *Península de Hicacos, Matanzas Province*. AMNH 89536, Punta Hicacos, D. C. Leber, 24 September 1960; IB 371, Varadero (not mapped), O. H. Garrido, December 1964; ASFS V22322, Punta Hicacos, Rincón Francés, O. H. Garrido, 6 July 1966; IB 1293, same data as holotype.

Name in honor of MARIO S. BUIDE, whose interest in the *Península de Hicacos* herpetofauna and in Cuban herpetology in general is hereby acknowledged.

DEFINITION: A subspecies of *Anolis equestris* characterized by a combination of 1) moderate size (males to 176 mm, females to 148 mm snout-vent length; only three males and two females known), 2) low number of vertical dorsal scales (12-15), 3) body bright green to bottle green, without scattered pale scales or prominent streaking between scales, 4) dewlap pink, 5) axillary stripe broad sulfur-yellow or mustard-yellow posteriorly, whitish anteriorly, and with a slate black border, 6) casque with very extensive bright yellow markings on canthal ridges, and occiput (often entire casque) and lips bright yellow (Fig. 6B), 7) a postlabial bar obscure but at times confluent with the yellow occipital area, and 8) lores and nuchal area bright blue.

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 165 mm and tail length of 250 mm, tip regenerated; vertical dorsal scales 12, horizontal dorsal scales 16, caudal scales 16, 8/8 supralabials to eye center, 31 fourth toe lamellae.

Color (as preserved): Dorsum dull gray and without body dotting or flecking except for a few scattered brownish scales on the lower sides; tail above concolor with dorsum but fairly prominently marked with brownish scales arranged in a series of rings, at least

dorsally, and becoming obscure distally; head gray, but the casque (including the canthal ridges, most of the supraocular area, and the entire occiput) pale (bright yellow in life); rugose postocular scales pale; lips pale gray, lores and temporal region dull blue-gray; venter gray. The preserved specimen lacks the vivid blue face and neck characteristics of living examples. Dewlap pale pink.

VARIATION: The holotype and four paratypes have the following counts: vertical dorsals 12–15 (13.2), horizontal dorsals 12–15 (13.4), caudals 14–18 (16.0), supralabials 7/9 to 9/9 (no mode), fourth toe lamellae 26–30 (30.2).

The short series of *Anolis equestris buidei* is constant in having extensive bright yellow areas on the head, most especially involving the canthal ridges and the occiput; there may also be a pale (yellow in life) area on the neck. The axillary stripe is sulfur-yellow to mustard-yellow posteriorly, grading to white anteriorly, and has a slate-black edge. The postlabial stripe is poorly defined, but when present (as in ASFS V22322), it tends to be continuous with the pale occipital region. Having a few brownish scales on the lower sides and brown scales arranged in rings about the proximal portion of the tail are common features of the series. Although the preserved specimens do not show it, all were vivid sky blue on the lores and neck in life.

COMPARISONS: The major differences between *buidei* and nominate *equestris* are the presence in the former of a blue face and neck and the extensively yellow casque. These characters have never been observed in any other population of *Anolis equestris* and are confined, as far as we are aware, to the population on the Península de Hicacos. Both *equestris* and *buidei* apparently reach the same size in males; we presume that the same is true of females, although of our two female *buidei* the largest (148 mm) is considerably smaller than the largest female *equestris* (167 mm). *A. e. buidei* averages less in dorsal and caudal scale counts than *A. e. equestris*, but this may be an artifact of the short series of the former subspecies.

REMARKS: Despite the few specimens herein assigned to *buidei*, we are confident that it is a very distinct and nameworthy entity. Its restriction to the Península de Hicacos is important. This north-eastward projecting spit from the northern Matanzas coast has

been shown (BUIDE, 1966) to have been insular and to have but only relatively recently been rejoined to the Cuban mainland. Today, the base of the peninsula is swampy and low, and prevents the meeting of *Hicacos buidei* and mainland *equestris*. It seems likely *buidei* evolved its peculiar coloration on the peninsula when the latter was completely insular, and, with subsequent continuity of the land masses, has still remained cut off from *equestris* by the swampy base of the peninsula. The Península de Hicacos is noteworthy for the presence there of one of the disjunct populations of *Leiocephalus raviceps* Cope as well as an endemic subspecies of *Ameiva auberi* Cocteau (see SCHWARTZ, 1960, for the former and SCHWARTZ, 1970, for the latter).

Specimens of *Anolis equestris equestris* from Matanzas Province (Cárdenas, Perico) show no evidence of influence of *buidei*, and the former locality is relatively close (15 km) to the base of the Península de Hicacos. There is no evidence of intergradation between *buidei* and *equestris*.

***Anolis equestris persparsus*, new subspecies**

HOLOTYPE: AMNH 78116, an adult male, from 4 km E Trinidad, *Las Villas Province, Cuba*, taken 28 July 1957 by native collector.

PARATYPES: All from Las Villas Province. AMNH 78115, Finca Morales, 8 mi. (12.8 km) NW Trinidad, J. R. Feick, 27 July 1957; AMNH 78118-24, 3 km E Trinidad, native collector, 30 July 1957; AMNH 78125, Finca la Pastora, 2 km NW Trinidad, A. Echevarría, 30 July 1957; AMNH 78127, Finca la Pastora, 2 km NW Trinidad, A. Schwartz, 31 July 1957; AMNH 78126, Trinidad, native collector, 30 July 1957; AMNH 78128-29, Trinidad, native collector, 30 July 1957; AMNH 89542-52, Trinidad, native collector, 12-15 July 1960; MFP, Finca Camarones, road to Topes de Collantes, M. L. Jaume, 18 December 1966; AMNH 1612, Trinidad, F. M. Chapman, no date; USNM 138203-05, Trinidad, J. D. Hardy, 10-12 September 1956; AMNH 78117, Punta Casilda, native collector, 28 July 1957; IB 11754-76, ASFS V22323, Cayaguazán, Casilda, T. Naranjo, 26 September 1966.

ASSOCIATED SPECIMENS: Las Villas Province, Santa María, Manacas, Santo Domingo, 1 (MFP); Baños de Ciego Montero, 1 (AMNH 6518); Soledad, 10 (AMNH 89537-41, MCZ 21872-73, MCZ 25938, MCZ 22355, UMMZ 76110); vicinity of Soledad, 3 (UMMZ 70041, 70042 - 2 specimens); 2 km S Encrucijada, 2 (IB 446-47); road from Caibarién, 1 (IB 370); 1.2 mi. (1.9 km) S Yaguajay, 1 (AMNH 78144); San José del Lago, 14 (AMNH 78130-43); Cueva de Caguanes, Punta Caguanes, 3 (AMNH 82867-69); Arriero, 15 km S Cabaiguán, 2 (UMMZ 109516-17); Mapo, Sancti Spiritus, 1 (IB 1272).

INTERGRADES between *A. e. equestris* and *A. e. persparsus*: Las Villas Province. Sagua la Grande, 1 (IB 438); Cuatro Bocas, Sagua la Grande, 5 (IB 362-64. IB 436, IB 439); La Rubia, Sagua la Grande, 1 (IB 365); Santa Rosa, Sagua la Grande, 2 (IB 437, IB 440); Finca Quinta Elvira, Sagua la Grande, 2 (IB 441-42); road from Central Guipuzcoa to La Playa, road from Sagua la Grande, 3 (MFP).

Name from Latin "sparsus" (scattered, strewn) and the intensive "per", in allusion to its wide distribution.

DEFINITION: A subspecies of *Anolis equestris* characterized by a combination of 1) large size (males to 188 mm, females to 170 mm snout-vent length), 2) high number of vertical dorsal scales (11-19), 3) body green with scattered white to pale green or pale blue dots on posterior half to quarter of body, at times giving a somewhat tigroid effect, 4) dewlap pink, 5) axillary stripe bright yellow, 6) casque mottled and without yellow markings on occiput and canthus (Fig. 6C), and 7) a postlabial yellow bar, usually poorly defined posteriorly and flecked with dark green, not directed dorsad, and including the auricular opening.

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 180 mm and tail length of about 245 mm, distal third regenerated; vertical dorsal scales 13, horizontal dorsal scales 13, caudal scales 19, 8/10 supralabials to eye center, 31 fourth toe lamellae.

Color (as preserved) dull brownish green (bright green in life) with head less green (more brown) than body; head without occipital or canthal pale markings, more or less concolor with dorsal color; supralabial bar pale grayish green (yellow in life), diffusely edged and flecked with dark grey (dark green in life), especially posteriorly; axillary stripe white (bright yellow in life), narrow and long, extending about half way along the flank; fore- and hindlimbs dark greenish gray, somewhat marbled with greenish; tail variegated green and dark gray, but not banded; throat pale grayish green, venter and underside of tail slightly darker grayish green; dewlap pink in life.

VARIATION: The series of 73 *Anolis equestris persparsus* has the following counts: vertical dorsals 11-19 (14.3), horizontal dorsals 11-17 (13.8), caudals 14-22 (18.5), supralabials 7/8 to 11/11 (mode 9/9), fourth toe lamellae 27-37 (31.8).

Anolis equestris persparsus is a variable subspecies insofar as pattern

is concerned. However, there are never indications of pale (yellow) canthal scales or yellow on the occipital region, the casque being uniformly colored (greenish gray, brownish gray, dull green) and without brightly colored associated areas. The axillary stripe and supralabial bar are regularly bright yellow, and the bar is rarely sharply delimited posteriorly and is (at least posteriorly) flecked with dark green. The axillary stripe is at times bordered above and below by some black scales, thereby setting the stripe off even more sharply from the green lateral color. The eyeskin may be dull pale gray, in sharp contrast to the ground color. The major variable feature is the posterior spotting. In the usual *persparsus* condition, the posterior half to quarter of the body has isolated pale green, bluish or whitish scales which contrast fairly sharply with the balance of the dorsal color. These pale scales may extend onto the basal half of the tail and onto the upper surfaces of the hindlimbs. In many lizards, however, notably those from the northern Las Villas coast in the San José del Lago area, the body and tail are practically tigriform. In a lizard from Finca Morales, the axillary stripe was greenish yellow, and the dewlap of this specimen was recorded as pink (Pl. 51C1). Other dewlap designations include Pl. 2A2 (4 km E Trinidad) and Pl. 2B1 (San José del Lago).

COMPARISONS: *Anolis equestris equestris*, *A. e. buidei*, and *A. e. persparsus* are easily distinguished by their head patterns. In *equestris* and *buidei* the head has conspicuously pale (bright yellow in life) canthal scales or a yellow casque and some sort of bright occipital figure; *persparsus* lacks any such bright head figures, and the head is uniformly colored and usually duller and darker than the body itself. Likewise, *persparsus* has at least some pale posterior body and tail scales; this feature occurs occasionally in *equestris* but never reaches the heavily spotted or somewhat tigriform condition of *persparsus*. Of the two forms, *persparsus* reaches a larger size (188 versus 179 mm) than does *equestris*. As far as scutellation is concerned, vertical dorsals and caudals average slightly higher in *persparsus* than in *equestris*.

REMARKS: We consider the material from the vicinity of Sagua la Grande in northwestern Las Villas Province to be intermediate between *equestris* and *persparsus*. Of the series of 14 specimens from

this region, three lizards are clearly *equestris* in that they have the contrastingly patterned heads as well as the clearly delineated postlabial bar of that subspecies. Eight specimens are just as clearly *persparsus*, without brightly patterned heads and with conspicuous postlabial bars. Three lizards are, however, intermediate between these two subspecies in that there are some pale head markings, especially on the canthus, and the postlabial bar is more sharply defined, especially posteriorly, than is usual in *persparsus*. Specimens from adjacent localities (Perico, Manacas, Encrucijada, none of which is close to Sagua la Grande) are easily referable to *equestris* to the west or *persparsus* to the south and east.

As pointed out above, the geographic relationships between *Anolis luteocularis calceus* and *A. l. jaumei* and *A. equestris persparsus* remain unknown. SCHWARTZ (1958:6) reported four specimens as being intermediate between *A. e. persparsus* (= *A. e. equestris sensu* Schwartz, 1958) and *A. e. thomasi*, the subspecies next to the east. These intergrades were from the vicinity of Morón, Camaguey Province, and from 15 km E Cabaiguán, Las Villas Province. Reinspection of the Cabaiguán lizards convinces us that they are more properly assigned to *A. e. persparsus* whereas the Moron lizards are certainly far closer to *thomasi* than to *persparsus*, and data from them have been included with the former subspecies. There are thus no clear intergrades between *persparsus* and *thomasi*, and the distance separating these two subspecies is relatively narrow (70 km, between San José del Lago and Loma de Cunagua).

***Anolis equestris juraguensis*, new subspecies**

HOLOTYPE: IB 1152, an adult male, from Monte Alto, 3 km SW Juraguá, *Las Villas Province, Cuba*, taken 19 September 1966 by native collector.

PARATYPES: All from Las Villas Province. IB 443, Juraguá, native collector, 19 May 1966; IB 444-45, Juraguá, native collector, 20 May 1966; IB 1151, IB 1153, ASFS V22324-25, MCZ 119388, NMC 12278, USNM 167305, same data as holotype; IB 1198, Cinco Tiras, west of Juraguá, native collector, 15 August 1966.

Name from the type locality, Juraguá, Las Villas Province.

DEFINITION: A subspecies of *Anolis equestris* characterized by a combination of 1) moderate size (males to 177 mm, females to 154

mm snout-vent length), 2) high number of vertical dorsal scales (12–16), 3) body pure green with a gray-green dorsal stripe and with scattered white scales on body and tail, most especially on the posterior half of the body where the pattern is tigroid, lateral and ventral scales separated by a white longitudinal band, and with a chocolate brown phase, 4) dewlap clear pink, 5) axillary stripe white, very long and broad, with a small yolk-colored “tongue”, 6) casque mottled and without yellow markings on occiput and canthus (Fig 6D), and 7) postlabial bar white, sharply delimited posteriorly and including the auricular opening, not flecked with green or brown, and not directed dorsad.

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 177 mm and tail length of 330 mm; vertical dorsal scales 16, horizontal dorsal scales 17, caudal scales 18, 8 supralabials to eye center on left side, 34 fourth toe lamellae.

