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VARIATION IN LIZARDS OF THE LEIOCEPHALUS
CUBENSIS COMPLEX IN CUBA AND THE ISLA DE PINOS

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VARIATION IN LIZARDS OF THE LEIOCEPHALUS CUBENSIS COMPLEX IN CUBA AND THE ISLA DE PINOS

ALBERT SCHWARTZ 1

Synopsis: Leiocephalus cubensis Gray has been regarded as one of four species of this genus in Cuba and the Isla de Pinos, and has been known to occur throughout both islands in suitable habitats. Collection of 388 specimens and study of additional material from various museums resulted in the partition of L. cubensis into two species, each with four subspecies. L. cubensis is now known from Cuba and the Isla de Pinos, the Doce Leguas keys, and the Archipiélago de los Canarreos, whereas the new species occurs in western Cuba and the Isla de Pinos. The status of Oriente lizards of this complex remains uncertain. A history of the two species leading to their contemporary distribution is offered.

Introduction

Of the four species of the genus Leiocephalus currently recognized on the island of Cuba, L. cubensis Gray has the widest distribution, occurring in suitable habitats from Cabo de San Antonio to Cabo Maisí. Under a National Science Foundation grant I made herpetological collections during the summer of 1957 in the Cuban provinces of Pinar del Río, Habana, Las Villas, and Camagüey, during the Christmas holidays of 1957-58 on the Isla de Pinos, and during the summer of 1958 in the provinces of Matanzas, Las Villas, Camagüey, and again on the Isla de Pinos. Among the amphibians and reptiles collected are 388 specimens of what has been considered as L. cubensis. The present paper discusses the variation demonstrable in this material. Specimens in several museum collections are also employed in the analysis.

I have had assistance in the field from the following persons, without whose help and fellowship the large number of these lizards could not have been collected: Messrs. Edwin B. Erickson, John R. Feick, William H. Gehrmann, Jr., Dennis R. Paulson, Willard M. Stitzell, Richard Thomas, George R. Zug, Dr. Robert S. Howard, Srs. Armando García, Porifiro Azcuy, Octavio Noda, and the late Alfredo Alvarez Mola. Many Cuban children and farmers helped greatly in collecting specimens. Mr. Willard M. Stitzell made many calculations of averages and chi square tests, and Mr. George R. Zug gave great as-

¹ Albert Schwartz is an Instructor in the Department of Biology at Albright College, Reading, Pennsylvania. The present paper is a result of collections made in Cuba and the Isla de Pinos under a National Science Foundation grant. Manuscript received 10 December 1958.—Ed.

sistance in counting scales on several lots of specimens. Mr. William H. Gehrmann, Jr. took kodachromes in the field for me. The black and white photographs are the work of Mr. Gary Stone and Mr. John A. Falkenstein. The drawings of hemipenes were done by Mr. Ronald F. Klinikowski. All have my sincere thanks for their endeavors on my behalf.

In the United States and Cuba I have examined specimens of the L. cubensis complex from the following collections, and wish to express my gratitude to the respective curators for allowing me access to material in their care:

ANSP—Academy of Natural Sciences of Philadelphia (Dr. James Böhlke)

AMNH—American Museum of Natural History (Mr. Charles M. Bogert and Dr. Richard G. Zweifel

CM-Carnegie Museum (Mr. Neil D. Richmond)

MCZ—Museum of Comparative Zoology (Dr. Ernest Williams)

MJ-Sr. Miguel L. Jaume García, Habana

UH—Universidad de la Habana (Dr. Carlos G. Aguayo y de Castro and Dr. Isabel Pérez Farfante)

UMMZ—Museum of Zoology, University of Michigan (Dr. Norman E. Hartweg and Mr. Richard Etheridge)

USNM—United States National Museum (Dr. Doris M. Cochran)

METHODS AND TERMINOLOGY

The usual scale counts and measurements have been made on all adult specimens used in this study. All measurements are in millimeters. To simplify describing the patterns of these typically zoned or lined lizards, I have numbered the longitudinal zones beginning at the dorsal midline and proceeding ventrally as follows: Zone 1. a narrow, usually dark middorsal area lying on either side of the dorsal crest scales; Zone 2, a light longitudinal band about two to three scales in width; Zone 3, a dark longitudinal band usually about four scales in width, called the dorsal field; Zone 4, a white (or at least very pale) longitudinal line beginning above the postorbital blotch and extending to the sacral region; Zone 5, a broad lateral band extending from the temporals and the posterior edge of the postorbital blotch posteriorly over the side of the body, called the lateral field; Zone 6, a white or pale longitudinal line extending from below the eye posteriorly to the groin. Below zone 6 the lateral coloration usually blends into that of the venter. These zones are

expressed to their fullest extent in the smaller species, and are combined, obscured, or indistinguishable in *cubensis*.

ANALYSIS OF CHARACTERS

The lizards currently regarded as L. cubensis are actually separable into two distinct species on the basis of size, coloration and pattern, and hemipenial structure. No scale count taken will separate the two species, although average differences between them do occur. Each species is likewise divisible into four subspecies. The name cubensis Gray is obviously properly applied to the larger of the two species which, in addition to large size, is characterized by a rather inconspicuously lined or unicolor dorsum, brightly colored venter, orange or red sides with vertical rows of green scales extending onto the venter, a prominent black or dark brown postorbital blotch, and with the throat clouded, mottled, dotted, stippled, or generally very dark in color. The other species is small, has a prominently lined dorsum, unicolor pale venter, pinkish to reddish sides without vertical green rows of scales, postorbital blotch absent or at best poorly defined, and throat pale with distinct black or brown markings, seldom clouded or obscured.

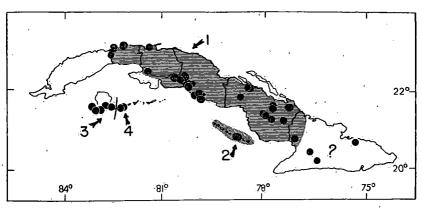


Figure 1.—Distribution of Leiocephalus cubensis on Cuba and the Isla de Pinos. Subspecies as follows: 1) cubensis-horizontal lines; 2) paraphrus-stippling; 3) gigas; 4) pambasileus. Certain locality records have been combined for greater clarity. The three locality dots in eastern Cuba represent specimens which are considered L. c. cubensis only tentatively.

It is not surprising that these two species have been long confused. On Cuba L. cubensis is found from western Habana to eastern

Oriente (fig. 1), the smaller form occurs in Pinar del Río (fig. 2); the two species are completely allopatric and no intermediates have been encountered. On the Isla de Pinos live a large subspecies of cubensis and two races of the smaller form; here the distributions present an interesting and confusing pattern, but the two species are ecologically isolated, and again no intermediates have been seen. Study of old preserved material has been misleading; observations on these lizards in the field and comparison of fresh material, the colors and patterns of which were studied in life, have clarified their relationships.

As in other Cuban members of the genus Leiocephalus, coloration and pattern play an important part in differentiating the subspecies of

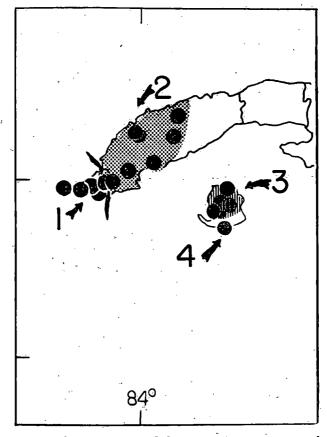


Figure 2.—Distribution of Leiocephalus stictigaster in Western Cuba and the Isla de Pinos. Subspecies as follows: 1) stictigaster; 2) sierrae-stippled; 3) exotheotus-vertical lines; 4) astictus. Certain locality records have been combined for greater clarity.

both these species. However, the situation here is not so difficult as in *L. carinatus*, because the basic pattern differences in the *cubensis* complex are more striking than in *L. carinatus*, and many old preserved specimens show some details satisfactorily. Color notes in life and kodachrome photographs taken in the field have aided my study greatly. The presence or absence of a postorbital blotch and its extent posteriorly, the spotting of the dorsum of the hindlimbs, underside of the base of the tail, and venter of the lizard can be determined easily on specimens that have been preserved for some time. Even such details as the light-colored scales which are greenish in life on the sides of the abdomen in *cubensis* are determinable after many years in preservative.

The throat pattern in each species of the *L. cubensis* complex varies tremendously within populations, and its significance on a subspecific level is open to question. As noted above, throat pattern differences do separate the two species involved. The sex of individual specimens of the *cubensis* complex, in contrast to *carinatus*, is easily determinable; males possess two pairs of enlarged postanal scales which the females lack. The presence or absence of these enlarged scales allows even very small lizards to be sexed with ease.

Both species of the complex show other differences between males and females. Males reach a larger size than females, adult males are more heavily built than adult females and have broader heads. The postorbital blotch is usually better developed in males. Adult males and females differ, with one exception, in that the longitudinal zones of females are persistent and seldom become obscured with increasing size, and the dorsal fields usually show many dark paired blotches. Generally juveniles show an intensification of the adult female pattern. On the belly, especially laterally, females usually have many diffuse grey dots or spots, which are not to be confused with the brown or black ventral dots of the males of some races of the smaller species.

Throughout the range of cubensis the number of dorsal crest scales in the occiput-vent length varies from 48 to 66; the number of dorsal crest scales in the occiput-axilla distance varies between 16 and 31. The number of scales at midbody, counted on one half the body from the midventral line to but not including the dorsal crest scales, varies from 18 to 30, and the number of tricarinate subdigital scales on the fourth toe varies from 21 to 28. The same data for the smaller species are: dorsal crest scales in occiput-vent length, 43 to 62; dorsal crest scales in occiput-axilla distance, 15 to 28; midbody scales, 20 to 32;

tricarinate fourth toe scales, 19 to 28 (See Table I). None of these scale counts will separate the two species.

The presence or absence of contact between the parietals and whether or not the supraorbital semicircles separate the supraocular series completely from the two pairs of frontals have proved significant in differentiating between the subspecies. In *cubensis* the number of loreals on one side varies between 4 and 12 and the number of temporals on one side from 9 to 16. In the smaller form the loreals range from 3 to 10, the temporals 8 to 16. All of these characteristics have proved useful in analyzing the various populations heretofore assigned to *L. cubensis*.

ACCOUNTS OF THE SPECIES

Five species of the genus Leiocephalus are now known to occur in Cuba; three of these occur as well on the Isla de Pinos. Of the five species, L. raviceps Cope and L. macropus Cope have been reported only from Oriente Province (Barbour and Ramsden, 1919), although macropus has been collected since at several other localities in Cuba. Leiocephalus cubensis Gray and L. carinatus Gray occur both on Cuba and the Isla de Pinos, as does also the species described as new below.

Barbour and Ramsden (1919: 169) presented a useful key to the four species then known to occur in Cuba. They characterized L. cubensis as having the caudal crest not higher than the dorsal, no minute granules behind the ear opening, the side of the neck entirely covered with pointed, imbricate, keeled scales, and about 12 dorsal scales equal to the head length. The height of the caudal versus dorsal crest by which they differentiate cubensis from carinatus is of doubtful significance. In both the caudal crest is slightly higher than the dorsal, and it is especially well developed in adult males. However, the two species can be distinguished by the great difference in size of dorsal scales, those of carinatus being much larger, the entire lizard having a distinctly rough and "scaley" appearance, whereas those of cubensis are smaller and the aspect of the animal is more smooth.

The pattern and coloration of these two species is radically different as well: carinatus is in general dull in color, with more or less (depending upon the subspecies) well-defined cross bands and a dull yellowish to gray venter, whereas cubensis is either unicolor or with poorly defined longitudinal zones dorsally, and has a multicolored or vivid yellow venter. L. cubensis possesses a postorbital black or

TABLE 1

Measurements and scale counts of four subspecies of *L. cubensis* and four subspecies of *L. stictigaster*, expressed as means and observed ranges. Combined data for both sexes except for snout-vent length.

cubensis	paraphrus						
37 & , 28 ♀)	(9 ₺, 17 ♀).	gigas (23 8 , 30 ♀)	pambasileus (11∂,7♀)	stictigaster (26 ♂, 27 ♀)	sierrae (33 & , 30 ♀)	exotheotus (19∂, 16♀)	astictus $(15\delta,10\Omega)$
	• •			•			
8.4 (64-110)	83.9 (55-98)	100.7 (80-121)	83.4 (66-95)	66.1 (57-79)	73.2 (60-81)	59.5 (46-70)	69.2 (58-79)
8.0 (56- 81)	63.7 (56-69)	72.1 (61- 83)	65.4 (64-67)	54.9 (48-72)	62.8 (57-67)	49.9 (43-57)	58.7 (55-62)
•		-					•
.8%	53%	56%	45%	59%	78%	47%	27%
12%	47%	44%	55%	41%	22%	53%	73%
						• .	
7%	69%	76%	100%	40%	66%	55%	86%
3%	31%	24%	0%	60%	34%	45%	14%
	•	•					
64.5 (48- 62)	55.6 (48-62)	57.4 (50- 64)	57.9 (52-63)	54.2 (48-62)	49.9 (45-55)	48.7 (43-53)	49.2 (45-54
1.8 (17- 28)	22.1 (16-26)	23.9 (20- 27)	25.9 (22-28)	22.7 (19-28)	19.3 (16-24)	21.1 (15-26)	21.5 (17-26
25.1 (18- 28)	25.4 (23-27)	27.1 (23-30)	26.3 (23-28)	24.8 (22-28)	24.9 (21-32)	23.3 (19-26)	22.0 (20-25
5.4 (3- 10)	4.8 (4- 7)	4.9 (4- 12)	7.2 (6- 9)	4.8 (3- 8)	`4.8 (3-10)	4.5 (2- 7)	5.0 (3- 7
2.0 (9- 15)	10.9 (10-13)	13.1 (10- 16)	13.5 (11-16)	12.7 (10-16)	12.5 (10-16)	11.4 (8-15)	11.0 (9-12)
3.4 (21- 27)	25.4 (23-28)	24.5 (24- 28)	25.8 (24-28)	23.4 (20-27)	23.8 (21-28)	22.2 (19-27)	22.8 (20-25
	8.0 (56- 81) 8% 2% 7% 3% 4.5 (48- 62) 1.8 (17- 28) 5.1 (18- 28) 5.4 (3- 10) 2.0 (9- 15)	8.0 (56- 81) 63.7 (56-69) 8% 53% 2% 47% 7% 69% 3% 31% 4.5 (48- 62) 55.6 (48-62) 1.8 (17- 28) 22.1 (16-26) 5.1 (18- 28) 25.4 (23-27) 5.4 (3- 10) 4.8 (4- 7) 2.0 (9- 15) 10.9 (10-13)	8.0 (56- 81) 63.7 (56-69) 72.1 (61- 83) 8% 53% 56% 2% 47% 44% 7% 69% 76% 3% 31% 24% 4.5 (48- 62) 55.6 (48-62) 57.4 (50- 64) 1.8 (17- 28) 22.1 (16-26) 23.9 (20- 27) 5.1 (18- 28) 25.4 (23-27) 27.1 (23- 30) 5.4 (3- 10) 4.8 (4- 7) 4.9 (4- 12) 2.0 (9- 15) 10.9 (10-13) 13.1 (10- 16)	8.0 (56- 81) 63.7 (56-69) 72.1 (61- 83) 65.4 (64-67) 8% 53% 56% 45% 2% 47% 44% 55% 7% 69% 76% 100% 3% 31% 24% 0% 4.5 (48- 62) 55.6 (48-62) 57.4 (50- 64) 57.9 (52-63) 1.8 (17- 28) 22.1 (16-26) 23.9 (20- 27) 25.9 (22-28) 5.1 (18- 28) 25.4 (23-27) 27.1 (23- 30) 26.3 (23-28) 5.4 (3- 10) 4.8 (4- 7) 4.9 (4- 12) 7.2 (6- 9) 2.0 (9- 15) 10.9 (10-13) 13.1 (10- 16) 13.5 (11-16)	8.0 (56- 81) 63.7 (56-69) 72.1 (61- 83) 65.4 (64-67) 54.9 (48-72) 8% 53% 56% 45% 59% 2% 47% 44% 55% 41% 7% 69% 76% 100% 40% 3% 31% 24% 0% 60% 4.5 (48- 62) 55.6 (48-62) 57.4 (50- 64) 57.9 (52-63) 54.2 (48-62) 1.8 (17- 28) 22.1 (16-26) 23.9 (20- 27) 25.9 (22-28) 22.7 (19-28) 5.1 (18- 28) 25.4 (23-27) 27.1 (23- 30) 26.3 (23-28) 24.8 (22-28) 5.4 (3- 10) 4.8 (4- 7) 4.9 (4- 12) 7.2 (6- 9) 4.8 (3- 8) 2.0 (9- 15) 10.9 (10-13) 13.1 (10- 16) 13.5 (11-16) 12.7 (10-16)	8.0 (56- 81) 63.7 (56-69) 72.1 (61- 83) 65.4 (64-67) 54.9 (48-72) 62.8 (57-67) 8% 53% 56% 45% 59% 78% 22% 47% 44% 55% 41% 22% 7% 69% 76% 100% 40% 66% 3% 31% 24% 0% 60% 34% 4.5 (48- 62) 55.6 (48-62) 57.4 (50- 64) 57.9 (52-63) 54.2 (48-62) 49.9 (45-55) 1.8 (17- 28) 22.1 (16-26) 23.9 (20- 27) 25.9 (22-28) 22.7 (19-28) 19.3 (16-24) 5.1 (18- 28) 25.4 (23-27) 27.1 (23- 30) 26.3 (23-28) 24.8 (22-28) 24.9 (21-32) 5.4 (3- 10) 4.8 (4- 7) 4.9 (4- 12) 7.2 (6- 9) 4.8 (3- 8) 4.8 (3-10) 2.0 (9- 15) 10.9 (10-13) 13.1 (10- 16) 13.5 (11-16) 12.7 (10-16) 12.5 (10-16)	8.0 (56- 81) 63.7 (56-69) 72.1 (61- 83) 65.4 (64-67) 54.9 (48-72) 62.8 (57-67) 49.9 (43-57) 8% 53% 56% 45% 59% 78% 47% 44% 55% 41% 22% 53% 7% 69% 76% 100% 40% 66% 55% 3% 31% 24% 0% 60% 34% 45% 4.5 (48- 62) 55.6 (48-62) 57.4 (50- 64) 57.9 (52-63) 54.2 (48-62) 49.9 (45-55) 48.7 (43-53) 1.8 (17- 28) 22.1 (16-26) 23.9 (20- 27) 25.9 (22-28) 22.7 (19-28) 19.3 (16-24) 21.1 (15-26) 51.1 (18- 28) 25.4 (23-27) 27.1 (23- 30) 26.3 (23-28) 24.8 (22-28) 24.9 (21-32) 23.3 (19-26) 55.4 (3- 10) 4.8 (4- 7) 4.9 (4- 12) 7.2 (6- 9) 4.8 (3- 8) 4.8 (3-10) 4.5 (2- 7) 2.0 (9- 15) 10.9 (10-13) 13.1 (10- 16) 13.5 (11-16) 12.7 (10-16) 12.5 (10-16) 11.4 (8-15)