Color in life pure green with casque gray and without any yellow canthal or occipital markings; posterior half of body and all of tail heavily marked with white scales giving a tigroid effect posteriorly; venter pale green, sharply set off from dorsal darker green by a longitudinal band of white scales; dewlap clear pink, chin pale green, heavily flecked with dark green scales laterally; eyeskin white; supralabials white, spotted with green; axillary stripe long (extending along anterior third of body), broad, and white with an included yolk-yellow “tongue” anteriorly; postlabial stripe white, clearly delimited from gray head and green body colors, extending behind and including the auricular opening; fore- and hindlimbs green, heavily banded with white crossbands.

VARIATION: The series of 12 *Anolis equestris juraguensis* has the following counts: vertical dorsal scales 12–16 (13.9), horizontal dorsal scales 15–19 (17.1), caudal scales 15–20 (17.3), supralabials 8/8 or 8/9 (mode 8/9), fourth toe lamellae 24–35 (30.1).

In color and pattern, the series of paratypes resembles the holotype closely. The body is always pure green above and paler green below, the two colors separated by a longitudinal white ventrolateral line. The casque is gray with either white or gray eyeskin, and there are no occipital or canthal markings. The posterior half to one third of the body is heavily marked by white scales, so that in

extreme individuals, the total effect is tigroid, and the hindlimbs and tail continue this same general tigroid theme. The axillary stripe is long and bold, sharply set off from the surrounding body color, and is white with an included anterior "tongue" of yolk-yellow, mustard-yellow, or yellow-brown. The postlabial stripe is likewise bold and white, and extends posteriorly to behind the auricular opening which it includes. The throat is pale green with often very dark green (to brown in the chocolate phase) isolated scales concentrated in an ill-defined band at about the level of the eyes. The dewlap was recorded as clear pink. Although preserved specimens do not show it, the junior author's notes in life indicate that a middorsal gray-green stripe is a common feature in the living animals while in the green phase. There are no small juveniles, but the smallest individuals (snout-vent length between 125 and 142 mm) are patterned and colored like adults.

COMPARISONS: *Anolis equestris juraguensis* is easily differentiated from both *equestris* and *buidei* in that it lacks the bright occipital and canthal areas of the latter and also lacks any sky-blue facial coloring as in *buidei*. *A. e. juraguensis* most closely resembles *A. e. persparsus*; both subspecies lack head markings. *A. e. juraguensis* differs from *persparsus* in being much more heavily spotted with white scales posteriorly and on the tail (*i.e.*, is much more tigroid than are most *persparsus*, but see the discussion of variation in that subspecies), and in having a ventrolateral white longitudinal stripe separating the dorsal and ventral colors, in being brighter (= more pure) green with a middorsal gray-green area in the green phase, in having a white axillary stripe with an included yellow tongue in contrast to a bright yellow stripe, and in having a white postlabial stripe in contrast to a yellow stripe in *persparsus*. In addition, *persparsus* reaches a larger size in both sexes, 188 versus 177 in males, 170 versus 154 in females); *juraguensis* has higher counts of horizontal dorsals (15 to 19 versus 11 to 17 in *persparsus*) with a consequently lower mean (13.9) in *persparsus* than in *juraguensis* (17.1).

REMARKS: Although *persparsus* and *juraguensis* resemble each other in several features, they are nonetheless equally distinctive; it seems likely that *juraguensis* is a derivative of the more widespread *persparsus*. Juraguá lies on the west side of the Bahía de

Cienfuegos; *Anolis equestris* from north (Baños de Ciego Montero) and east (Soledad) of this bay are typical *persparsus*. There are no specimens of giant anoles available between Juraguá and the Península de Zapata; this latter area is occupied by *A. l. jaumei* and *A. l. calceus*. Of these subspecies, it is pertinent to recall that *jaumei* (which occurs at Playa Larga, some 70 km west of the Juraguá area), has, like *juraguensis*, an axillary stripe with an included yellow tongue. There is thus a possibility that we are associating *jaumei* incorrectly with *A. luteogularis*; perhaps it might more appropriately be considered a subspecies of *A. equestris*. Other features of its color and pattern, however, ally it with the more western species. Until more material becomes available from this entire west-central south coast of Cuba, the affiliations of these populations must remain somewhat problematical.

***Anolis equestris thomasi* Schwartz**

Anolis equestris thomasi SCHWARTZ, 1958, *Herpetologica* 14: 3.

TYPE LOCALITY: 2 km SE Banao, Camagüey Province, Cuba.

DEFINITION: A subspecies of *Anolis equestris* characterized by a combination of 1) moderate size (males to 181 mm, females to 153 mm), 2) low number of vertical dorsal scales (9–16), 3) body bottle green, without scattered pale scales posteriorly, but with the skin between the enlarged dorsal scales white, giving a laterally streaked appearance, 4) dewlap very pale pink to almost white, 5) axillary stripe white, 6) casque bottle green with vivid yellow canthus and some yellow on occiput, and 7) supralabials and postlabial bar vivid yellow, sharply delimited posterior to auricular opening (Fig. 6E), and with dark green blotches on most of the anterior supralabials.

DISCUSSION: Both living and long preserved *Anolis equestris thomasi* are the most distinctive of the subspecies of *A. equestris*. The very large size of the scales and the streaked sides easily distinguish this subspecies from all others. Even specimens which have been preserved for many years often show the characteristic side streaking. In life, the white axillary stripe, the yellow supralabials and

postlabial bar and the yellow occipital area all serve to distinguish *thomasi*.

Anolis equestris thomasi occurs throughout Camagüey Province, along the northern Oriente coast as far east as Banes and into the western Oriente lowlands at least as far south as El Jobo between Holguín and Bayamo. In the extreme southwestern portion of Oriente (Cabo Cruz) occurs another subspecies which is clearly a *thomasi* derivative, but which differs from the more northern subspecies in several salient features.

Meristic data (means and extremes) for 38 *A. e. thomasi* are: vertical dorsals 9–16 (12.9), horizontal dorsals 10–17 (12.8), caudals 13–22 (17.6); the largest male has a snout-vent length of 181 mm, the largest female 153 mm. Supralabials to eye center vary between 7/7 and 10/10 (mode 8/9); fourth toe lamellar counts vary between 26 and 38 (32.4).

The amount of yellow on the casque is somewhat variable. The canthals are regularly bright yellow (Pl. 9I5, Pl. 11L3 at the type locality), and there is most often a W or U shaped yellow occipital figure. Most specimens from Camagüey Province lack a pair of large postorbital pale (= yellow in life?) blotches whereas all Oriente *thomasi* have them. Exceptional Camagüey specimens are two from Martí (UMMZ 70931, AMNH 45676) which have the postorbital blotches; Martí is about 25 kilometers from the Oriente-Camagüey line; occasional Camagüey specimens have very small pale flecks in their postorbital regions. A very few individuals from both provinces have a paramedian pair of yellow blotches at about the level of the forelimb insertion at the dorsal midline. It is possible that the Camagüey specimens should be nomenclatorially separated from those from Oriente, since they are easily distinguishable, but we are reluctant to do so at this time.

The dewlap color is very pale pink (Pl. 2B1, Pl. 3D1) to almost white. Specimens collected by the junior author at Gibara agree in dewlap color with those from the type locality and its environs. The throats are heavily blotched with dark green in living specimens, almost to a point of forming a reticulum.

Two juveniles (MCZ 59328 – snout-vent 52 mm, MCZ 59327 – 58 mm) show the juvenile pattern of four pale body bands, despite

the fact that the smaller of these two lizards is an albino. A slightly larger specimen (AMNH 78151) with a snout-vent length of 72 mm, shows no indication of the dorsal crossbands.

Anolis equestris thomasi differs from all other subspecies of *A. equestris* in much paler dewlap color, in having bottle green sides streaked with interstitial white, and in having distinctly larger scales. The latter character is once again one to which the vernier does little justice, since the differences between *thomasi* on one hand and the remaining subspecies on the other are more striking than the mean differences shown by the counts imply.

We have already discussed the lack of intergradient material between *thomasi* and *persparsus*. Specimens from Morón in north-western Camagüey Province, considered by SCHWARTZ (1958: 6) to be intergradient between these two subspecies, agree very well with our somewhat expanded concept of the variation in *A. e. thomasi* and we no longer consider them intermediate. It is of course possible that *persparsus* and *thomasi* represent populations of two species rather than both being subspecies of *A. equestris*. We have considered this possibility but have rejected it since once again we would be faced with relationships of other populations to the east. It seems preferable to keep *thomasi* as a subspecies of *A. equestris* despite the apparent lack of intergrades.

SPECIMENS EXAMINED: *Camagüey Province*. Loma de Cunagua, 12 mi. (19.2 km) E Morón, 2 (AMNH 78145-46); south of Morón, 1 (IB 1162); 2 km SE Banao, 2 (AMNH 78148); 2 km NW Banao, 1 (AMNH 89533); 5.5 mi. (8.8 km) NE Banao, 1 (AMNH 78151); Paso de Lesca, Sierra de Cubitas, 1 (AMNH 89534); Los Paredones, Sierra de Cubitas, 2 (MCZ 59327-28); ca. 8 km W Camagüey, 4 (AMNH 72645); Finca Santa Teresa, 9 km W Camagüey, 3 (MCZ 57929-31); 9 km W Camagüey, 1 (MCZ 59442); 20 mi. (32 km) SW Florida, 1 (AMNH 89535); Nuevitas 1 (AMNH 1611); Martí, 2 (AMNH 46576, UMMZ 70931). - *Oriente Province*. Gibara, 3 (AS 285 - 2 specimens, IB 486); Banes, 5 (AS 286 - 4 specimens, USNM 164272); nr. Banes, 4 (MCZ 55628-29, MCZ 55631-32); polo field, United Fruit and Sugar Company, Banes, 2 (MFP); Los Angeles, 5 mi. (8 km) E Banes, 2 (MCZ 25153-54); El Jobo, between Holguín and Bayamo, 1 (MFP).

Anolis equestris verreonensis, new subspecies

HOLOTYPE: IB 488, an adult male, from Verreón, Cabo Cruz, *Oriente Province, Cuba*, taken 31 March 1965 by O. H. Garrido.

PARATYPES: All from Oriente Province. ASFS V22326, same data as holotype; AMNH 83632, Cabo Cruz, R. F. Klinikowski, 5 July 1959; USNM 138090, between Cabo Cruz and Niquero, J. D. Hardy, 1 September 1956; USNM 138129-32, Jucaral (not mapped), J. D. Hardy, 6 September 1956.

Name from the type locality, Verreón, Oriente Province.

DEFINITION: A subspecies of *Anolis equestris* characterized by a combination of 1) small size (males to 168 mm, females to 152 mm snout-vent length), 2) low number of vertical dorsal scales (10-14), 3) body green (shade unrecorded) without scattered pale scales posteriorly but with white interstitial lateral streaking, 4) dewlap pink, 5) axillary stripe yellow, 6) casque very dark (black in some cases), marked with tiny white dots which may extend onto the neck and shoulders, canthus and occiput not set off from balance of casque by yellow (Fig. 6F), and 7) postlabial yellow bar moderately sharply set off from temporal color and including auricular opening.

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 168 mm and tail length of 320 mm; vertical dorsal scales 10, horizontal dorsal scales -, caudal scales 17, 9/10 supralabials to eye center, 35 fourth toe lamellae.

Color (in life) green (almost black as preserved), with white streaking prominent between the large squarish scales; axillary stripe broad, long, and bright yellow; casque black in life, dotted with many tiny white flecks which extend posteriorly over the occiput and onto the neck; lores likewise dotted with white; supralabial stripe truncated anteriorly and beginning under eye, the anterior supralabials marbled yellow and dark green; supralabial stripe and postlabial bar bright yellow, including and extending behind the auricular opening; upper surfaces of limbs concolor with dorsum; throat diffusely marbled with dark green, venter (as preserved) blackish green; dewlap pink.

VARIATION: The series of *Anolis equestris verreonensis* has the following counts: vertical dorsals 10-14 (11.7), horizontal dorsals 10-14 (12.3), caudals 14-19 (16.9), supralabials 8/8-9/10 (mode 8/9), fourth toe lamellae 32-39 (34.1).

The seven paratypes are like the holotype in that none shows the yellow canthals and extensive yellow occipital region of *A. e. thomasi*. One individual (IB 487) has somewhat more pale area on the occiput

than do the others, but even this lizard lacks the large pale occipital regions of *thomasi*. The casque, on the other hand, is regularly dark and more or less flecked with tiny pale dots. The supralabial line is moderately prominent and includes the auricular opening, and the axillary stripe is always present and bold. In contrast to Oriente *A. e. thomasi*, which always have a bold pale postorbital area, *A. e. verreonensis* lacks this feature. One individual (USNM 138090) differs from the balance of the *verreonensis* in that there are two sets of paramedian blotches, one set located above the forelimb insertion and the other further posteriorly, which seem almost to be remnants of the juvenile bands which we assume that juvenile *verreonensis* possess (there are no young individuals known). However, USNM 138090 has a snout-vent length of 151 mm. Another lizard (USNM 138130) has a pair of small pale blotches above the forelimb insertion.

COMPARISONS: *Anolis equestris verreonensis* bears the same relationship to *A. e. thomasi* as does *A. e. persparsus* to *A. e. equestris*. The latter members of both pairs have brightly patterned heads, whereas the former members of both pairs have casques which lack any bright adornments. *A. e. verreonensis* differs from *thomasi*, of which it is obviously a local derivative, in that the axillary stripe is yellow rather than white, the dewlap is a brighter pink rather than pale pink to almost white, and the bright head decorations are suppressed and the casque is dotted. From *A. e. persparsus*, *A. e. buidei*, and *A. e. juraguensis*, *verreonensis* differs in lacking pale scales on the posterior body and tail, in having a dotted casque and streaked sides, and in smaller size; the body scales are larger in *verreonensis* than in these other subspecies. From *A. e. equestris*, *verreonensis* differs in lacking head pattern, larger scales, and smaller size.

REMARKS: The Cabo Cruz area is one of high local endemism. When the senior author took the first specimen from this region, he was impressed both with its resemblances to *thomasi* and the differences between it and *thomasi*. More recent material collected by JERRY D. HARDY and the junior author amply confirm these differences.

All localities for *Anolis equestris verreonensis* center about the

Cabo Cruz region. There are, however, two additional specimens of large-scaled *thomasi*-like anoles from Oriente which merit discussion. One of these has already been referred to – USNM 58855, from Santiago de Cuba. SCHWARTZ (1964: 414–15) commented on this specimen in that its large scales and pattern prevented its being associated with “*A. e. smallwoodi*”, the taxon known from the city of Santiago de Cuba. Re-inspection of the specimen, a subadult female with a snout-vent length of 126 mm, shows that it is a *thomasi*-like lizard with large scales, apparently without bold casque markings, and with an isolated pair of pale nuchal spots. The second specimen (IB 485) is from Finca La Celia, Los Cayos, 28 km W Bayamo, Oriente Province. This individual was observed in life by the junior author. In the green phase, the lizard was bright emerald green (not bottle green), the head more yellow-green with the center of the casque and the neck splashed with black. The axillary stripe was yellow, and the sides were streaked with yellow rather than with white. In the dark phase, the sides were streaked with lemon yellow, the upper lips and postlabial bar were bright yellow, as were also the occipital protuberances on each side. There was a brown postorbital blotch and the canthus was extensively yellow with a profusion of scattered sulfur yellow flecks on the casque itself. The dewlap was pink. The entire schema of pattern of the Bayamo lizard is quite different from that of *verreonensis*: the presence of occipital pale areas and the marbled casque with its prominent pale canthus, as well as the vermiculate posterior casque and neck, all serve to distinguish this lizard from both *thomasi* and *verreonensis*. Yet it is surely a member of this complex of large-scaled subspecies of *A. equestris*. Barely conceivably, this specimen is to be interpreted as intergradient between *thomasi* and *verreonensis*, but we doubt that this is its true status. It seems more likely that both the Bayamo and “Santiago de Cuba” lizards represent a population of *A. equestris* which extends eastward in the lowlands associated with the Río Cauto along the northern edge of the Sierra Maestra. If so, then the “Santiago de Cuba” specimen is not from the immediate environs of that city but rather from the Palma Soriano-San Luis area. Only additional material from this

region of Oriente can clarify the status of these two lizards as well as that of *A. equestris* in eastern Cuba.

THE ORIENTE SITUATION

We feel that, up to this point, our interpretation of the relationships between *Anolis luteogularis* and *A. equestris* are reasonably secure. Although we have been faced with lack of intergrades between subspecies of several of the forms associated with either *A. luteogularis* or *A. equestris*, nevertheless the picture presented appears to us to be as correct as it can be under the present circumstances; the single major exception to this statement is the complex of subspecies associated with *A. luteogularis*, as we have previously pointed out.

Once within the confines of Oriente Province, however, the situation becomes far more difficult than it is elsewhere in Cuba. SCHWARTZ (1964: 407) has given a brief resumé of the physiography of this easternmost Cuban province; geographically, Oriente is structurally the most complicated area of Cuba, and ecologically it is tremendously diverse, from high mountains clothed in rainforest to cactus-studded and bleak coastal regions. In this area, giant anoles are quite common at some localities and apparently rather rare in others. In one instance, only two specimens are now known of one subspecies (*noblei*), and in another (*baracoae*) we now have long series for study. There are still many regions of Oriente whence there is no material available, however, and for this reason our conclusions must remain in some measure tentative.

As presently understood, there are six forms in Oriente Province, in the order of their description, distributed as follows:

- 1) *noblei* – the Sierra de Nipe
- 2) *galeifer* – the Sierra Maestra from Las Mercedes in the west to Loma del Gato in the east
- 3) *smallwoodi* – coastal areas between the Bahía de Santiago and the Bahía de Guantánamo and in the region about Hongolosongo on the northern slope of the Sierra Maestra to the west of the Bahía de Santiago

4) *palardis* – the Cuenca de Guantánamo, east along the southern coast to Baitiquirí

5) *baracoae* – the region about Baracoa on the northern mesic coast

6) *saxuliceps* – the region about Moa on the northern coast.

It would seem most logical if the Oriente populations could be arranged as subspecies of (presumably) *Anolis equestris*, since that species occurs in northern and western Oriente. But several facts make such a course of arrangement improbable; we wish once more to emphasize that in several instances we are forced to rely upon the accuracy of locality data for specimens which we have not ourselves collected. There is no choice in such instances, for we cannot in complete honesty discard *all* specimens whose locality data violate our ideas about the relationships of the Oriente taxa. Our arrangement of the Oriente populations is based upon the following premises.

1) From Hongolosongo, Loma del Gato, we have examined specimens which are clearly *galeifer* and others which are clearly *smallwoodi*. These two forms are easily distinguishable on the basis of casque and body patterns; this is especially true of *smallwoodi* where the pea-green occipital blotches and heavily spotted dorsum contrast strongly with the absence of occipital blotches and with scattered body spots in *galeifer*. If these two taxa are sympatric without intergradation, then it is most unlikely that they are conspecific (except possibly through a *Rassenkreis* of some sort, of which we have no evidence whatsoever). Therefore, *galeifer* and *smallwoodi* belong to two separate species.

2) Of the Oriente populations, *galeifer* and *noblei* most closely resemble *A. equestris*, and we would have little hesitancy in associating these two taxa with *A. equestris* were it not for the following situation. *A. equestris* is known from a single specimen (data reliable) from Finca La Celia, Los Cayos, 28 km W Bayamo, whereas *galeifer* is known from Las Mercedes, 27 km S Yara (data reliable). These localities are separated from each other by a distance of about 25 kilometers airline; the latter locality is in the lower northern foothills of the Sierra Maestra. Neither of the specimens involved shows characteristics of the other taxon. Although it is possible

that *galeifer* intergrades with the local *thomasi*-like *equestris*, and thus that *galeifer* should be regarded as an *equestris* subspecies, we are reluctant to assume so. Coupled with this situation is the *thomasi*-like *equestris* purportedly from Santiago de Cuba. If this lizard came from that area, it indicates that *thomasi*-like anoles occur there in close juxtaposition to *smallwoodi* (and presumably with *galeifer* also).

3) In extreme eastern Oriente, *palardis* is known from Baitiquirí and *baracoae* from Imías; once again we are dealing with two readily identifiable forms, the former leopard-spotted on the body, the latter with an axillary stripe which is composed of disjunct orange spots in an otherwise black field. The distance separating these two localities is about 22 km; the specimens involved show no genetic influence of the one form on the other.

4) Along the northern Oriente coast, *saxuliceps* is known from the region about Moa, at Cupeyal, at a locality 8 mi. NE Felicidad, and from Caña on the road between Guantánamo and Sagua de Tánamo. There is an hiatus between the localities for *saxuliceps* and *baracoae* of about 26 kilometers, but *palardis* and *saxuliceps* approach each other fairly closely. Most important is that *noblei* occurs sympatrically with *saxuliceps* at Cupeyal. There is no question of the distinctness of *noblei*, *saxuliceps*, *smallwoodi*, or *baracoae* (although we have to some extent modified our concepts of each of these taxa since the descriptions of three of them by Schwartz).

If the above facts are kept in mind, there are several interpretations open to us:

a) *galeifer* and *noblei* are both subspecies of *A. equestris*. This implies that intergradation occurs within the 27 kilometer hiatus between the *thomasi*-like anole and *galeifer* at Las Mercedes. It also implies that *noblei* intergrades with *A. e. thomasi* (presumably between the Sierra de Nipe and Banes) or possibly to the south (assuming that *A. equestris* follows the Río Cauto lowlands). If such is the case, then *smallwoodi* and *palardis* are a species distinct from *A. equestris* (because of *galeifer-smallwoodi* sympatry at Hongolo-songo).

b) *baracoae* and *palardis* are two species. The lack of demonstrable

intergradation between these two taxa in the Baitiquirí-Imías region and elsewhere, as well as their different styles of pattern, suggest that these are two species rather than two subspecies.

c) *saxuliceps* is a species different from both *baracoae* to the east and *noblei* to the west. The isolated position of *saxuliceps*, its (as far as known) fairly circumscribed geographic range, and lack of intermediates between it and any other named taxon suggest that *saxuliceps* is a species distinct from all others. However, as noted above, *saxuliceps* and *palardis* approach each other closely (Felicidad and Monte Líbano – 16 km), and it may be more reasonable to consider them to be subspecifically related – there is no contrary evidence, either as far as characteristics or sympatry are concerned.

Taking all of the above facts into consideration, we have adhered to a *via media* in our arrangement of Oriente populations. We regard *noblei* and *galeifer* as one species, *smallwoodi*, *palardis*, and *saxuliceps* as another, and *baracoae* as a third species. We suggest that this may very well be a simplification of what is an even more complex situation. We are least sure about specific status for *noblei* and *galeifer*, and most sure of the specific status of *baracoae*. In fact, when separating *noblei* and *galeifer* from *equestris*, we are very hard put to find meaningful characteristics which will distinguish the two species. Recognition of *A. noblei* is dependent primarily upon the status of *thomasi* and *thomasi*-like specimens from Oriente, and the lack of intergradation between *thomasi* and *galeifer* in this province. We may be accused of inconsistency here, since we have regarded *thomasi* as a subspecies of *equestris*, despite the absence of intergradation between *A. e. persparsus* and *A. e. thomasi* along the Las Villas-Camagüey border. The accusation is correct, but we feel that this is our privilege in treating a very puzzling situation.

***Anolis noblei* Barbour & Shreve**

Anolis equestris noblei BARBOUR & SHREVE, 1935, Occ. Papers Boston Soc. Nat. Hist. 8: 250.

TYPE LOCALITY: Sierra de Nipe, Oriente Province, Cuba.

DEFINITION: A giant species of the genus *Anolis* characterized

by a combination of 1) moderate number of vertical dorsal scales, 2) moderate number of caudal scales, 3) size large, 4) dewlap pink, 5) axillary stripe yellow, 6) upper and lower jaws dark (green) with pale postlabial bar prominent, 7) tail without broad transverse banding, 8) body often with widely scattered pale dots, and 9) canthus pale or dark, and occasionally with an occipital pale figure.

DISTRIBUTION: The Sierra de Nipe, east to the Cuchillas de Toa, and the Sierra Maestra, in Oriente Province, Cuba (Fig. 3).

***Anolis noblei noblei* Barbour & Shreve**

DEFINITION (based only upon the holotype, MCZ 22653, which we have not re-examined, and one other specimen): A subspecies of *Anolis noblei* characterized by a combination of 1) moderate size? (only male \pm 152 mm snout-vent length, only female 156 mm snout-vent length), 2) low number of vertical dorsal scales (19–20), 3) caudal scales 22 in both specimens, 4) body green with scattered pale scales, but without a distinctly leopard-like aspect, and 5) canthus pale, with a pair of pale nuchal blotches, and a pale postlabial bar which includes the auricular opening (Fig. 7A).

DISCUSSION: Obviously, with but two specimens (one of which, the holotype, we have not re-examined but of which a detailed color and pattern description as well as drawing are available in SCHWARTZ, 1964) we can say very little about *Anolis noblei noblei* or even to contrast it satisfactorily with *A. n. galeifer*. The second specimen was not seen in life by the junior author, but it was observed freshly preserved. At that time, the body was green, and there were scattered obscure paler spots on the sides. The axillary stripe was yellow and the dewlap pink. As preserved today, the body spots are still faintly visible and brownish against a dark green ground. The casque is very pale green with black pigment in the sutures between the casque scales. The canthus and supraciliary region are pale cream, and there is some cream on the occipital region. The postorbital protuberances are pale, bounded below by a well delimited green postorbital blotch, which in turn is bounded below by a bold (pale green) postlabial bar; the lips and loreal

region are dark green-brown. The throat is suffused with dark brown-green, and the belly is dull greenish gray. The forelimbs are unmarked; the hindlimbs have a series of fine pale transverse lines across the thigh. The neck is marbled with dark gray-green and cream, and there is a pair of paramedian elongate pale spots on either side of the neck.

Meristic data on the two specimens are: vertical dorsals 19–20, horizontal dorsals 24–± 28, caudals 22 in both specimens; the male has a snout-vent length of about 152 mm, the female 156 mm. There are 10/10 supralabials to eye center and 32 fourth toe lamellae in the new specimen.

We consider the fresh specimen as *A. noblei noblei* partially because of its provenance and partially because it agrees well with the description of the holotype of *A. n. noblei* (as *A. equestris noblei*) in SCHWARTZ (1964: 407–408). These two individuals are obviously different from *A. e. thomasi* to the west (closest localities for the two species are about 50 kilometers airline across the Bahía de Nipe) and equally distinct from *saxuliceps* which occurs with *noblei* at Cupeyal.

SPECIMEN EXAMINED: *Oriente Province*, Cupeyal, Sagua de Tánamo, 1 (IB 1218).

***Anolis noblei galeifer* Schwartz**

Anolis equestris galeifer SCHWARTZ, 1964, Bull. Mus. Comp. Zool. 131: 409.

TYPE LOCALITY: Nr. Buey Arriba, SW of Bayamo, Oriente Province, Cuba.

DEFINITION: A subspecies of *Anolis noblei* characterized by a combination of 1) large size (males to 190 mm, females to 148 mm snout-vent length), 2) high number of vertical dorsal scales (18–26), 3) caudal scales 20–29, 4) body green without spotting, or with spotting much reduced, and 5) canthus pale, without a pair of pale nuchal blotches but occasionally with some pale nuchal marbling, and a pale postlabial bar which includes (rarely) or lies above (usually) the auricular opening (Fig. 7B).

DISCUSSION: Of the Oriente members of the *equestris* complex,

we are least certain of the recognizability of *Anolis noblei galeifer*. This is in part due to the lack of series of *A. n. noblei*, in part due to the scattered nature of the records of *galeifer*, and in part due to the fact that we have seen only a very few specimens of this taxon alive. Apparently the distribution of *galeifer* encompasses the uplands of the Sierra Maestra and at least the northern slopes of that range, as well as the northern slopes of the Sierra de la Gran Piedra. There are but two specimens from the southern slopes of the Sierra Maestra (Guama; coast south of Pico Turquino) and the latter is a juvenile lizard (snout-vent length 47 mm) with four pale crossbands between the neck and the hindlimbs and thus valueless for comparison with adults from elsewhere. It seems not unlikely that there is another form of *A. noblei* on the xeric southern coast between Cabo Cruz and the Bahía de Santiago, but specimens are lacking from this entire region. The relationships, on this southern coast, between *A. noblei* and *A. e. verreonensis* which occurs at its western extreme at Cabo Cruz remain to be determined. To the east, *A. n. galeifer* occurs with *A. smallwoodi* in the region about Loma del Gato, and there are specimens from El Cristo, Río Frío, and Alto Songo which are clearly *galeifer* and not *smallwoodi*. The possibility of the occurrence of a large-scaled *thomasi*-like subspecies of *A. equestris* in the Santiago de Cuba region should also not be discarded.