brown blotch which is absent in carinatus. L. cubensis likewise differs from raviceps and macropus in scalation, coloration, and pattern. L. macropus has an area of small granules behind the tympanic opening; this area is covered with miniature keeled scales in cubensis. The pattern of macropus includes a supra-axillary black blotch with a central white vertical bar, as well as at least an indication of nuchal and sacral transverse black bars; all these distinctive features are absent in cubensis. L. raviceps differs from cubensis in the much smaller dorsal scales, smaller size, presence of paired dark dots, blotches, or herringbone pattern in the dorsal fields, and pale rather than brightly colored venter.

The new species herein described differs from carinatus, macropus, and raviceps in much the same way as does cubensis. Although smaller than cubensis, it is exceeded by both carinatus and macropus in adult size. It lacks the distinctive pattern features of carinatus, macropus, and raviceps noted above. Its scales are smaller than those of carinatus, but larger than those of macropus and raviceps. The distinctly longitudinally lined dorsal pattern distinguishes it from the transversely banded carinatus, the herringbone patterned raviceps, or the peculiar supra-axillary, nuchal, and sacral markings of macropus. Comparison with cubensis, to which it is most closely allied, is made in the systematic account below. In both species emphasis has been placed on the coloration and pattern in males; females of both species and all subspecies are remarkably similar and differ from each other only slightly if at all.

Leiocephalus cubensis Gray

Tropidurus (Leiolaemus) cubensis Gray (1840: 110).

Holotropis microlophus Cocteau and Bibron (1838 or 1839: 56, part). Holotropis vittatus Hallowell (1856: 151).

Leiocephalus vittatus Boulenger (1885: 163, part). Barbour (1914: 300, part).

Leiocephalus cubensis Barbour (1916: 304, part). Stejneger (1917: 273, part). Barbour and Ramsden (1919: 89, 171, part). Barbour (1930: 98, part). Cochran (1934: 35). Barbour (1937: 136, part). Alayo (1951: 109). Sutcliffe (1952: 7). Alayo (1955: 16). Schwartz and Ogren (1956: 103, part).

Leiocephalus raviceps Cochran (1934: 39, part).

The material on which Gray based his original description was collected in Cuba by W. S. Macleay; the type description mentions no locality other than Cuba. As coloration is important in differentiat-

ing between forms of the *L. cubensis* complex, it is interesting to note that Gray (1840: 110) mentioned the following color details: "bluish chin and throat bluish white spotted; belly and underside of tail white." The apparent unicolor condition of the venter restricts the name *cubensis* to the populations of the central portion of Cuba, where these lizards show an unspotted white (in preservative) belly. Although no precise locality is given for the original specimen, it probably came from near Guanabacoa, Habana Province. According to Conde (1958: 261), Macleay lived at Guanabacoa from 1827 to 1836, and only at this locality while in Cuba. Accordingly, I restrict the type locality of *L. cubensis* to the vicinity of Guanabacoa, Habana Province, Cuba.

Hallowell (1856) described Holotropis vittatus from a single specimen collected in Cuba by a Dr. Morris. This specimen, stated by Hallowell to be in the Philadelphia Academy of Natural Sciences, cannot be located today. However, the details of color and pattern (p. 151), and the observation of a "large black blotch on each temple" and "abdomen, under parts of extremities and tail of a much lighter color than that upon the back" leaves no doubt that the lizard described by Hallowell is the same as that described earlier by Gray.

Diagnosis: A species of Leiocephalus characterized by:

1) large size (snout-vent length in adult males as much as 121 millimeters, in females to 83 millimeters); 2) unicolor brown or metallic bronzy dorsum with zonation absent or poorly defined; 3) color of sides red to orange with vertical green lines extending onto the yellow or multicolored venter; 4) a prominent black or brown postorbital patch or blotch which may extend posterior to the tympanic opening as a series of black vertical bars in the lateral fields; 5) throat with variable patterns of lines, dashes, dots, or mottlings, with a bluish ground color, and the entire pattern usually much obscured or obliterated by clouding or stippling with black; 6) structure of the hemipenis, as illustrated (fig. 3). The hemipenis has its ventral surface, as extruded from the vent at preservation, covered with numerous calvees for about two-thirds its length; the more proximal of the calvees are larger than the distal. The calvees extend dorso-laterally; basally the calvculate area is separated from the smooth or slightly wrinkled proximal portion of the hemipenis by a series of large About 10 well-defined flounces cover the medial surface of the structure; these merge gradually with the calvculate region midventrally, and distally as well. Dorsally the sulcus spermaticus is a simple, rather wide and not deeply indented groove covered by a

membranous flap and bounded on each side by the smooth (without flounces or calyces) surface of the hemipenis. The distal portion of the hemipenis is smooth and wrinkled. Viewed from the free end the hemipenis is roughly triangular, with the sulcus lying in the longer side of the triangle.

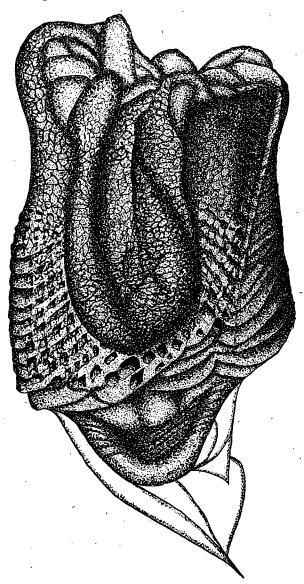


Figure 3.—Hemipenis of L. cubensis (AMNH 81009).

Leiocephalus cubensis cubensis Gray

Type locality: Cuba; restricted to the vicinity of Guanabacoa, Habana Province, Cuba.

Distribution: from western Habana Province throughout the central portion of the island of Cuba to western Oriente. Specimens from three Oriente localities are presently referred to this form doubtfully (see fig. 1).

SPECIMENS EXAMINED: Habana, La Habana, 3 (CM 694-96), 2 miles east of Boca de Jaruco, 2 (AMNH 77941, 78583); Caimito, 2 (USNM 27612-13); Marianao, 8 (USNM 28008-09, 28011-16). Matanzas, Zapata Swamp, 1 (AMNH 49218); 13 kilometers northeast of Matanzas, 2 (AMNH 81001-02). Las Villas, 21.6 miles northwest of Rodas, 2 (AMNH 77938-39); Rodas, 2 (ANSP 26047-48); Baños de Ciego Montero, 2 (AMNH 7404-05); Caracas Sugar Mill, 2 miles west of Cruces, 1 (AMNH 7311); Soledad, 7 (UMMZ 65325 (3); 72414 (4)); 8 miles southeast of Soledad, 1 (AMNH 77940); 2.9 miles southwest of Soledad, 1 (AMNH 81003); Trinidad, 34 (AMNH 77952-77961, 77964-77978; 77980-77986; 77988-89); 4 kilometers west, 8 kilometers north of Trinidad, 1 (AMNH 77942); 7.2 kilometers northwest of Trinidad, 9 (AMNH 77943-77951); Finca Morales, 8 miles northwest of Trinidad. 2 (AMNH 77961-62); Punta Casilda, nr. Trinidad, 1 (AMNH 77979); Finca La Pastora, 2 kilometers northwest of Trinidad, 1 (AMNH 77987); Finca San José, Corralillo, Cumanayagua, 1 (MJ 98). Camagüey, 12 miles east of Morón, Loma de Cunagua, 3 (AMNH 77990-92): 14 miles east of Moron, Loma de Cunagua, 2 (AMNH 77993-94); 2 kilometers southeast of Banao, 1 (AMNH 77996); 5.5 miles northeast of Banao, Paso de Lesca, Sierra de Cubitas, 1 (AMNH 77995): Nuevitas, 1 (AMNH 32299); 21 kilometers west of Camaguey, 1 (AMNH 77997); 20 kilometers west of Camaguey, I (AMNH 81004); Camagüey, 4 (UMMZ 70927-30); Ciego de Avila, 1 (ANSP 19448); Martí, 1 (UMMZ 72409), El Salto de la Tinaga, 1 (USNM 75831). Oriente, Birama, 1 (AMNH 57460); Sagua de Tánamo, 1 (MCZ 8961): Los Negros, Jiguaní, 3 (MCZ 8601-03); Finca Palmarito, El Jobo, Bayamo, 2 (UH).

Description: A subspecies of *L. cubensis* characterized by large size; metallic brown dorsal coloration with a green or yellow wash giving a bronzy appearance (see fig. 4) and without yellow or orange dots; sides dull red; venter immaculate yellow centrally and grading to reddish laterally; postorbital blotch present in subadult and adult males usually extending posteriorly as far as above the insertion of

the forelimb and represented behind the temporals by a series of wide black vertical bars; parietals usually (82%) not in contact.

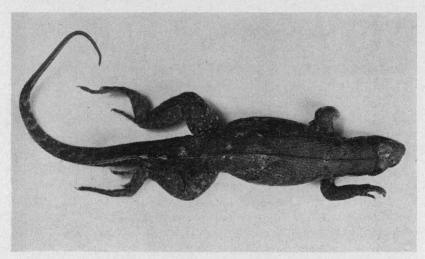


Figure 4.—Leiocephalus c. cubensis, dorsal view; male, from 12 miles east of Morón, Loma de Cunagua, Camagüey Province, Cuba (AMNH 77990); snoutvent length 90 mm.

Variation: In snout-vent length 37 male $L.\ c.\ cubensis$ average 88.4 (64-110), 28 females average 68.0 (56-81). Dorsal crest scales in occiput-vent length (combined data for both sexes) average 54.4 (48-62), and dorsal crest scales in occiput-axilla length average 21.8 (17-28). One half scales at midbody average 25.1 (18-28), loreals 5.4 (3-10), temporals 12.0 (9-15), subdigital fourth toe tricarinate scales 23.6 (21-27). The parietals are usually not in contact (82%) and the supraorbital semicircles are usually complete (77%).

The general color of the dorsum and the red sides and green lines from the lateral fields onto the sides of the belly are constant characters of *L. c. cubensis*. However the precise pattern of the dorsum varies greatly. In males the usual dorsal pattern involves a complete fusion and obliteration of all six zones, and thus the lizard is not longitudinally lined. The area of the lateral field (zone 5) in such unicolor specimens is manifested in many cases by black-tipped scales on the sides of the body and by broad black vertical bars anteriorly; these bars represent the posterior continuation of the postorbital blotch. Likewise in such unicolor lizards the dorsal fields may contain a few scattered paired black spots, usually widely spaced, and never prominent. The next step toward a longitudinally lined pat-

tern is the appearance of zone 6 as a whitish or dusky lateral line separating the dorsal color from that of the belly. The lizards thus have a single unicolor dorsal area bounded laterally by zone 6. Zone 4 appears next, cutting off the lateral field from the dorsal concolor area; in such individuals zone 4 is relatively broad and bold. Finally, the remaining unicolor dorsal area is divided into zones 2 and 3, zone 2 being much the lighter and almost the same color as zones 4 and 6. The median dorsal zone 1 is always poorly defined in males; if manifest, it is present only as a faint darkening along the dorsal crest scales. The appearance of these zones results at their most complete expression in a boldly striped lizard (AMNH 32299 for example). different patterns in male L. c. cubensis occur randomly, both geographically and ontogenetically. Specimens of the same snout-vent length may show the two radically different patterns—the unicolor dorsum and the striped dorsum. Of four juvenile males one has the pattern of longitudinal lines completely expressed, one has a unicolor dorsum with zone 6 defined, the remaining two show the intermediate condition.

Females show the same sort of variation as males, though adults do not exhibit the longitudinally striping so extremely as do lined males. If lines are present, they are almost invariably zone 6 alone, only one female (UMMZ 72414) has the zone 4 lines boldly delineated against the ground color. The lateral fields vary from a speckled appearance to diffuse vertical barring. The dorsal fields are either unicolor or have from faint and few (UMMZ 72409) to prominent and many (UMMZ 72414) paired black spots. In the latter specimen these black blotches are organized into a herringbone pattern. Five juvenile females show a more prominent longitudinal pattern than adult females, but the variation in this small lot is comparable to that of the juvenile males.

In summary, the variation in color of *L. c. cubensis* is not striking. The brown and bronzy dorsal coloration, red sides, yellow venter, the green lateral scales extending onto the sides on the belly, and the bluish throat are typical of the subspecies. On the other hand the pattern varies greatly in both sexes, although both show some similarities; the dorsal pattern ranges from completely unicolor to a longitudinally zoned appearance.

REMARKS: L. c. cubensis occurs throughout central Guba from at least Caimito east to Oriente Province, and from the north to the south coast. In its range cubensis occurs in a variety of habitats, from hot sandy coastal beaches to at least 1200 feet elevation along the grassy

roadways in the Sierra de Trinidad. Although the region occupied has a variety of edaphic habitats, apparently no physical or climatic barriers act as isolating mechanisms, and the uniformity of the lizards' characteristics suggest gene flow to be unrestricted throughout the entire region. More specimens may permit further racial subdivision of this subspecies, which is not warranted by the material now at hand. Two adult males from near Matanzas (AMNH 81001-02) were pale sandy dorsally in life and much flecked with brown; in this respect they differ from specimens from adjacent coastal Habana. As they agree with this race in all other characteristics, they are best regarded as ecotypes.

Six specimens of L. cubensis from Oriente merit special comment; these are from Sagua de Tánamo (MCZ 8961), Los Negros, Jiguaní (MCZ 8601-03), and Finca Palmarito, El Jobo, Bayamo (UH). first is a juvenile, and the Los Negros lot includes two males and one female, all adult or subadult. In color, so far as can be determined. as all are old specimens, and in pattern these individuals are all typical of the race cubensis. On the other hand, the Los Negros specimens have unusually high dorsal crest counts (57 to 66), midbody scales (27 to 30), and dorsals in occiput-axilla distance (26 to 31) for cubensis. The two Bayamo specimens, an adult male and an adult female, are even more peculiar; they are distinctly lined dorsally, have well defined zones 4 and 6, and lack a postorbital spot. The male is dotted ventrally and has dots in the lateral fields; both individuals have heavily marked throats, but apparently lacked in life the usual clouding. The dorsal crest scales are 51 and 56 and thus below the counts on the other Oriente specimens listed above. The specimens are suggestive of the new species described below, but lack of material precludes any decision at this time. So few specimens of the L. cubensis complex are available in collections from extreme eastern Cuba that precise allocation of these six individuals must await further material. Meanwhile I am regarding them provisionally as L. c. cubensis.

Messrs. Feick and Gehrmann collected specimens of L. cubensis on the Doce Leguas keys off the south shore of Camaguey Province. Cochran (1934) reported Leiocephalus carinatus and L. raviceps as occurring on the Doce Leguas, and noted two specimens of raviceps from a "cayo" west of Cachiboca. I have not examined these specimens, but have been informed by Dr. George B. Rabb (in litt.) that they are actually L. cubensis. There are thus no valid records of raviceps from the Doce Leguas keys, and Schwartz and Ogren (1956:

103) were in error in including Camaguey Province within its range. L. raviceps is presently known to occur solely in Oriente province.