Meristic data for 15 *Anolis noblei galeifer* are: vertical dorsals 18–26 (21.8), horizontal dorsals 19–26 (22.0); the largest male has a snout-vent length of 190 mm, the largest female 148 mm (only four females known). Supralabials to eye center vary between 9/9 and 10/11 (mode 10/10); fourth toe lamellar counts vary between 32 and 42 (35.7).

Judging from the series available to us, *Anolis noblei galeifer* seems a rather variable subspecies. Most specimens lack any indications of body dotting or spotting, but four lizards (three from Hongolosongo and one from El Cristo, all preserved in the green phase) show some indications of pale dotting on the back and sides; the remote possibility exists that these lizards show tendencies toward intergradation with *smallwoodi* to the east (geographically they are ideally intermediate between *galeifer* and *smallwoodi*), but

they lack the very characteristic occipital pattern of the latter subspecies. Additionally, other Hongolosongo specimens are clearly either *galeifer* or *smallwoodi*, without any intergradient characteristics, so we assume that some dorsal dotting is part of the variation in *galeifer*; it should be noted that *A. n. noblei* shows dorsal spotting also.

The canthus is regularly pale, and the occipital rugosities are regularly pale also. The casque itself is more often dark than light, or has more dark than light areas; one lizard (MFP) from Río Frío, El Cobre, has the casque extensively pale rather than dark. The postlabial bar is indistinct in preserved specimens and only rarely includes the auricular opening; rather, the bar extends dorsad to the opening and ends rather abruptly on the side of the neck. The axillary stripe is long and fairly prominent. There is at times an indication of some pale nuchal spotting or flecking, but there rarely is any indication of a pair of clear pale nuchal blotches or spots.

In life, *Anolis noblei galeifer* is a green lizard with a pink dewlap. We have no data on the color of the spots (if present) or the color of the pale canthus, but we assume that at least the latter is some shade of yellow in life. Likewise the color of the postlabial bar and the axillary stripe is unknown. The lores and anterior labials are dark in preserved specimens, and we assume that they are dark green or concolor with the body coloration in the living animal.

Comparisons of *galeifer* with nominate *noblei* are extremely difficult. The meagre data suggest that *galeifer* has smaller dorsals and smaller caudals than does *noblei*, but direct comparison of the Cupeyal *noblei* with comparably sized *galeifer* shows that in fact the dorsals of at least this *noblei* are smaller than those of *galeifer*. No *galeifer* has the marbled neck of *noblei*. Both specimens of *noblei* have the hindlimbs finely crossbanded; such crossbanding is absent in *galeifer*. It is futile to pursue such comparisons further, since the *noblei* sample is inadequate.

Since it is possible that *Anolis noblei galeifer* occurs sympatrically with a *thomasi*-like subspecies of *A. equestris* and *A. e. smallwoodi*, it is profitable to compare these three subspecies. From the local *A. equestris* population (if there is one) *galeifer* differs in having much smaller scales and in lacking the pale lateral streaking of

thomasi-like anoles; from *A. s. smallwoodi*, *galeifer* can be easily differentiated by the absence of the pale pea-green and marbled occipital regions and the absence of prominent leopard-like spotting. More detailed comparisons will be made in the discussion of *A. s. smallwoodi*.

SPECIMENS EXAMINED: *Oriente Province*. Las Mercedes, 27 km S Yara, 1 (AMNH 83627); nr. Buey Arriba, SW of Bayamo, 1 (MCZ 59325); 10 km S Bueycito, Limonar, 1 (IB 609); Jiguaní, 1 (MCZ 96726); La Emajagua, Pico Turquino, 1 (MFP); coast south of Pico Turquino, 1 (MCZ 42480); Guama, 1 (USNM 29784); San Andrés, Jutinicú, Alto Songo, 1 (MFP); Río Frío, El Cobre, Carretera Central, 2 (MFP); Loma del Gato, Hongolosongo, 2 (MFP); nr. Loma del Gato, Hongolosongo, 2 (MFP, MBZH 142); El Cristo, 1 (MFP).

***Anolis smallwoodi* Schwartz**

Anolis equestris smallwoodi SCHWARTZ, 1964, Bull. Mus. Comp. Zool. 131: 412.

TYPE LOCALITY: Laguna de Baconao, Oriente Province, Cuba.

DEFINITION: A giant species of *Anolis* characterized by a combination of 1) moderate to high number of vertical dorsal scales, 2) moderate number of caudal scales, 3) size large to moderate by population, 4) dewlap pink, faintly orange, pale pink, or rosy, 5) axillary stripe yellow to green, 6) upper and lower jaws with a prominent pale labial stripe with included dark (green) blotches on the supralabials but without a subangular blotch, and 7) tail without broad transverse bands.

DISTRIBUTION: Oriente Province, in the south from the region near Loma del Gato around the head of the Bahía de Santiago and thence as far east as Baitiquiri; north from Guantánamo across Oriente Province to the region about Moa on the northern coast (Fig. 4); replaced east of the Imías-Moa line by *A. baracoae*; to the west of Moa replaced by and sympatric with *A. n. noblei*, and on the south sympatric with *A. n. galeifer* and possibly with *A. equestris* (*thomasi*-like specimens previously discussed).

***Anolis smallwoodi smallwoodi* Schwartz**

DEFINITION: A subspecies of *Anolis smallwoodi* characterized by a combination of 1) moderate size (males to 172 mm, females to

158 mm snout-vent length), 2) body green with paler green spotting, the spots encompassing as many as six adjacent scales and the entire aspect leopard-like, 3) dewlap faintly orange to pink, 4) axillary stripe long, broad, prominent and bright yellow, 5) occiput pale pea-green with bold darker green vermiculations, 6) casque gray, tan, or blue and without pale dotting, flecking, or spotting, and 7) postlabial stripe pale green, bordered by darker green (Fig. 8A).

DISCUSSION: *Anolis smallwoodi smallwoodi* is one of the most easily recognized forms of giant anole in Cuba. The combination of leopard spotting, with pale green or greenish yellow spots on a medium to dark green ground, the bold, broad and bright yellow axillary stripe in strong contrast to the green ground, and the large pea-green to grayish green occipital blotches with a bold and prominent darker green reticulum, all serve to distinguish the nominate subspecies. Some specimens show some of these features less prominently than do others; for instance, AMNH 89529 is spotted but in addition has three fairly prominent crossbands between the axilla and groin, these bands composed of appressed spots. ASFS V14941 has the occipital spots heavily and less distinctly reticulate or vermiculate than most other specimens; a specimen (MFP) from Vista Alegre has the dorsal spotting very fine. But despite such relatively minor variants, the concept of *A. s. smallwoodi* is remarkably easy to formulate.

A young individual (AMNH 89532; snout-vent length 61 mm) has one nuchal and three body crossbands, the bands composed of appressed spots rather than being solid; this individual (seen by the senior author in life) lacked pale occipital areas. A slightly larger specimen (MFP; snout-vent length 88 mm) shows both remnants of the juvenile body bands and in addition has developed spots between the bands, so that the typical adult body pattern has been established. Finally, a larger but still juvenile lizard (MCZ 6924; snout-vent length 95 mm) is banded and spotted and has the pale occipital areas. These three lizards show the sequential series of the development of the spotted adult pattern and the pale occiput.

In all specimens for which we have color data, the dorsum was green with pale green leopard-like spotting, the axillary stripe was

bright yellow, the casque greenish yellow, gray, tan, or blue, with pale pea-green occipital blotches, the lores pale green, usually mottled with darker, the labials pale green with a prominent postlabial stripe bordered by dark green, and a dark green venter. The eyeskin is often grayish green and thus in bold contrast to the color of the lores and face. The canthus rostralis is never set off from the balance of the head color by bold yellow or other bright pigment. The dewlap is usually pink (P1. 2A9) but there are some specimens with faintly orange dewlaps.

Meristic data (means and extremes) for 19 *Anolis smallwoodi smallwoodi* are: vertical dorsals 18–25 (20.4), horizontal dorsals 18–26 (21.2), caudals 19–28 (24.7); largest male 172 mm, largest female 158 mm snout-vent length. Supralabials to eye center vary between 8/9 and 10/12; the mode is 9/9. Fourth toe lamellar counts vary between 30 and 39 (mean 34.1).

A recently collected specimen (ASFS V13808) showed the following coloration in life (notes by Peter J. TOLSON). The dorsum was green, either light pea-green in the pale phase to dark green in the dark phase. In the pale phase, the dorsal spots were yellow, changing to buffy yellow in the dark phase. The axillary stripe was buffy, edged with yellow-buffy in the dark phase, changing to bright yellow in the pale phase. The lores and casque were sky-blue, marbled with black, the eyeskin was charcoal brown, and the snout was gray. The occiput and supraocular areas were yellow to pea-green, and the nuchal blotches or marbling were yellow. The limbs were green, the intensity depending upon the dorsal intensity, with prominent narrow yellow crossbands, and the tail shows the same narrowly crossbanded pattern. The venter was green-brown and the dewlap pink (P1. 2B9). As far as we are aware, *A. s. smallwoodi* lacks a brown phase, the two basic phases involving changes in green hues, rather than green on one hand and brown on the other. *A. s. smallwoodi*, as the above description indicates, is an exceptionally bright and colorful lizard.

Geographically, *A. s. smallwoodi* occurs from the eastern end of the Sierra Maestra (Hongolosongo), thence around the head of the Bahía de Santiago east to the Bahía de Guantánamo. Most specimens are from the lowland xeric areas in the coastal rain shadow of the

high Sierra de la Gran Piedra. In this region, the species has been taken in mangrove swamps and associated mesic woodlands at the type locality and in shaded but xeric woodlands as at Playa Juraguá. Two recent specimens from the U. S. Naval Base were collected in xeric wooded situations. That *A. s. smallwoodi* is not restricted to lowland habitats is shown by its occurrence at Hongolosongo, and on the road to La Gran Piedra, and finally a specimen from La Gran Piedra itself at an elevation of 1100 meters.

As far as specimen labels are concerned, *A. s. smallwoodi* and *A. n. galeifer* occur together at Loma del Gato and its vicinity in the Sierra del Cobre. *A. s. smallwoodi* and *A. n. galeifer* must also come in contact in the region of the Sierra de la Gran Piedra, since there are specimens of *galeifer* from the northern slopes and associated lowlands (Río Frío, El Cristo, Alto Songo) of this range, whereas *smallwoodi* seems to occupy its southern slopes and the high interior. There is no problem distinguishing these two taxa where they are sympatric, since the pale occipital areas and very conspicuous dorsal spotting in *A. s. smallwoodi* at once distinguish that species from *A. n. galeifer*. The precise situation as far as these two taxa are concerned in these two regions of contact will be most interesting to ascertain.

SPECIMENS EXAMINED: *Oriente Province*. Hongolosongo, 1 (MBZH 260); Loma del Gato, Hongolosongo, 1 (MFP); 4 km N Santiago de Cuba, 1 (AMNH 89531); Boniato, Santiago de Cuba, 1 (MFP); Vista Alegre, Santiago de Cuba, 2 (MFP); Santiago de Cuba, 1 (MCZ 6924); Playa Juraguá, 1 (AMNH 89532); hills above Firmeza, 1 (MFP); 9.4 mi. (15.0 km) W Laguna de Baconao, 1 (AMNH 89525); Laguna de Baconao, 4 (AMNH 89527-30); road to La Gran Piedra, 1 (MFP); La Gran Piedra, 1100 meters, 1 (MFP); "Toro", Finca Quera (= Osleo's Ranch), 5 mi. (8 km) W U. S. Naval Base, about 0.25 mi. (0.4 km) in from coast, 1 (ASFS V14941); U. S. Naval Base, west side, behind corral, 1 (ASFS V15042); U. S. Naval Base, 500 meters NE Watertower Hill, 1 (ASFS V13808).

Anolis smallwoodi palardis Schwartz

Anolis equestris palardis SCHWARTZ, 1964. Bull. Mus. Comp. Zool. 131(12): 416.

TYPE LOCALITY: Río Yateras, 5 mi. (8 km) N river mouth, Oriente Province, Cuba.

DEFINITION: A subspecies of *Anolis smallwoodi* characterized by a combination of 1) large size (males to 190 mm, females to 165 mm

snout-vent length), 2) body green to brown and with large pale (yellow, green, yellowish green) spots, often encompassing many more than six scales and closely appressed to give an almost reticulate dorsal pattern, 3) dewlap pale pink, 4) axillary stripe long, broad, prominent and yellow-green, 5) occipital blotches absent, 6) casque brown to black with much fine white stippling, dotting, or even a pale reticulum, and 7) postlabial stripe yellow-green, usually not bordered by darker green (Fig. 8B).

DISCUSSION: At the time of the description of both *smallwoodi* and *palardis*, the latter taxon was represented by but two specimens (the holotype and a single specimen from the U. S. Naval Base at Guantánamo Bay). There were five other specimens (Imías; Baitiquiri; and three from "near Guantánamo") whose taxonomic status was uncertain. Since we have had access to the RAMSDEN collections in the Museo Felipe Poey, our concepts of *palardis* are much expanded since 1964. In addition, through the cooperation of the United States Navy and Marine Corps, the senior author was able to visit the U. S. Naval Base; with the competent and enthusiastic assistance of PETER J. TOLSON, three living specimens of *palardis* were obtained (prior to this, neither SCHWARTZ nor GARRIDO had seen *palardis* in life). Finally, LANDO & WILLIAMS (1969) published color data for the paratype of *palardis* (MCZ 68921) which we have re-examined; thus our current knowledge of the variation and distribution of *palardis* is much more extensive than it has been.

Meristic data (means and extremes) for 27 *Anolis smallwoodi palardis* are: vertical dorsals 18–24 (21.2), horizontal dorsals 18–26 (22.4), caudals 20–29 (23.8); largest male 190 mm, largest female 165 mm snout-vent length. Supralabials to eye center vary between 7/8 and 10/11 (modes 9/9 and 10/10). Fourth toe lamellar counts vary between 22 and 42 (mean 32.4).