The specimens of L. cubensis taken during the summer of 1957 on the Doce Leguas keys represent a new subspecies, which may be called

Leiocephalus cubensis paraphrus, new subspecies

Type: AMNH 78005, adult male, from southernmost point of large unnamed key 3 kilometers northwest of Cayo Cachiboca lighthouse, Camaguey Province, Cuba, taken 24 August 1957, by John R. Feick and William H. Gehrmann, Jr. Original number 4301. See figure 4.

PARATYPES: AMNH 77998-99, Cayo Cachiboca, at lighthouse, Camagüey Province, Cuba, 25 August 1957, J. R. Feick, W. H. Gehrmann, Jr., AMNH 78000-04, 78006-13, same data as type.

DISTRIBUTION: Known only from two localities in the Laberinto de Jardines de la Reina, but presumed to occur on suitable islands through the Doce Leguas chain (see fig. 1).

Diagnosis: A subspecies of *L. cubensis* characterized by smaller size; bronzy brown dorsal coloration with yellow or orange dots; immaculate venter with suffusions of yellow, blue, and purple; scales in the groin often vivid rust or orange; black postorbital blotch present in males and not extending into lateral fields; parietals usually (53%) in contact.

Description of Type: An adult male with the following measurements and counts: snout-vent length 83, tail 137 with distal third regenerated, snout to anterior border of tympanic opening 18.9, head width 15.7, supraocular scales 6/6, loreals 7, temporals 11, enlarged auricular scales 4/4, median head scales 5, frontal row complete, 3 scales, frontoparietal row complete, 6 scales, parietals in contact, semicircles complete, dorsal crest scales occiput to vent 55, dorsal crest scales occiput to axilla 22, scales around one half of body at midbody 25, fourth toe subdigital tricarinate scales -/26.

COLORATION: The dorsal color in life is bronzy brown with scattered orange dots. The zonation is obscured, with only zone 6 clearly defined as a lighter area along the sides from the tympanic opening to the hindlimb insertion (fig. 5). The sides are olive with isolated bluish scales forming thin vertical bars in the darker lateral field and extending onto the sides of the belly; no dark blotches occur in the dorsal fields. The postorbital blotch is black, slightly browner centrally, extends from the eye to the edge of the temporals, and is rep-

resented on the side of the neck as a dark, poorly delineated, U-shaped figure. The dorsal surface of the hindlimbs is speckled with orange on a rusty background, and the same rusty coloration is shown in the groin. The throat is unicolor metallic blue without dark markings of any sort; the venter is varicolored yellow, blue, and purple. The sides of the tail have scattered yellow scales, most concentrated on the proximal third, and scattered pale yellow scales on the distal two thirds; the dorsum of the tail is unicolor brown without chevrons.

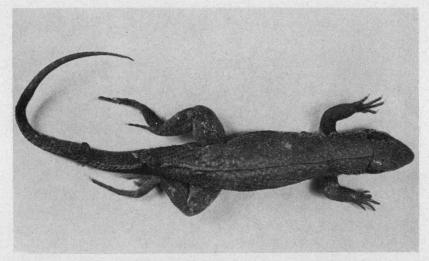


Figure 5.—Leiocephalus c. paraphrus, dorsal view, type (AMNH 78005); snout-vent length 83 mm.

Variation: In snout-vent length, 9 male *L. c. paraphrus* average 83.9 (55-98); 7 females average 63.7 (56-69). Dorsal crest scales (combined data for both sexes) in occiput-vent length average 55.6 (48-62), and dorsal crest scales in occiput-axilla length average 22.1 (16-26). One half scales at midbody average 25.4 (23-27), loreals 4.8 (4-7), temporals 10.9 (10-13), subdigital fourth toe tricarinate scales 25.4 (23-28). The parietals are more often in contact (53%) than not, and the supraorbital semicircles are more often complete (69%) than not.

The general metallic brown dorsal coloration with yellow or orange dots is a distinctive feature of all males, though some show this character more plainly than others. The immaculate venter with varicolored suffusions likewise is distinctive, as is also the absence of dorsal chevrons on the tail. The unmarked blue throat of the type is unique among specimens of *paraphrus*. In no male does the post-

orbital blotch extend prominently behind the temporals as a series of bars or as an elongate blotch; three individuals show a small, restricted, triangular black area immediately behind the temporals in the lateral field. Zone 6 is the only longitudinal zone developed in any specimen showing evidence of the longitudinal pattern. Two large males show a slightly darker lateral field bounded below by zone 6, but this is not the usual situation. Females have the zonation better expressed and likewise have some expression of black blotching in the dorsal fields, but this is never prominent.

Comparisons: Although both races are close in uniform dorsal ground color, L. c. paraphrus differs from nominate cubensis in dorsal pattern (yellow or orange dots on a bronzy dorsum), in brightly colored venter, restriction of the postorbital blotch, and absence of vertical bars in the lateral field. L. c. cubensis males and females reach a somewhat larger size than do those of paraphrus, at least insofar as the present small series of paraphrus indicates. More cubensis (82%) have the parietals not in contact than paraphrus (47%); these differences are significant by the chi square test (P = < .01).

REMARKS: Specimens of L. c. paraphrus were collected by Messrs. Feick and Gehrmann in scrub growth on two of the Doce Leguas keys. The lizards were less numerous on Cayo Cachiboca than on the unnamed nearby key which is the type locality. Specimens from the two keys do not differ in color or in scale characters, although additional material from throughout the Doce Leguas chain may show some interkey variation.

Leiocephalus cubensis gigas, new subspecies

Type: AMNH 81056, adult male, from Caleta Grande, Isla de Pinos, Habana Province, Cuba, taken 26 July 1958, by Albert Schwartz and George R. Zug. Original number 6137.

PARATYPES: AMNH 81050-55, 81057, same data as type; AMNH 78581-82, Caleta Grande, Isla of Pinos, Habana Province, Cuba, 30 December 1957, W. M. Stitzell.

Specimens examined and not designated as paratypes: (all from the Isla de Pinos) AMNH 81005-19, 78568, Paso de Piedras, ca. 20 kilometers southwest of Santa Fé; AMNH 78576-80, Puerto Francés; AMNH 81020-43, Jacksonville; AMNH 81044, 7 miles east of Jacksonville; AMNH 81045-49, Punta del Este; CM 617, 656, 665, "Isle of Pines".

DISTRIBUTION: Known from the area of the Ciénega de Lanier (Paso de Piedras), and from various localities on the south coast of

the Isla de Pinos, (see fig. 1) but not the only member of the L. cu-bensis complex from the south coast (see below).

DIACNOSIS: A subspecies of *L. cubensis* characterized by large size (largest of the species), bronzy dorsal coloration without orange or yellow dots, immaculate bright yellow venter, no orange or rust in the groin, and black postorbital blotch present in males and extending into lateral fields. The parietals are usually (56%) in contact.

Description of Type: An adult male with the following measurements and counts: snout-vent length 121, tail with distal half regenerated 141, snout to anterior border of tympanic opening 25.7, head width 20.0, supraocular scales 6/6, loreals 12, temporals 10, enlarged auricular scales 2/3, median head scales 5, prefrontal row complete 4 scales; frontoparietal row complete 6 scales, parietals in contact, semicircles complete, dorsal crest scales occiput to vent 62, dorsal crest scales occiput to axilla 26, scales around one half of body at midbody 24, fourth toe subdigital tricarinate scales 23/23.

COLORATION: The dorsal coloration in life is metallic greenish bronze. The zonation is obscured, and zones 1, 2 and 3 are unicolor. The lateral fields are extensive, abruptly set off from the dorsal bronzy color, and are red with the usual vertical rows of green scales extending onto the sides of the vellow belly. The dorsal fields have no dark blotches. The postorbital blotch is black and prominent posteriorly as far as the tympanic opening; thence it is represented by a series of about four vertical black blotches or bars in the lateral field. Both upper and lower lips are black, and the black upper lip is separated from the postorbital blotch by a bluish line from beneath the eye to and including the median auriculars. The dorsal surface of the hindlimbs is speckled with isolated greenish scales. The throat is vellow, and most scales have a small but conspicuous dark gray dot: these dots, by virture of the regular alignment of the throat scales, are arranged into about 10 longitudinal rows extending posteriorly onto the chest. Anteriorly the chin is light blue and mottled with black. The sides of the tail have scattered green scales, and isolated reddish brown dots are prominent on the lower lateral surfaces of the unregenerated portion of the tail. The dorsum of the tail is reddish brown without chevrons.

Variation: In snout-vent length 23 male *L. c. gigas* average 100.7 (80-121), 30 females average 72.1 (61-83). Dorsal crest scales (combined data for both sexes) in occiput-vent length average 57.4 (50-64), and dorsal crest scales in occiput-axilla length average 23.9 (20-27). One half scales at midbody average 27.1 (23-30), loreals 4.9 (4-

12), temporals 13.1 (10-16), subdigital fourth toe tricarinate scales 24.5 (21-28). The parietals are more often in contact (56%) than not, and the supraorbital semicircles are more often complete (76%) than not.

The bronzy or greenish dorsum and red sides with vertical green or blue scales arranged in rows are typical of all adult males. Young males (snout-vent length 92 mm, and less) regularly have an ill defined pale zone 6 manifest from the posterior edge of the tympanic opening to the groin. This feature may even persist in larger males, but becomes more obscure with larger size, and is not demonstrable in the type or other very large individuals. The belly is always yellow, and in some specimens the reddish pigment from the sides encroaches onto the ventral surface, so that as few as six longitudinal rows of ventrals may be yellow. The throat pattern varies from the dotted condition described for the type (four specimens) to a solid dusky throat (five specimens); even in the extremely dark-throated individuals the discrete gray dots on the throat and some chest scales may be discerned. The ground color of the throat varies from pale blue to pale yellow. Even in young males the postorbital spot extends into the lateral fields above the forelimb insertion. The amount of light and dark flecking on the sides of tail is variable. Some males have the undersurface of the hindlimbs much flecked with reddish brown, but this is not constant.

Females are like the males in dorsal color, having a distinctly greenish or bronzy dorsal zone. Some have paired blotches or flecks in the dorsal area, but these never form a herringbone pattern. life the venters of females are pinkish in contrast to the yellow bellies of males. Zonation is much obscured, but a rare individual shows faintly the presence of pale zones 4 and 6, especially anteriorly. Some females also show distinct vertical black barring in the lateral fields and zone 6, but this is not constant. The postorbital blotch is well expressed for females, but this may be either hollowed, and then brown. centrally, or very obscure to absent. Usually the belly is immaculate centrally with brown isolated dots peripherally; however six females have either the chest or the entire venter covered by these diffuse The throat varies from an almost immaculate pale blue to a much mottled and almost entirely dark gray. No females examined have the individual dark dots seen on the throat scales of some males, and their throat patterns appear more random than the throat patterns of males.

Eight juvenile gigas have a unicolor dorsum with zones 1 through 4 blended into a metallic brown dorsal band. The lateral field, zone 5, is dark brown and prominent against the lighter brown dorsum, and is not delimited above by a lighter zone 4. The dorsal band may be immaculate (AMNH 78576) or may be much flecked with black (AMNH 78582). Zone 6 is pale and prominent. No color differences between the sexes are apparent in the juveniles. Both sexes have gray flecks on the sides of the belly which persist in adult females and young adult males.

Comparisons: L. c. gigas is larger (males 121, females 83) than both cubensis (110, 81) and paraphrus (98, 69). Of the two Cuban races, gigas resembles cubensis more closely, and indeed the two subspecies do not differ strikingly in any feature of color or pattern. In addition to size, gigas differs from cubensis principally in having the parietals usually in contact (56%), whereas in cubensis they are usually not in contact (82%). This difference is statistically significant ($P = \langle .01 \rangle$). Compared to paraphrus, gigas has a yellow venter in contrast to a multicolored one, and in the lateral fields posterior to the tympanic opening has vertical bars that paraphrus lacks. Also paraphrus has the dorsum spotted with yellow or orange dots and orange or rust-colored scales in the groin.

In December 1957 we collected seven Leiocephalus on the south coast of the Isla de Pinos at two localities (Caleta Grande, Puerto Francés), and an eighth at Paso de Piedras. The Isla de Pinos lies 53 kilometers south of Cuba and is on the same insular platform. The area of the Isla is 3,061 square kilometers, of which two thirds comprise the so-called "north coast", separated from the "south coast" by the Cienega de Lanier, a narrow swampy band which extends from the Boca de la Ciénega on the east 23 kilometers to the Ensenada de la Siguanea on the west. Only at the Paso de Piedras (or Cayo Piedras, as it is sometimes called), a narrow band of "monte" (dense broadleaf forest) between the eastern and western sections of the Cienega, is there continuity between the xeric and rocky south coast and the somewhat more mesic and gravelly north coast. The south coast itself varies greatly in flora, and deciduous forests yield in many places to palm forest and beach shrub or scrub growth. The more mesic sections of the south coast support the forests, and it is probable that the forest at the Paso de Piedras is continuous with similar associations at Jacksonville and Caleta Grande, Punta del Este, and Puerto Francés.

As the eight specimens collected in mid-winter were all juveniles (snout-vent lengths 52 mm. and less), the status of the southern popula-However, these specimens obviously differed tions was uncertain. from others collected at the same season on the north coast, which I now realize are not cubensis, but its smaller relative. At the same time, three specimens from the Carnegie Museum (CM 617, 656, and 665), all part of a large series collected by G. A. Link in 1910 and referred to L. cubensis by Barbour (1916: 304) with the comment that they "seemed to average decidedly smaller in size than the Cuban specimens, and seemed in general to be of a sandier, more bleachedout color, often lacking the rich maroon on the sides of the head and body", were observed to be markedly larger than the rest of this lot of specimens. As the Link material is labeled merely "Isle of Pines", the exact source of these three specimens of gigas is unknown. Though Link visited the south coast on a later trip to the Isla in 1912-13 (Todd: 1916), that he went there in 1910 is not known definitely. Again, he may well have taken the three gigas somewhere along the Ciénega de Lanier, or even on the north coast, although we searched for it there in vain.

During the summer of 1958 I found L. c. gigas abundant at Paso de Piedras, Jacksonville, and Caleta Grande, and rather scarce at Punta del Este. At the first three localities it inhabits dense broadleaf forest, and it is not unusual to see these lizards during the heat of the day along the dirt roads that penetrate this jungle. It is the only Leiocephalus known from Paso de Piedras and Jacksonville; at Caleta Grande L. carinatus occurs along the beach under large rocks, in the palm jungle (which is occupied by a few gigas), and in the stone walls surrounding a deserted house. At Punta del Este gigas occupies rocky areas in the woodlands in company with L. carinatus, which also inhabits the exposed beach cliffs where gigas does not occur. The ecological relationships of L. c. gigas with the subspecies of the smaller species of the L. cubensis complex are discussed later in this paper.

From 29 July to 31 July George R. Zug and I visited the keys in the Archipielago de los Canarreos, which extend from Punta del Este eastward about 145 kilometers. This archipelago consists of several major keys and numerous smaller islets, many of which are low and support only a growth of mangroves. We collected from west to east along the chain at Cayo Matias, Cayo Hicacos, Cayo Campos, Cayo Avalos, Cayo Cantiles, Cayo del Rosario, and Cayo Largo. Most of these keys are sandy with scattered limestone rock formations, and

support a dense growth of palms and xerophytes with a coastal fringe of mangroves. Some have beautiful beaches; Cayo Cantiles however is extremely rocky with little sand, and is covered by an almost impenetrable jungle of broadleaved trees, lianas, and shrubs. Sutcliffe (1952) discussed the occurrence of six reptiles on some of the keys, especially Cayo Largo, and Cochran (1934) reported two species. Neither of these authors had specimens of *Leiocephalus* from the keys. We were fortunate in obtaining series of L. cubensis on two keys near the Isla de Pinos, Cayo Hicacos and Cayo Campos. We saw none on Cavo Matias, which is close to Punta del Este, nor on any of the keys further along the chain to the east, although Cayman Islanders resident on the Isla de Pinos reported having seen "lion lizards" on Cayo Avalos. Study of these lizards from the Archipiélago de los Canarreos indicates that they represent a new form to be known as 1.

Leiocephalus cubensis pambasileus, new subspecies

TYPE: AMNH 81068, adult male, from Cayo Hicacos, Habana Province, Cuba, taken 28 July 1958, by George R. Zug. Original Number 6193.

PARATYPES: AMNH 81058-67, same data as type.

Specimens examined and not designated as paratypes: AMNH 81069-79, Cayo Campos, Habana Province, Cuba.

DISTRIBUTION: known only from Cayo Hicacos and Cayo Campos, Archipiélago de los Canarreos, off Punta del Este on the east shore of the Isla de Pinos (see fig. 1).