Anolis smallwoodi palardis differs in three striking ways from *A. s. smallwoodi*: 1) *palardis* is much more heavily spotted dorsally than is *smallwoodi*; 2) *palardis* lacks the pale occipital blotches with their dark green reticula whereas *smallwoodi* has these patches well developed; and 3) the casque in *palardis* is dark brown to black with some sort of white dotting, flecking, spotting, or even a white reticulum, whereas the casque in *smallwoodi* lacks any such dorsal

pattern and is gray to tan or even blue, rather than brown to black. There are no meristic differences between the two subspecies, but *palardis* appears to reach a larger size in both sexes than *smallwoodi*. In contrast to *smallwoodi*, *palardis* has a brown or black phase, and the dorsal body spotting may be extensive, leaving only a darker reticulum (as in MCZ 68921 or ASFS V16354) or the spots may be much smaller (MFP from Bayate) and the lizard much less leopard-like than in typical specimens. In general, there seems to be a tendency for interior (in contrast to coastal) material to be less heavily spotted dorsally, and this possibly shows the genetic effects of *saxuliceps* (or even of *smallwoodi*) on these more interior specimens. However, taken as a group, we are confident that all the lizards we assign to *palardis* represent a single taxon.

LANDO & WILLIAMS (1969: 180) noted that MCZ 68921 was overall bright green in life, with mottled black on dark brown background dorsally, the cream to white spotted scales remaining through all color phases. They reported that the eyelids and temporal region were bright orange, and the venter white to cream. Briefly, the lizard assumed a color phase wherein the lower sides, legs, and tail were bright blue.

A female (ASFS V16354) was described in life as having the dorsal ground color very dark green (almost black) with the spots yellow-green and thus very prominent. The upper surface of the casque was brown, the neck black, and both these members were contrastingly flecked with clear white. The eyeskin was mustard, and both upper and lower labials pale blue, each scale with a blackish green smudge. Both the labial and axillary stripes were yellow-green, bold and prominent, the labial stripe extending so far posteriorly onto the neck (above the ear opening) that it formed a conspicuous nuchal pattern element. The posteriormost dorsal spots are arranged into a series of about three crossbands. The forelimbs were pale yellow with dark gray and narrow bands, and the hindlimbs were pea green with narrow darker gray crossbands; this same color scheme was continued onto the tail. The dewlap was pale pink, and the ventral color pale green. The gular region, even in many old specimens, is covered by dark (presumably green in life) longitudinally aligned dashes on a paler (green?) ground. Like

smallwoodi, *palardis* is an exceptionally handsome lizard in life.

There are six lizards which are juveniles, ranging in snout-vent lengths from 44 mm (MCZ 8977) to 116 mm (MFP from Bayate). The smallest of these has one pale nuchal band and three pale body bands between the limbs, but the nuchal and first body band are composed of pale spots, whereas the two posterior body bands are solid. The next largest juvenile (MFP, Bayate, snout-vent length 91 mm) has four bands also, the posteriormost forming a wide pale sacral U from the inguinal region onto the base of the tail; this band is solid whereas the three more anterior bands are composed of spots, and there is some faint spotting in the interband spaces. The third lizard (MFP, Bayate, snout-vent length 95 mm) shows the same configuration of pattern as the preceding lizard, including the solid pale sacral U. The three remaining specimens (snout-vent lengths between 100 mm and 116 mm) lack bands entirely and are dorsally spotted; these specimens are from Bayate (MFP), Río Frío de San Carlos (MFP), and Guaso (ASFS V14942). Apparently the body banding and the prominent sacral U are lost between snout-vent lengths of 95 and 100 mm; however, even some fully adult lizards still have a sacral U, composed of large appressed spots, more or less vaguely indicated within the adult pattern.

Although we are most familiar with coastal *palardis* and tend to associate it with the hot and dry lowlands to the south of the Sierra de Purial, the subspecies evidently is not restricted to such xeric situations and occurs inland as far as Monte Líbano in the forested and mesic interior. We have seen no specimens which we consider truly intergrades between *smallwoodi* and *palardis*, but intergradation between them presumably occurs in the region about the Bahía de Guantánamo. Specimens from the west (*smallwoodi*) and east (*palardis*) sides of the Bahía de Guantánamo on the U. S. Naval Base are easily differentiated from each other, but material from the city of Guantánamo itself is *palardis*; the distance between the two closest localities (exclusive of on both sides of the Bahía de Guantánamo) for the two subspecies is only about 20 kilometers. On the east, *palardis* approaches *baracoae* closely (Baitiquirí and Imías); these two taxa, which we regard as separate species, differ from each other in many ways, the most obvious distinction being

the orange and black axillary stripe, as well as the (at times) blue-green dewlap in *baracoae*. To the north, *palardis* seems to intergrade with *saxuliceps*; details of this situation are discussed beyond.

The recently collected specimens by the senior author were secured in two situations: one was shot as it rested on the trunk of a fan-palm in a hot and dry ravine; two other specimens were secured from the same large spreading *Ficus* which was one member of a row of these trees bordering a grassy field. The predilection of *A. s. palardis* for trees, even in such a rigorous habitat as most of this southern Oriente coast, is demonstrated by these occurrences.

SPECIMENS EXAMINED: *Oriente Province*. U. S. Naval Base, Bahía de Guantánamo, 1 (MCZ 68921); U. S. Naval Base, east side, 3 (ASFS V16354, ASFS V21994, ASFS V22151); near Guantánamo, 1 (MCZ 8977); Guantánamo, 5 (ASFS V11770, BYU 30325, MCZ 57928, MFP, USNM 58857); Bayate (not mapped), 12 (MFP); San Carlos, *batey* by the river, 1 (MFP); Río Frío de San Carlos, 1 (MFP); Monte Líbano, Cedro Grande, 1 (MFP); Monte Líbano, above Guantánamo power plant, Guaso, 1 (ASFS V14942); Baitiquirí, 1 (MCZ 42551).

***Anolis smallwoodi saxuliceps* Schwartz**

Anolis equestris saxuliceps SCHWARTZ, 1964, Bull. Mus. Comp. Zool. 131: 422.

TYPE LOCALITY: Moa, Oriente Province, Cuba.

DEFINITION: A subspecies of *Anolis smallwoodi* characterized by a combination of 1) probably moderate to large size (largest male about 150 mm, females to 162 mm snout-vent length), 2) body emerald green dotted with light green to orange, rarely encompassing more than one or two scales and apparently absent or restricted in juveniles and subadults, 3) dewlap pink to rosy, 4) axillary stripe short, broad, conspicuous, clear bright green, and at times with a few scattered orange scales along its edges, 5) occipital blotches absent, 6) casque brown with many (usually fine) cream to white dots or marblings giving an overall effect of pebbling in extreme instances, the white casque markings extending onto the occiput and neck as either flecks, spots, or streaks, and 7) postlabial stripe green, not bordered with darker green and with the auricular opening within its lower border (Fig. 8C).

DISCUSSION: The status of the name *saxuliceps* is perhaps one of the most puzzling of the entire Oriente complex. The taxon was named from a series of four specimens from the vicinity of Moa on the northern Oriente coast, all of which are females. The senior author had at that time a specimen of *Anolis* from north of Felicidad (south of Moa) of whose status he was unsure (SCHWARTZ, 1964: 421). We now consider this specimen (AMNH 83631) *saxuliceps*. There is also a specimen from Caña on the road between Guantánamo and Sagua de Tánamo (MFP) and still another from Cupeyal (IB 1898) which resemble each other and also resemble the single paratype of *saxuliceps* (MCZ 59324) available to us. SCHWARTZ's color notes in life on AMNH 83631 and those of GARRIDO on IB 1898 are remarkably similar, and thus we have no hesitancy in affirming that these two lizards represent the same taxon. As preserved, the Caña specimen resembles the two more recent lizards and the young MCZ paratype resembles all three in having a streaked neck, but it has a more pebbled casque, a diagnostic feature of the subspecies.

Meristic data (means and extremes) for 7 *Anolis smallwoodi saxuliceps* (including the holotype and two paratypes in the Hamburg Museum, which had been previously examined by SCHWARTZ) are: vertical dorsals 18–23 (20.1), horizontal dorsals 21–27 (23.2), caudals 23–29 (25.1); only male \pm 150 mm snout-vent length, largest female 162 mm snout-vent length. Supralabials to eye center vary between 8/9 and 10/– (mode 9/9). Fourth toe lamellar counts vary between 29 and 36.

Anolis smallwoodi saxuliceps is easily distinguishable from both *smallwoodi* and *palardis*. The white-flecked or marbled or pebbled casque, the emerald green coloration with small green to orange dots, the lack of occipital blotches but the presence of white flecks or streaks on the occiput and neck, the short, broad and green axillary stripe – all serve in one way or another to differentiate *saxuliceps* from its related subspecies. Although we have only one male *saxuliceps*, we suggest that in size (judging from the snout-vent length of the largest female) *saxuliceps* is comparable to *palardis*. There are no strong scale differences between *saxuliceps*

and the other subspecies of *A. smallwoodi*, but the number of *saxuliceps* is small.

Since there are so few *saxuliceps* in collections, we quote in full the color data for two living specimens:

AMNH 83631. Dorsum green with light green dots which after death turned brown; head brown with cream colored dots extending onto the nape and a few on the dorsal crest scales; lips and shoulder stripe bright green; dewlap scales pale yellow, skin pink (Pl. 1E7); no occipital or shoulder blotches.

IB 1898. Dorsum uniform emerald green with some scattered orangish spots on the sides and limbs; venter and underside of limbs clearer green than dorsum; lateral zone, which separates the greens of the dorsum and venter, narrow and whitish green; axillary stripe well visible, although of the same green hue as the venter, and delimited by brownish orange scales along its edges; supra- and infralabials green; the postlabial stripe extends behind the ear as a well marked stripe; the neck on either side of this band is brownish with greenish and yellowish dots; the casque is rich brown as are the sides of the face as far as the supralabials and is marked with white dots and flecks; base of dewlap rosy pink with rows of green scales.

The distribution of *Anolis smallwoodi saxuliceps* extends from Felicidad to Moa in a series of localities which form almost a straight north-south line. The relationships of *saxuliceps* with adjacent taxa are puzzling, since it lies between or with *noblei*, *palardis* and *baracoae*. Sympatry with *noblei* at Cupeyal precludes regarding these two forms as being conspecific. The hiatus between the closest known localities for *saxuliceps* and *baracoae* (ca. 7 km E Moa; Cayo Güín) is about 26 kilometers. There is no evidence that *saxuliceps* and *baracoae* intergrade in this region; the axillary styles of the two taxa are only very slightly similar, but *baracoae* is so different in several characters that we consider it distinct from *saxuliceps*. The distance between the two closest localities for *saxuliceps* and *palardis* is 15 kilometers (8 mi. NE Felicidad; Monte Líbano) and the styles of pattern and coloration of these two forms are much closer than are those of *saxuliceps* to any other taxon. Although our deduction may be incorrect, we consider *palardis* and *saxuliceps* conspecific.

There are no habitat or altitudinal data for the series of *Anolis smallwoodi saxuliceps*, but at least the two recent specimens were collected in regions of hardwood forest and *cafetales*. It seems likely that this sort of situation is the one inhabited by *saxuliceps*. The Moa region is one of lowland pine forests; presumably the specimens from Moa were taken in stream-side deciduous woods rather than in the pines themselves.

SPECIMENS EXAMINED: *Oriente Province*. Moa, 3 (Hamburg Museum 5374, HM 5376 – 2 specimens); ca. 7 km E Moa, 1 (MCZ 59324); Cupeyal, 1 (IB 1898); Caña, on road between Guantánamo and Sagua de Tánamo, 1 (MFP); 8 mi. (12.8 km) NE Felicidad, 1 (AMNH 83631).

Anolis baracoae Schwartz

Anolis equestris baracoae SCHWARTZ, 1964, Bull. Mus. Comp. Zool. 131: 419.

TYPE LOCALITY: Baracoa, Oriente Province, Cuba.

DEFINITION: A giant species of *Anolis* characterized by a combination of 1) high number of vertical dorsal scales, 2) high number of caudal scales, 3) size small, 4) dewlap variable, ranging from blue-green to whitish blue or green spots on a brownish ground, or pink, 5) axillary stripe composed of orange flecks within a black field, 6) upper jaw banded yellow and green, 7) in dark phase two yellow postnuchal spots and one at each ear and another posteriorly (Fig. 8D), and 8) tail without broad transverse bands.

DISCUSSION: Certainly the most easily recognizable species of giant Cuban anole is *Anolis baracoae*. The axillary stripe composed of orange flecks in a black field and the dewlap shades often involving greens, blues, or browns, immediately distinguish *baracoae* from all other taxa. It is perhaps pertinent to note that the taxon immediately adjacent to the west (*saxuliceps*) also has some orange scales bordering the axillary stripe, but the general configuration of the stripes in the two forms is quite different.

When SCHWARTZ named *baracoae*, there were but five specimens available. Through the efforts of the junior author, there are now long series of this species present in collections, and we are thus far

more able to determine the variations and parameters in meristic counts than was SCHWARTZ.

Meristic data (means and extremes) of 59 *Anolis baracoae* are: vertical dorsals 22–29 (25.2), horizontal dorsals 24–33 (28.2), caudals 21–32 (26.7); largest male 172 mm, largest female 155 mm snout-vent length. Supralabials to eye center vary between 8/8 and 10/11; the mode is 9/10. Fourth toe lamellae counts vary between 30 and 42 (mean 35.6).

Compared with the other species of Cuban giant anoles (*luteocularis*, *equestris*, *noblei*, *smallwoodi*) *baracoae* has smaller dorsal scales (vertical counts between *baracoae* and *equestris* do not overlap, so that complete separation is achieved by number of vertical dorsals). In caudal counts, *baracoae* stands at the upper extreme, but these counts overlap to some extent those of the other four species.

Anolis baracoae shows metachrosis. In the green phase, the dorsum is emerald green with many (usually fine) white dots over the entire body, each dot on one or two adjacent scales. Some individuals (IB 463) are much more heavily spotted dorsally and are reminiscent of *smallwoodi* or *palardis*. In an intermediate darker green phase, these white dots become orange, and in the brown phase, the dots are dark red. The casque and head lack any sort of marbling or discrete flecking, but almost invariably there is present a pair of yellow nuchal or postnuchal spots, a large postorbital spot on each side, and at times a spot at the auricular opening (although this may be confluent with the very prominent yellow postlabial stripe). The upper labials are vertically barred with yellow and dark green, since each supralabial has a dark green center. The axillary stripe is composed of orange dots (at times forming a fine orange line – ASFS V22363) in a black field, and this feature immediately distinguishes *baracoae* from all other taxa. The tail and limbs are usually finely crossbarred with rows of pale green to yellowish green scales, and the venter is yellow-green.

The strangest feature of *Anolis baracoae* is the variation in the dewlap color. Although some other taxa of giant Cuban anoles have slightly variable dewlap colors (for instance, *thomasi* varies from white to very pale pink), the situation in *baracoae* is more complex. SCHWARTZ's (1964: 420) description of *baracoae* noted

that the dewlap color in his short series was bluish green. The junior author has recorded dewlap colors in *baracoae* as blue-green, whitish blue, green spots on a brownish ground (in the dark phase) and pink, at times with a greenish peripheral suffusion. In any sample, the amount of variation is often great, and we cannot segregate various populations by dewlap shades or colors with any assurance whatsoever. It is possible that blue green (or perhaps non-pink) dewlaps occur in females; all of the typical series was composed of females. If such is the case (and we cannot confirm this suggestion from our present data), then perhaps pink or pink-and-green dewlaps are the male feature, and thus dewlap color may be a sexually dichromatic feature in *A. baracoae*.

A single tiny juvenile (IB 455, snout-vent length 45 mm) lacks the customary three or four pale transverse bands of juvenile *luteogularis* and *equestris*, and shows a pale flecked or dotted dorsum, with the flecks and dots arranged in many vague series of transverse rows across the sides and back. Another juvenile (MCZ 42520) with a snout-vent length of 48 mm has no dorsal or lateral markings whatsoever. It is possible that *baracoae* differs from other species in lacking boldly crossbanded young.

Anolis baracoae occurs from sealevel at the type locality and its vicinity to interior situations at moderate elevations. The northern Oriente coast, it should be recalled, is well forested, with hardwood stands extending to the very coastline. Thus, *A. baracoae* is typically a denizen of shaded and wooded situations. The specimens from Imías, on the southern xeric Oriente coast are puzzling, but presumably they were taken from riverine deciduous woods in this hot and dry area. There is no doubt that they are *baracoae* rather than *palaridis*, since the axillary stripes are typical of the former species and not of *A. smallwoodi*.

We have previously commented on the relationships between *baracoae* and its neighbors *saxuliceps* and *palaridis*. *A. baracoae* and *A. smallwoodi* approach each other closely on the southern coast (Imías and Baitiquirí, a distance of about 22 kilometers) without any indication of intergradation. The hiatus on the north coast and interior is somewhat broader (Cayo Güfn and 7 km E. Moa on the coast; La Poa and Caña in the interior; distances of 26 km and 43

km respectively). In these cases also we see no indications of intergradation between *baracoae* and *saxuliceps* or *palaridis*. We feel very secure in our assignment of specific status to *A. baracoae*.

SPECIMENS EXAMINED: *Oriente Province*. Cayo Güín, 5 (IB 463–65, ASFS V22361–62); Zapote de Mandinga, 5 (IB 451–54, IB 456); El Guayabo, 2 (IB 466, IB 468); La Poa, 20 (IB 1281, IB 1289–90, IB 1311–14, IB 1316–18, IB 1320, MFP – 9 specimens); Sabanilla, 19 (IB 469–77, IB 482–84, [NMC 12279–80, USNM 167306–07, IB 1310, IB 1315, IB 1319]; La Florida (not mapped), 6 (IB 457–60, ASFS V22364–65); Baracoa, 5 (AMNH 83628–30, MCZ 42520, IB 467); Boca de Miel, Baracoa, 1 (IB 455); Baracoa, Joar, 1 (MCZ 47050); La Tinta, Jauco, Baracoa, 1 (MFP); about 5 km W Maist, 2 (IB 1309, ASFS V22363); Imías, 2 (MCZ 42552, MFP).

DISTRIBUTION: Extreme eastern Oriente Province, east of a line drawn vertically between Cayo Güín on the north coast and Imías on the south coast (Fig. 4).

DISCUSSION

The results of our investigations may be briefly summarized: *Anolis equestris*, formerly considered the only species of giant anole on Cuba and the Isla de Pinos, has been shown to be composed of five species, of which four are polytypic. The taxa and their arrangement as we regard them are:

- 1) *Anolis luteogularis*
 - Anolis l. luteogularis*
 - Anolis l. nivevultus*
 - Anolis l. hassleri*
 - Anolis l. delacruzii*
 - Anolis l. sectilis*
 - Anolis l. coctilis*
 - Anolis l. calceus*
 - Anolis l. jaumei*
- 2) *Anolis equestris*
 - Anolis e. equestris*
 - Anolis e. buidei*
 - Anolis e. persparsus*
 - Anolis e. juraguensis*
 - Anolis e. thomasi*
 - Anolis e. verreonensis*

- 3) *Anolis noblei*
 Anolis n. noblei
 Anolis n. galeifer
- 4) *Anolis smallwoodi*
 Anolis s. smallwoodi
 Anolis s. palardis
 Anolis s. saxuliceps
- 5) *Anolis baracoae*

Since, as we have discussed each form, we have presented the available evidence for its relationships with other forms, we need not once more go over these details. However, it should be recalled that in several cases (notably in the complex of subspecies we assign to *Anolis luteogularis*; the relationships of *thomasi*; and most especially the *thomasi-noblei-galeifer* situation) there are problems which at present remain insoluble for lack of material from crucial localities. The transition from one species (*A. equestris*) with ten subspecies to our present conclusion of five species with nineteen taxa is dramatic and unprecedented in Antillean anoline classification. We feel that we have amply defended our points of view as far as the taxa are concerned in the body of the present paper; for those who still feel that scutellological and morphological (rather than color and pattern) differences are required before species or subspecies of anoles (or other lizards) are mandatory before nomenclatural separation is attempted, let us only say in our defense that anyone who has observed living specimens of such forms as *baracoae*, *palardis*, *persparsus*, and *luteogularis* cannot fail to be impressed with the differences between them. As has been pointed out (WILLIAMS, 1963, 1965; UNDERWOOD, 1959; THOMAS & SCHWARTZ, 1967) anoles are eye-minded and sight-oriented lizards; the roles that color and design of both the body and dewlap play in species (and presumably subspecies) selection and evolution seem to be great. This fact, coupled with the complex geological history of the Cuban insular platform and the extremely varied ecological background against which the *equestris* complex has evolved, accounts in no small part for the diversification of these lizards in Cuba. Parenthetically, we might mention that WILLIAMS & RAND (1969: 15)

pointed out the distinct possibility of a similar situation in the Hispaniolan giant anole *Anolis ricordi* Duméril & Bibron. Mounting evidence from Hispaniola suggests that *A. ricordi*, like "*A. equestris*" may also be a composite species. Considering that it has taken some 150 years for the material of the *equestris* complex to accumulate in sufficient quantity for any sort of analysis to be made even tentatively, we feel that the possibilities of several species of anoles masquerading under the name *A. ricordi* are great, but that it will require diligent and carefully documented collecting before this is a certainty.

SCHWARTZ (1970), in discussing Cuban *Ameiva auberi*, has suggested a theory of montane refugia to account in part for the very great diversity of that species on Cuba and the Isla de Pinos. During the Cenozoic, Cuba had an erratic history of alternating emergences and partial submersions, these latter resulting in archipelagos whose islands corresponded roughly to the present major montane masses. Cuba as a unit was finally (more or less) permanently re-established in the Middle Miocene, although it appears that the Sierra Maestra was not completely raised until Pliocene orogeny (data from MARRERO, 1951). Some areas today occupied by very distinctive subspecies of the Cuban herpetofauna (notably the Archipiélago de los Canarreos, the Laberinto de las Doce Leguas, and the *cayería* off the northern Matanzas-Las Villas-Camagüey coast) emerged during the Pliocene or even Pleistocene. The same may well be true of the Península de Zapata, the Península de Guanahacabibes, and the Isla de Pinos itself (although there are montane ranges of moderate relief on the latter island today). Thus, it is quite remarkable that some of the very distinctive subspecies of the *equestris* complex occur on these quite recently emerged land masses.

ETHERIDGE (1960) regarded "*Anolis equestris*" as a member of the *carolinensis*-group of island alpha anoles. The other giant Cuban anoline, *Chamaeleolis* (with two species), is likewise an island alpha anole, but it is more primitive than the *equestris* complex lizards. It seems reasonable to assume that, despite striking differences in scutellation, the *equestris* complex and *Chamaeleolis* are related

and that both represent relatively old persistent stocks of island alpha anoles on Cuba.

Given a long period of residency on Cuba and Cuba's alternation of emergences and submergences, the proto-*equestris* stock evolved along five basic lines: 1) *luteogularis* in the western Pinar del Río uplands; 2) *equestris* perhaps in the Sierra de Trinidad area; 3) *noblei* in the Sierra Maestra region; 4) *smallwoodi* in the Sierra de la Gran Piedra; and 5) *baracoae* in the extreme eastern Cuchillas de Toa. These assignments seem reasonable, but we are hard-pressed to consider wide-ranging *Anolis equestris* as having persisted in but a single refugium (see beyond). With the above postulations in mind, we can attempt to trace the evolutionary histories of the species, as follows.

Anolis luteogularis today occupies all of western Cuba, the Isla de Pinos, and at least one of the islands in the Archipiélago de los Canarreos (Cayo Cantiles). The distribution of the nominate subspecies is the broadest, since that subspecies occurs in the Sierra de los Organos-Sierra del Rosario massifs, as well as all associated lowland areas in Pinar del Río Province and as far west as the vicinity of Güines and La Habana in Habana Province. It seems certain that *A. l. luteogularis* is 1) the basic stock from which other subspecies of *A. luteogularis* have developed and 2) the primary isolate of the original proto-*equestris* complex of the western Cuban massifs. Once Cuba more or less attained its present configuration, and lowland areas were exposed and became habitable, *A. l. luteogularis* expended its range from the mountains into the lowlands themselves.

With the exceptions of the Pinar del Río ranges and the mountains on the Isla de Pinos, the remainder of the area occupied by *A. luteogularis* is low and thus presumably only recently emerged from the sea. Consequently, all subspecies of *A. luteogularis* (other than *A. l. luteogularis*) must be of relatively recent origin. This statement is all the more striking, since these other subspecies include several which are very distinctive and quite different in styles of pattern and scutellation from primary *A. l. luteogularis*. We feel that *nivevultus* is a direct derivative of *A. l. luteogularis* on

the Península de Guanahacabibes; its characteristics are an extension and amplification of those of the nominate subspecies and the only problem involved here is the recency of emergence of the Península. However, it should be recalled that the Península is a high center of endemism on the subspecific level and that at least one full species (*Anolis quadriocellifer*) is restricted to the Península. It seems certain that the Península de Guanahacabibes, cut off ecologically from the balance of Pinar del Río by the Plains of Remates, has been a strong center of herpetological differentiation (see GARRIDO & SCHWARTZ, 1968, for a detailed discussion of the Guanahacabibes herpetofauna).

We have pointed out previously that we are not certain about the relationships of *hassleri* with *A. luteogularis* (although we regard it as a subspecies of *A. luteogularis*). The northern portion of the Isla de Pinos, that area occupied by *hassleri*, today lacks any strong relief; there are several low mountain ranges, including the Sierra de Las Casas, the Sierra de Caballos, and the Sierra de la Cañada, as well as other isolated "hills" such as the hills at Santa Isabel where *delacruzii* occurs. Of these ranges and hills, the Sierra de la Cañada has the maximum elevation of 316 meters and the Cerro de Daguilla an elevation of 310 meters (MARRERO, 1951: 443-450). There are indications that the northern section of the Isla de Pinos was originally a dome which has been eroded to form a peneplain; the circular distribution of the modern Isla de Pinos ranges and the island's radial drainage are evidences of this history. It seems possible that *hassleri* and *delacruzii* represent remnants of an early *luteogularis* stock which were isolated on the present northern section of the Isla de Pinos, and that *hassleri* differentiated there and has persisted in the relict deciduous montane and *arroyo* flora. *A. l. delacruzii* on the other hand is a *hassleri* isolate on the hills at Santa Isabel; the geographical and vegetational picture of this particular region has been discussed previously.

The Ciénaga de Lanier separates the two sections of the Isla de Pinos; in fact, it is more than probable that the Isla de Pinos has at times been separated into a northern and a southern portion by the incursion of the sea across the low-lying Ciénaga. Other species of reptiles (*Ameiva auberi*, *Leiocephalus stictigaster*) have well marked

subspecies on the northern and southern portions of the Isla. *A. l. sectilis* is thus presumably a *hassleri* derivative on the southern Isla de Pinos island; establishment of connections between the two islands has allowed *sectilis* to come in contact with *hassleri* at selected ecologically suitable situations (as at Paso de Piedras) where the two forms intergrade.

The three remaining subspecies of *Anolis luteocularis* (*coctilis*, *calceus*, *jaumei*) present a problem. We have suggested that these may represent a sequential series (*sectilis-coctilis-calceus*) but such a sequence is not likely; it requires deriving a large form (*calceus*) from a dwarf subspecies (*coctilis*). It seems more likely that *coctilis* was derived directly from *sectilis* on the chain of the Archipiélago de los Canarreos, and that *calceus* and *jaumei* represent two separate re-invasions of the Cuban mainland from the Isla de Pinos. Although of the two Isla de Pinos subspecies, *sectilis* is the more remote geographically from the Cuban mainland, both *calceus* and *jaumei* appear much closer to *sectilis* than to *hassleri*. MARRERO (1951: 44) showed seasonal oceanic currents in June and December for the waters about Cuba. In June, there is a major current from the west between Cuba and the Isla de Pinos and thus objects could be carried from the northern portion of the Isla to the Península de Zapata. In December, this current is apparently reduced or absent, and a more southern current sweeps the southern Isla de Pinos and the Archipiélago de los Canarreos from the west. Although the Península de Zapata is not in the direct line of this current as it moves along the southern Cuban coast, it is not improbable that such winter currents may have been responsible for the arrival of the *luteocularis* stock on the Cuban mainland from the southern Isla de Pinos. After this arrival (and probably there was more than one overseas transportation of the Isla de Pinos stock to Cuba), *calceus* differentiated on the Península de Zapata and *jaumei* on the southwestern Las Villas coast in the Bahía de Cochinos area.