Diagnosis: A subspecies of *L. cubensis* characterized by smaller size, pale sandy green dorsal coloration, absence of dorsal dotting, vivid yellow venter, no orange or rust in groin, and a large black postorbital blotch extending uninterrupted to above forelimb insertion. The parietals are usually (55%) not in contact, and the number of loreals (6-9, average 7.2) is high.

Description of Type: An adult male with the following measurements and counts: snout-vent length 87, tail distal three-quarters regenerated 81, snout to anterior border of tympanic opening 19.4, head width 15.2, supraocular scales ?/6, loreals 8, temporals 16, enlarged auricular scales 3/4, median head scales 4, prefrontal row complete 3 scales, frontoparietal row complete 5 scales, parietals in contact, semicircles complete, dorsal crest scales occiput to vent 63, dorsal crest scales occiput to axilla 8, scales around one half of body at midbody 28, fourth toe subdigital tricarinate scales 26/26.

Coloration: The dorsal color in life is a pale sandy tan, with a faint metallic greenish overwash. Zonation is absent, and even zone 6 is not present. The sides are bright orange with the customary green scales arranged in vertical rows along the lower sides and extending onto the sides of the abdomen. The dorsal field, which is composed of zones 1 to 4, is irregularly flecked with dark brown and shows on the neck and shoulders three diffuse transverse bars, the hindmost of which is the best defined and resembles the nuchal band of L. macropus. The postorbital blotch is black and extends to above the insertion of the forelimb with only a slight interruption, thus presenting an almost uniform black band from the eye to the forearm. The chin is white in life, the throat pale vellow, and the venter vivid yellow. The throat has irregular black blotches anteriorly and two fragmented and irregular paramedian lines posteriorly. chest is irregularly spotted with black dots and blotches. The rest of the ventral surface is immaculate except for a few well defined reddish brown dots scattered on the ventral surfaces of both fore- and hindlimbs and within the orange of the lower sides and along the lateral surfaces of the tail. The fingers are pale yellow. The dorsal surface of the tail is without chevrons.

Variation: In snout-vent length 11 adult and subadult male L. c. pambasileus average 83.4 (66-95), 7 females average 65.4 (64-67). Dorsal crest scales average (combined data for all specimens) in occiput-vent length 57.9 (52-63), and dorsal crest scales in occiput-axilla length 26.3 (23-28), loreals 7.2 (6-9), temporals 13.5 (11-16), subdigital fourth toe tricarinate scales 25.8 (24-28). The parietals are less often in contact (55%), and the supraorbital semicircles are complete in all specimens.

The 10 adult and subadult males resemble the type closely in color and pattern, although some large specimens show zone 6 as a poorly defined whitish longitudinal stripe. The postorbital blotch is always black, well defined, prominent against the pale tan dorsum, and extends unbroken except for occasional pale greenish scales to the forelimb insertion. Although the type has some dark brown markings in the dorsal field, this is not constant in the series, and the dorsum varies from immaculate sandy to diffuse brown mottlings on a sandy ground color. This mottling is apparently a retention of the juvenile longitudinal banding in four young males (snout-vent lengths 50 to 58) in which zonation is prominent and zones 3 and 4 are visible. Ventrally all the adult and subadult males show white chins, pale yellow throats, and brilliant yellow venters. The chin and throat

pattern is variable, but none is immaculate nor entirely black. The anterior markings tend to be mottled and the posterior ones to be organized into a series of short longitudinal dashes or longitudinal Both fore- and hindlimbs have some ventral brown spotting, but this varies and is usually more prominent on the hindlimbs. The pale yellow fingers are a well marked feature in living specimens. Only the juvenile males have caudal chevrons. The seven females are typical of the species; the zonation is not particularly prominent, although one has zone 6 white and especially well delineated. The dorsum usually has some brownish mottling, and the lateral fields have irregular and inconspicuous vertical bars. The bellies are undistinguished, having the peripheral dark brown or black dots as do all female L. cubensis. The throats are heavily mottled with black, and posterior throat lines, when present, are relatively broad; the chests are also heavily spotted with black. Unregenerated tails have dorsal chevrons. Young males resemble the females in pattern.

COMPARISONS: L. c. pambasileus differs from both cubensis and gigas in smaller size and in color. The key race is sandy rather than metallic brown or bronzy, and has distinctly pale yellow toes. Although both pambasileus and cubensis are the only races in which lack of parietal contact is high (55% in pambasileus, 82% in cubensis), this difference is significant (P = between .02 and .01). The higher number of loreals is also significantly different in pambasileus.

L. c. pambasileus resembles paraphrus most closely. Both are pale and of medium size in the complex, but pambasileus has an extensive postorbital blotch which is restricted in paraphrus, a sandy dorsum instead of a metallic brown one with yellow or orange spots as in paraphrus, and lacks orange in the groin. It also has a higher number of loreals and a yellow venter in contrast to the multicolor venter in paraphrus.

REMARKS: Cayo Hicacos and Cayo Campos lie off the east coast of the Isla de Pinos, Hicacos about 18 kilometers, Campos about 22 kilometers east of the easternmost point of the Isla. Both are keys of moderate size, and have the usual mangrove fringe. The southern shore of Campos has an extensive sandy beach. Hicacos, although sandy, has no extensive beach area but is covered with scrub and palm forest. On both keys the lizards were abundant. They became active on Hicacos at 0700, and even at this early hour were wary and difficult to approach. On Cayo Matias, between Hicacos and the mainland of the Isla, apparently no Leiocephalus occur. Its beach is narrow, and its dense low herbaceous covering appears un-

suitable for these lizards. The interior of the key is low and apparently subject to extensive flooding during high tides. On Hicacos the *Leiocephalus* sought refuge under large limestone rocks on the beach, and were seen foraging among herbaceous plants and trees.

We found *Leiocephalus* only on Hicacos and Campos. We did not land on the Cayos Aguardientes, just east of Campos. Next in the chain is Cayo Cantiles which, having a rocky substrate covered with a dense, tropical hardwood jungle, is completely unsuitable for these lizards. The key has no beach and is bounded by a rocky shore.

L. c. pambasileus is certainly derived from L. c. gigas, of which we took specimens on Punta del Este. The relationship between these two forms is reminiscent of that between L. c. cubensis and paraphrus on the Cuban mainland and the Doce Leguas. In fact the resemblances between the two insular populations are striking. Some 170 kilometers separate the easternmost key of the Archipiélago from the westernmost of the Doce Leguas. Probably pambasileus represents a locally differentiated population of gigas derived from the Isla and occurring originally on Cayos Matias, Hicacos, and Campos, and perhaps on other keys to the east. Its original distribution has been modified in that it no longer occurs on Matias, and it is now isolated on the two keys from which specimens have been taken. The populations on these two keys appear to be indistinguishable.

Leiocephalus stictigaster, new species

Holotropis microlophus Cocteau and Bibron (1838 or 1839: 56, part). Leiocephalus vittatus Boulenger (1885: 163, part). Barbour (1914: 300, part).

Leiocephalus: cubensis Barbour (1916: 304, part). Steineger (1917: 273, part). Barbour and Ramsden (1919: 89, 171, part). Barbour (1930: 98, part). Barbour (1937: 136, part). Alayo (1955: 16, part). Schwartz and Ogren (1956: 103, part).

Diagnosis: A species of Leiocephalus characterized by: 1) small size (snout-vent length in adult males 81 millimeters or less, in females 72 millimeters or less); 2) dorsum prominently lined longitudinally; 3) sides orange, pink, or red, without vertical green lines extending onto pastel colored or white venter which is usually dotted with discrete brown or black dots; 4) postorbital blotch absent or at best poorly defined; 5) throat with variable pattern but usually composed at least in part of lines on a white or pastel ground color and seldom obscured by the deposition of additional dark pigment; 6) structure of the hemipenis as illustrated (fig. 6). The hemipenis has its ventral

surface, as extruded at preservation, covered with many calyces, the calyculate area set off from adjacent flounces as a raised oval region which adjoins directly the smooth basal portion of the hemipenis. Laterally and medially are large numbers of flounces, above 20 in number, the basal ones being the larger and more conspicuous. The sulcus spermaticus is simple, dorsal, covered by a membranous flap, and lies in a smooth area. The hemipenes of *L. cubensis* and *L.*

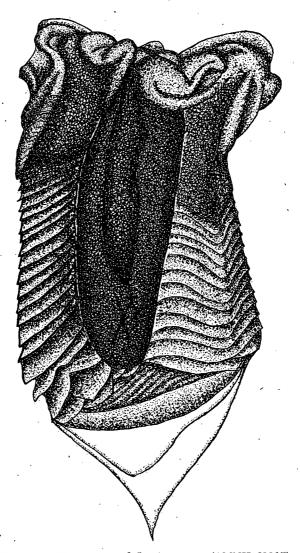


Figure 6.—Hemipensis of L. stictigaster (AMNH 81125).

stictigaster are similar in gross structure, but stictigaster's excessive calyces and flounces are at once apparent.