Of the species of the *equestris* complex, *Anolis equestris* has the broadest distribution; it is certainly known from Habana Province to eastern and northeastern Oriente Province. Within the species there are three basic styles of pattern: 1) bright casque and canthal markings (*equestris*, *buidei*); 2) no bright head or canthal markings

(*persparsus*, *juraguensis*); and 3) sides streaked with pale color between the scales (*thomasi*, *verreonensis*). We suggest that these three basic styles represent three isolates of the proto-*equestris* stock; these stocks, although divergent, have apparently not become reproductively isolated (there are intergrades between *equestris* and *persparsus* in northwestern Las Villas Province, but no intergrades are known between any of the other subspecies). We suggest that nominate *equestris* is the isolate of the Escaleras de Jaruco or perhaps the Bejucal-Madruga-Limonar Anticline (both ranges now of moderate relief). Apparently, *A. e. equestris* has moved westward to meet *A. l. luteogularis* in Pinar del Río (although no recently taken specimens confirm this movement) and *A. l. luteogularis* moved eastward to come into contact with *A. e. equestris* in Habana Province. *A. e. buidei* is a local derivative of *A. e. equestris* on the previously insular (but now peninsular) Península de Hicacos.

The refugium of the *persparsus-juraguensis* pair logically is the high Sierra de Trinidad. From this center, *persparsus* spread throughout Las Villas Province, coming into contact with *equestris* and intergrading with it in the northwestern portion of that province. *A. e. juraguensis* is a local derivative of *persparsus* to the west of the Bahía de Cienfuegos.

The center of *thomasi* differentiation is presumably the Sierra de Cubitas in northern Camagüey Province. From this refugium, *thomasi* has spread throughout Camagüey and north and western Oriente Province. Intergradation between *thomasi* and *persparsus* is unknown; the rationale for considering *thomasi* a subspecies of *equestris*, rather than as a distinct species, has already been made. Local differentiation of *verreonensis* from *thomasi* in the Cabo Cruz region is certain. The eastern limits of *thomasi*-like anoles in Oriente remain to be determined, but lizards with the *thomasi* style of lateral streaking occur in the Río Cauto lowlands north of the Sierra Maestra and probably farther east, in the region north of Santiago de Cuba.

Anolis noblei is surely the species for which the Sierra Maestra served as a refuge. It is the only species within the major portion of this range (*A. smallwoodi* has invaded the eastern portion of the range at Hongolosongo). *A. noblei* has also apparently been able to

reach the Sierra de Nipe (and thence the Cuchillas de Toa) across the Río Cauto lowlands on one hand, and on the other *A. noblei* has followed the Valle Central to inhabit the northern slopes of the Sierra de la Gran Piedra (which elsewhere is occupied by *A. smallwoodi*). Such a distribution probably was attained before the (presumed) arrival from the west of *thomasi*-like anoles which themselves appear to have invaded southern Oriente via the Río Cauto drainage.

Anolis smallwoodi we consider the Sierra de la Gran Piedra isolate; the species is distributed through that range (except apparently along its northern face where *A. noblei* occurs) and in the associated lowlands between Santiago de Cuba, Guantánamo, and Baitiquiri. *A. smallwoodi* has to some slight extent invaded the territory of *A. noblei* at Hongolosongo and at Cupeyal. Apparently *A. smallwoodi* has crossed from the southern to the northern coast of Oriente to reach the Cuchillas de Toa (where it is sympatric with *A. noblei* at Cupeyal). We regard *A. smallwoodi* as the "resident" member of the complex in the Cuchillas de Toa and *A. noblei* as an invader from the west (Sierra de Nipe).

The effect of the pocket embayments on the southern Oriente coast upon the herpetofauna of that region is by now well documented; examples include *Leiocephalus raviceps* (SCHWARTZ, 1960), *Sphaerodactylus torrei* (THOMAS & SCHWARTZ, 1966), and *Ameiva auberi* (SCHWARTZ, 1970). As far as *A. smallwoodi* is concerned, the Bahía de Guantánamo separates *smallwoodi* from *palardis*; *A. s. smallwoodi* has however been able to circumvent the head of the Bahía de Santiago to reach the Sierra del Cobre to the west. *A. s. saxuliceps* is a northern derivative of *A. s. palardis* in the mesic Cuchillas de Toa.

Anolis baracoae appears to be the isolate of the extreme eastern Cuchillas de Toa and perhaps the Sierra de Purial. Although we tend to associate *baracoae* with areas of high rainfall and forest cover, its occurrence at Imías suggests that it may also be a lizard of xeric conditions. Extreme eastern Cuba is gradually emerging as a subcenter of specific differentiation: the occurrence in the mountains north of Imías of *Anolis imias* Ruibal & Williams is one instance, and *Eleutherodactylus bresslerae* Schwartz is limited to

this region. Apparently, the extreme eastern tip of Cuba and its wet mountains have had a history which differs from that of the rest of eastern Cuba itself.

As we visualize it, the *equestris* complex has had a very complicated history. In the matter of refugia, the anoles compare favorably with the senior author's interpretation of the evolutionary history of *Ameiva auberi* (SCHWARTZ, 1970). But there is one striking difference: in *Ameiva*, there has apparently been no specific differentiation, and all forms are regarded as subspecies of *Ameiva auberi*. In the *equestris* complex on the other hand, differentiation has been more striking, with the evolution of five species.

We realize that our interpretations, both nomenclatural and zoogeographic, are subject to great modifications. We have not hesitated to state categorically where we simply were not certain of the relationships of various taxa to each other. Consequently, our historical outline may be incorrect in many details, since the infrastructure upon which it is based is of itself less secure than we could wish. On the other hand, we feel that we have presented a quite different (and more accurate) interpretation of the *equestris* complex than has been heretofore apparent. Much new material has allowed us to break with the traditional interpretation of "*Anolis equestris*" as a single polytypic unit. How correct our interpretations are will depend upon the acquisition of new material both from the ranges of the various taxa as we now define them and from areas which remain unrepresented by specimens of the *equestris* complex.

EXTRACTO

El chipoyo cubano *Anolis equestris* se considera que está compuesto de cinco especies distintas, cuatro de la cuales son polytípicas: *Anolis luteogularis*, que radica en la parte oeste de Cuba hasta la provincia de La Habana por el este, en la Isla de Pinos, el archipiélago de los Canarreos, y en la costa sur de Cuba en la región de la Ciénaga de Zapata (8 subespecies reconocidas); *Anolis equestris* radica desde el este de la provincia de Pinar del Río hasta el oeste de la provincia de Oriente (6 subespecies reconocidas); *Anolis noblei* en la Sierra de Nipe, las Cuchillas de Toa y la Sierra Maestra (2 subespecies reconocidas); *Anolis smallwoodi* en la costa sur de Oriente desde la Bahía de Santiago a Baitiquirí, y por el norte hasta la región de

Moa (3 subespecies reconocidas); y *Anolis baracoae* en el extremo este de la provincia de Oriente.

Simpatria ha sido demostrada entre *A. luteogularis* y *A. equestris* en las provincias de Pinar del Río y La Habana; entre *A. noblei* y *A. smallwoodi* en Hongolosongo y en el Cupeyal en la provincia de Oriente. Las mayores características de las especies y subespecies incluyen el tamaño de las escamas dorsales, detalles del color del cuerpo y patrón de ambos: cuerpo y casquete de la cabeza.

Una hipótesis histórica de la especiación y diferenciación de los miembros del complejo *equestris* es presentada de la siguiente manera: correlacionada con la historia Cenozoica (Mioceno en adelante) de Cuba y más tarde la permanencia relativa de masas de montaña las cuales sirvieron de refugio a porciones de una rama proto-*equestris*. Se sugiere que *luteogularis* evolucionó en las tierras altas del oeste de Pinar del Río; *equestris* en la Sierra de Trinidad, las Escaleras de Jaruco, y la Sierra de Cubitas; *noblei* en la Sierra Maestra; *smallwoodi* en la Sierra de la Gran Piedra y *baracoae* en el este de Cuchillas de Toa y la Sierra de Purial. Desde estos refugios básicos las diferentes especies migraron a ocupar su respectiva distribución actual.

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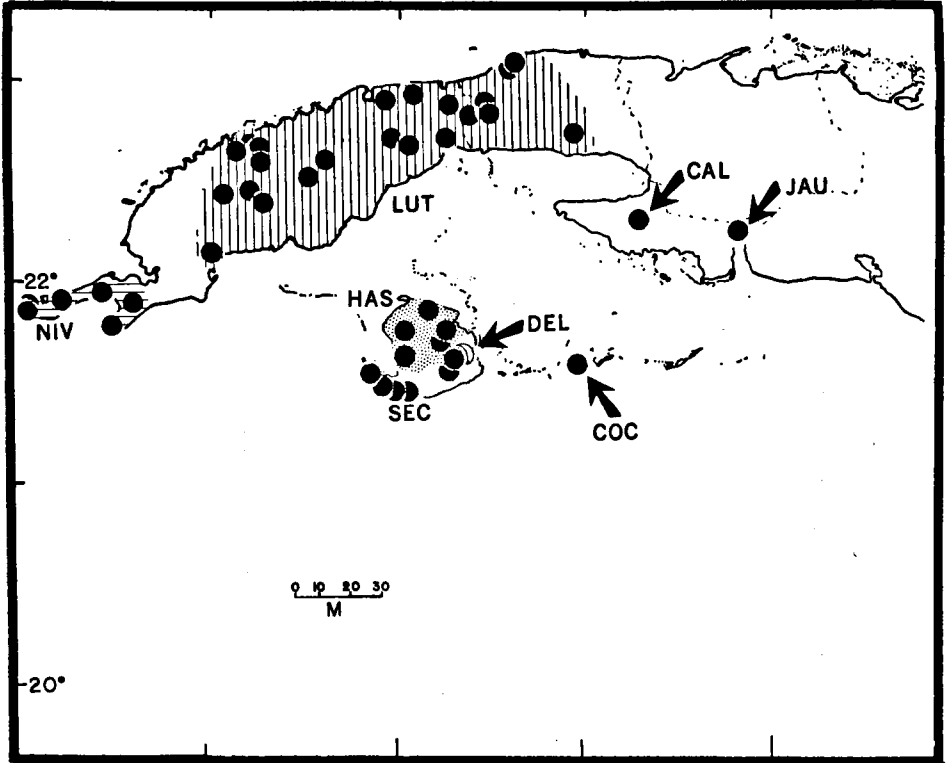


Fig. 1. Map of western CUBA, showing the distribution of the subspecies of *Anolis luteogularis*, as follow: *luteogularis* – wide vertical lines (LUT); *nivevultus* – wide horizontal lines (NIV); *hassleri* – stippling (HAS); *sectilis* – fine diagonal lines (SEC); *delacruzi* – open circle (DEL); *coctilis* (COC); *jaumei* (JAU); *calceus* (CAL).

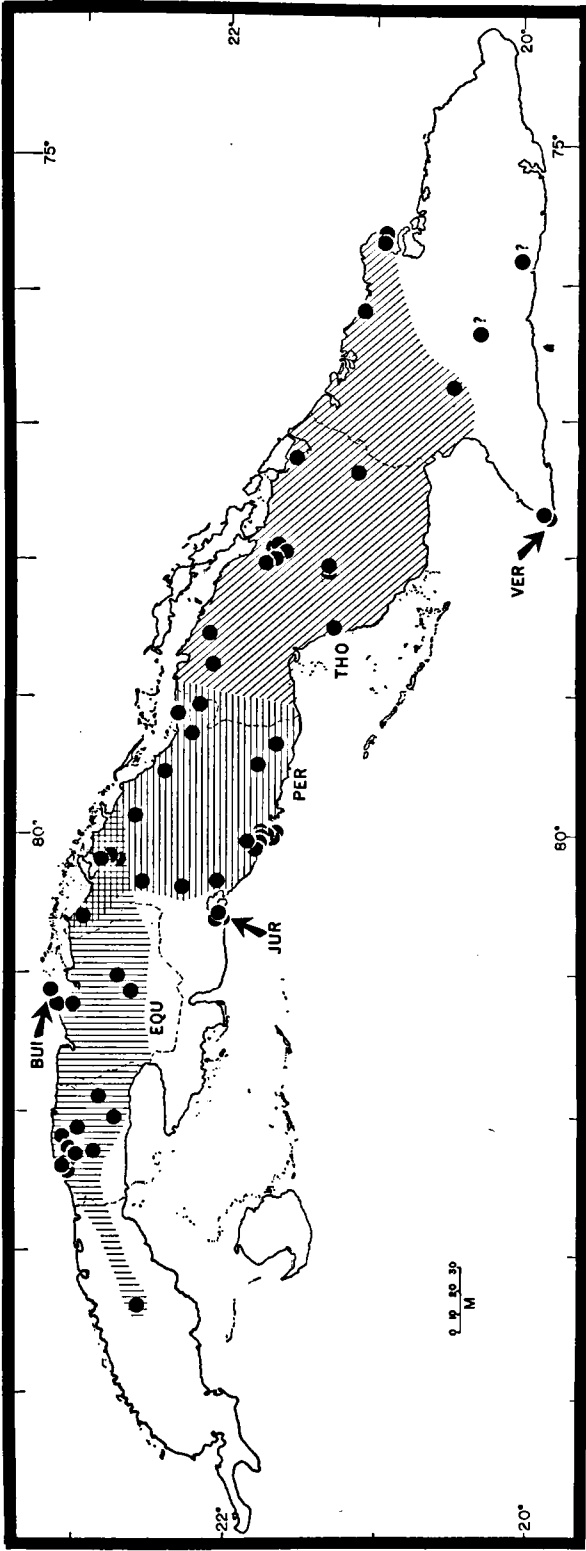


Fig. 2. Map of Cuba, showing the distribution of the subspecies of *Anolis equestris*, as follow: *equestris* - vertical lines (EQU); *buidai* (BUI); *persparvus* - horizontal lines (PER); *juraguensis* (JUR); *thomasi* - diagonal lines (THO); *verreauxensis* (VER). Questioned localities in Oriente Province are *thomasi*-like specimens noted in text. Overlap of symbols in northern Las Villas Province shows area of intergradation between *equestris* and *persparvus*.

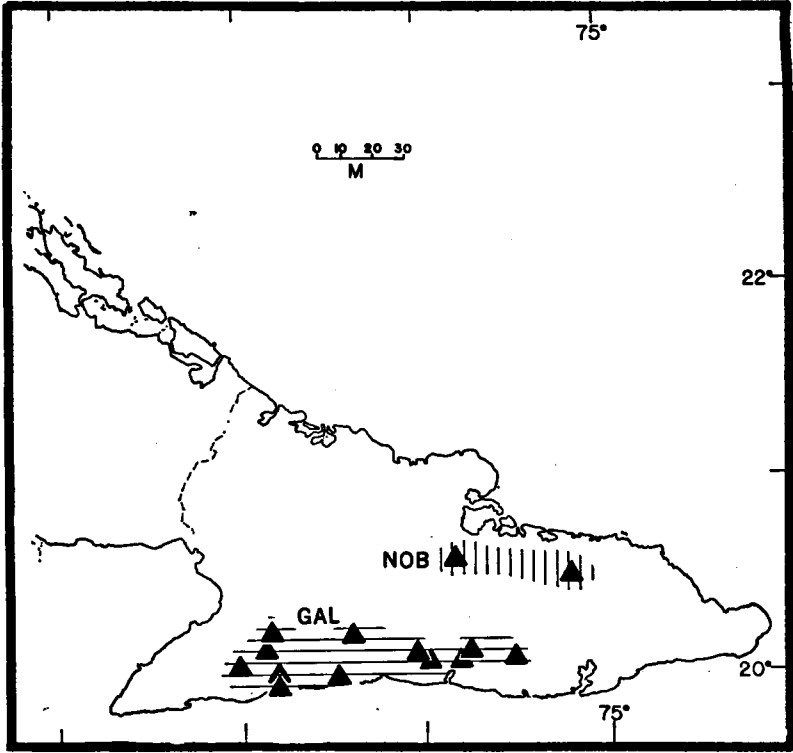


Fig. 3. Map of eastern Cuba, showing the distribution of the subspecies of *Anolis noblei*, as follow: *noblei* - vertical lines (NOB); *galeifer* - horizontal lines (GAL).

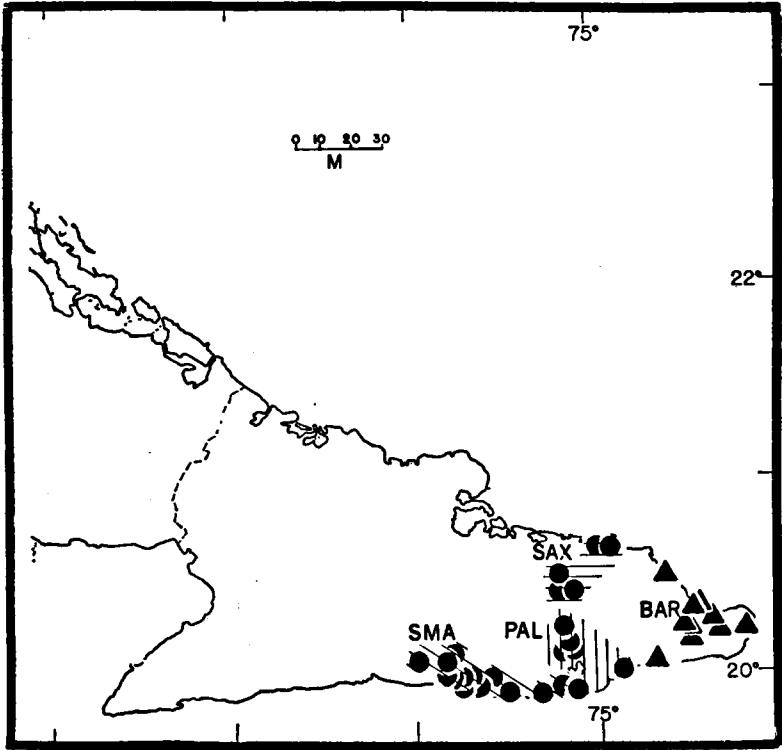


Fig. 4. Map of eastern CUBA, showing the distributions of *Anolis smallwoodi* (circles) and *Anolis baracoae* (triangles), as follow: *smallwoodi* - diagonal lines (SMA); *palardis* - vertical lines (PAL); *saxuliceps* - horizontal lines (SAX). *Anolis baracoae* (BAR).

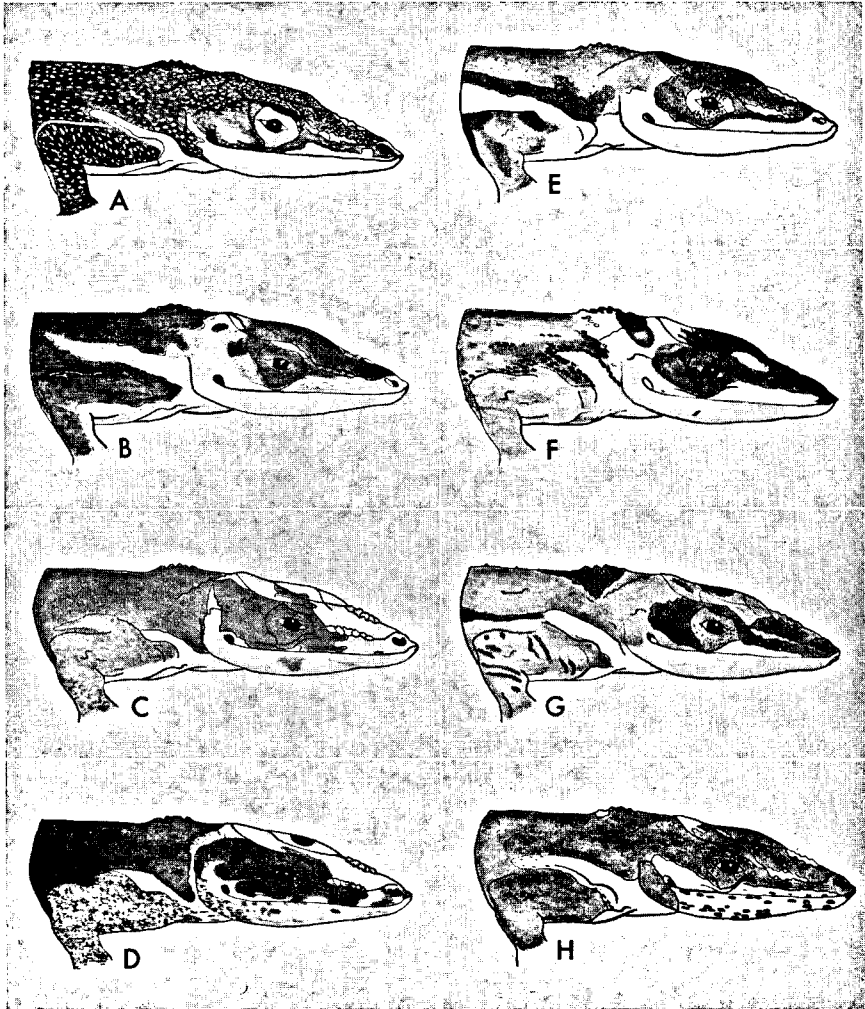


Fig 5. Laterodorsal views of heads of subspecies of *Anolis luteogularis*, as follow: A, *A. l. luteogularis*, AMNH 78150, 7.8 mi. SW Cabezas, Pinar del Río Province; B, *A. l. niveovultus*, IB 339, holotype, El Veral, Península de Guanahacabibes, Pinar del Río Province; C, *A. l. hassleri*, IB 1292, El Respiro, Santa Fé, Isla de Pinos; D, *A. l. delacruzii*, ASFS V22312, paratype, Santa Isabel, southeastern portion of northern two-thirds of Isla de Pinos, north of the Ciénaga de Lanier; E, *A. l. sectilis*, IB 388, holotype, Pedernales, Isla de Pinos; F, *A. l. coctilis*, IB 402, holotype, Punta del Inglés, Cayo Cantiles, Archipiélago de los Canarreos; G, *A. l. calceus*, IB 1295, holotype, Santo Tomás, Ciénaga de Zapata, Las Villas Province; H, *A. l. jaumei*, IB 369, holotype, Playa Larga, Ciénaga de Zapata, Las Villas Province.

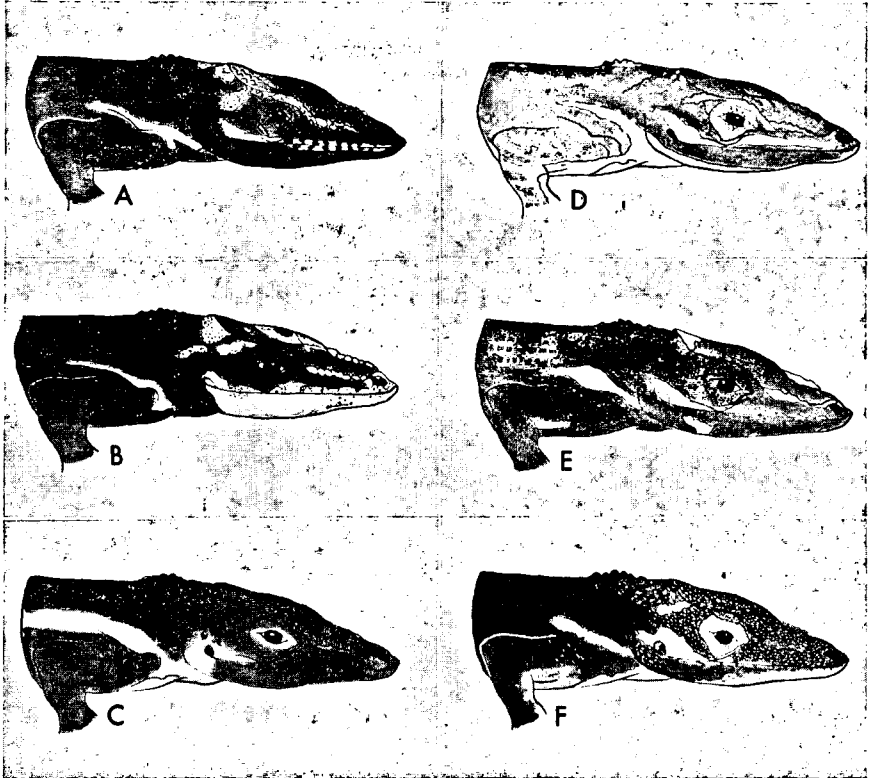


Fig. 6. Laterodorsal views of heads of subspecies of *Anolis equestris*, as follow: A, *A. e. equestris*, AMNH 78074, 9 km SW San José de la Lajas, Habana Province; B, *A. e. buidei*, AMNH 89536, paratype, Punta Hicacos, Matanzas Province; C, *A. e. persparsus*, AMNH 78116, holotype, 4 km E Trinidad, Las Villas Province; D, *A. e. juraguensis*, ASFS V22325, paratype, Monte Alto, 3 km SW Juraguá, Las Villas Province; E, *A. e. thomasi*, AMNH 78149, paratype, 2 km SE Banao, Camagüey Province; F, *A. e. verreonensis*, IB 488, holotype, Verreón, Cabo Cruz, Oriente Province.

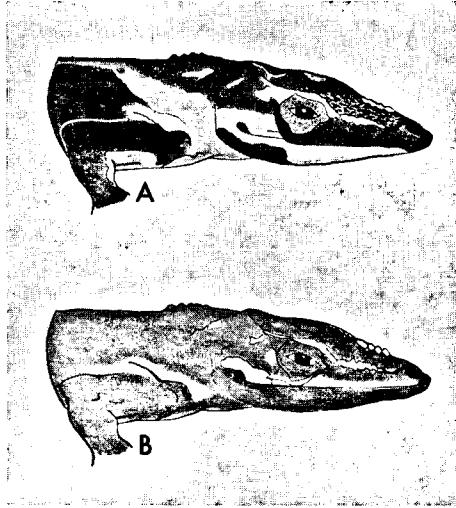


Fig. 7. Laterodorsal views of heads of subspecies of *Anolis noblei*, as follow: A, *A. n. noblei*, IB 1218, Cupeyal, Sagua de Tánamo, Oriente Province; B, *A. n. galeifer*, MFP, La Emajagua, Pico Turquino, Oriente Province.

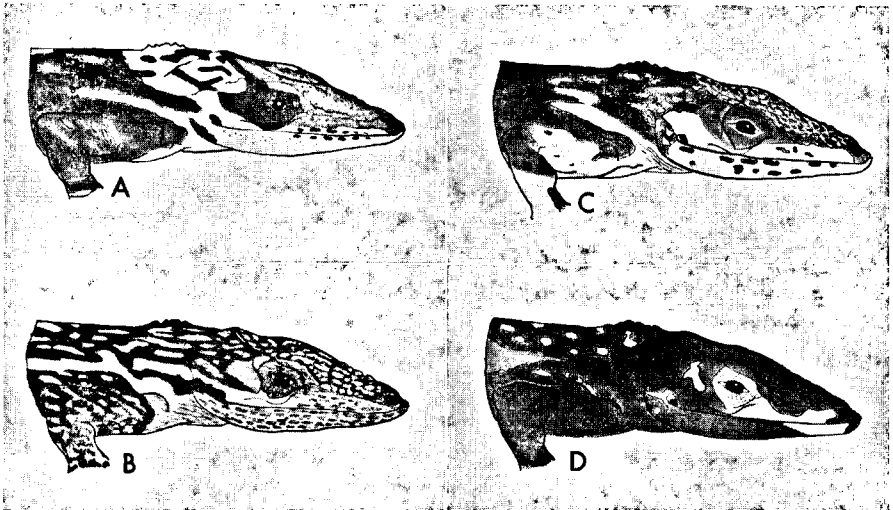


Fig. 8. Laterodorsal views of heads of subspecies of *Anolis smallwoodi* and *Anolis baracoae*, as follow: A, *A. s. smallwoodi*, ASFS V13808, U. S. Naval Base, Guantánamo Bay, Oriente Province; B, *A. s. palardis*, ASFS V16354, U. S. Naval Base, Oriente Province; C, *A. s. saxuliceps*, MCZ 59324, paratype, 7 km E Moa, Oriente Province; D, *A. baracoae*, IB 466, El Guayabo, Oriente Province.