Leiocephalus stictigaster stictigaster, new subspecies

Type: AMNH 77864, adult male, from beach on Cabo Corrientes, Pinar del Río Province, Cuba, taken 5 July 1957 by John R. Feick, William H. Gehrmann, Jr., and Armando García. Original number 2282. (Fig. 2).

PARATYPES: (all from Pinar del Río Province, Cuba) AMNH 77864-77908, same data as type; AMNH 77909-77921, north shore of Ensenada de Corrientes, 5 July 1957, J. R. Feick, W. H. Gehrmann, Jr., Armando García; AMNH 77927-28, north shore of Ensenada de Corrientes, 10 July 1957, J. R. Feick; AMNH 81080-85, north shore, Ensenada de Corrientes, 45 kilometers west of Cayuco, 19 August 1958, A. García, A. Schwartz; MCZ 10869-70, Cabo de San Antonio, April 1915, V. J. Rodriguez.

DISTRIBUTION: known only from the Península de Guanahacabibes, extreme western Cuba (fig. 2).

DIAGNOSIS: A subspecies of L. stictigaster characterized by pale sandy tan dorsal coloration, pinkish sides, and yellow ventral surface of males spotted with black dots.

Description of Type: An adult male with the following measurements and counts: snout-vent length 70, tail distal half regenerated 107, snout to anterior border of tympanic opening 15.5, head width 13.0, supraocular scales 6/6, loreals 5, temporals 12, enlarged auricular scales 4/3, median head scales?, prefrontal row complete?, number of prefrontals?, frontoparietal row complete 5 scales, parietals in contact, semicircles complete?, dorsal crest scales occiput to vent 53, dorsal crest scales occiput to axilla 22, scales around one half of body at midbody 24, fourth toe subdigital tricarinate scales 22/22.

Coloration: The dorsal color is generally pale sandy tan with zone 1 slightly darker than zone 2. The dorsal fields are grayish tan with 4 pairs of faint brown dots. Zone 4 is pale tan and sets off the rest of the dorsum from the slightly darker tan lateral fields, which are mixed with pinkish and extend onto the sides of the abdomen (fig. 7). Zone 6 is pale tan and not too prominently set off from the lateral belly color. The sides, posteriorly from the dark brown postorbital spot, are spotted with discrete black dots which extend over the entire ventral surface. The dorsal and ventral surfaces of the fore- and hindlimbs and the sides of the proximal portion of the tail have scattered discrete dark brown dots. The venter is yellow with

a pinkish suffusion on its sides. The throat is pale gray with scattered dark scales, arranged in rather poorly defined lines, 5 scales in length, in the chest region. The chin is pale yellow, the head shields light tan and immaculate. A postorbital blotch, brown in color, extends from the eye to the tympanic opening and is bordered below by a white band across the lower temporals; this in turn is bordered by a black line from the angle of the jaws to the anterior ventral edge of the tympanic opening. The tail has indistinct dark tan chevrons, their apices directed posteriorly, on a tan ground color.

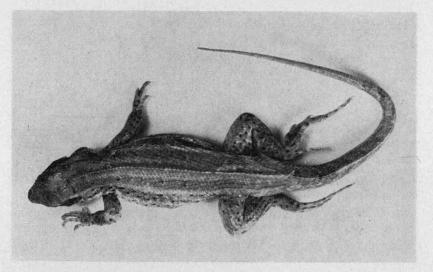


Figure 7.—Leiocephalus s. stictigaster, dorsal view, type (AMNH 77864); snout-vent length 70 mm.

Variation: In snout-vent length, 26 male paratypes average 66.1 (57-79), 27 female paratypes average 54.9 (48-72). Dorsal crest scales in occiput-vent length (combined data for both sexes) average 54.2 (8-62), and dorsal crest scales in occiput-axilla length average 22.7 (19-28). One half scales at midbody average 24.8 (22-28), loreals 4.8 (3-8), temporals 12.7 (10-16), subdigital tricarinate scales on the fourth toe 23.4 (20-27). The parietals are more often in contact (59%), the supraorbital semi-circles are more often incomplete (60%).

Color and pattern show relatively little variation. All individuals are pale tan, although some are a shade darker than the average. Some males show more black or dark brown spots in the dorsal tan fields than the type, and these spots are usually discrete and in only one individual form faint dorsal crossbars. Many males are com-

pletely immaculate dorsally; the type represents the average condition in this regard. The postorbital blotch is present, but pale in many specimens and only faintly expressed or absent in others. When present the blotch is often pale centrally, giving the effect of a hollow, dark, outlined block. All males show the black ventral dots and the brown limb and tail dots characteristic of the subspecies; the degree of ventral spotting varies somewhat, and occasional individuals have the center of the belly immaculate. However, all specimens show some ventral spotting, and in none is the venter immaculate.

Females are distinctly lined dorsally, usually with more black blotches or spots in the dorsal fields than males; some females have dark brown zigzag dots on either side of the dorsal crest scales, whereas others lack dorsal spotting entirely. The ventral and dorsal leg spotting of the males is absent in the females; the dorsal surface of the limbs is usually unicolor tan, rarely with diffuse dark blotches instead of dots. The postorbital blotch is usually poorly defined and, when more prominent, blends into the dark lateral field on the body and is not delimited posteriorly. Ventrally the yellow belly is much clouded with gray, giving it a dirty appearance, with concentrated gray pigment displayed as diffuse but discrete dull gray spots, quite different from the black ventral dots of males. The throat is dull gray, either spotted with black or with the pigment arranged in longitudinal dashes, sometimes organized into a pair of black paramedian lines with additional black or gray lines arranged anteriodorsally, their medial ends directed anteriorly and at times forming an acute V with the paramedian line on each side. The differences in pigmentation and pattern between males and females makes sex determination simple.

The five juveniles in the series of paratypes, two males and three females, are all pale tan and show between them the variation in the black dorsal blotches demonstrated in the adults. None has the post-orbital blotch present, and all are distinctly lined dorsally, an intensification of the lined pattern seen in adults. In each the venter is immaculate and lacks any indication of black dots. The snout-vent length at which dots first appear in the males must lie between 32 mm. (the snout-vent length of the largest male juvenile) and 57 mm. (the snout-vent length of the smallest male regarded as adult). The throat pattern of all juveniles, having diagonal dark lines on an immaculate background, resembles that of the females.

REMARKS: The series of L. c. stictigaster was collected in sandy and rocky situations in scrub growth on the Peninsula de Guanahaca-

bibes. The lizards were abundant, as the large series of both sexes attests. The pale tan coloration is protective, and the lizards blend well with the sandy substrate. The Península de Guanahacabibes is an area of below average rainfall, 115 to 125 cm. per year (Marrero, 1951: 442), compared to the average annual rainfall (137.5 cm.) of Cuba. The Peninsula may thus hardly be regarded as xeric, though the excessively rocky terrain makes plant growth scattered and stunted. That reptiles in xeric areas are often paler in color than their relatives in mesic regions is well known. In this instance the nominate race is paler than the next adjacent form, which inhabits in part the most mesic portion of Cubā.

L. stictigaster from the vicinity of San Vicente, Pinar del Río Province in the Sierra de los Organos, as well as from various localities in the lowlands of the province, are markedly different from stictigaster to the west. For these lizards I propose the name, in allusion to the local name "iguana de la sierra" and the mountain inhabiting proclivities of the form,

Leiocephalus stictigaster sierrae, new subspecies

Type: AMNH 77813, adult male, from San Vicente, Pinar del Río Province, Cuba, taken 27 June 1957 by a native for Albert Schwartz. Original number 2011. See fig. 2.

Paratypes: (all from Pinar del Río Province, Cuba) AMNH 77810, mountains north of San Vicente, 19 June 1957, D. R. Paulson; AMNH 77811-12, mountains north of San Vicente, 25 June 1957, native for A. Schwartz; AMNH 77814-15, San Vicente, 29 June 1957, native for A. Schwartz; AMNH 77816, San Vicente, 2 July 1957, native for A. Schwartz; AMNH 77817-22, San Vicente, 5 July 1957, native for A. Schwartz; AMNH 77823-38, San Vicente, 6 July 1957, native for A. Schwartz; AMNH 7783-45, San Vicente, 8 July 1957, native for A. Schwartz, AMNH 77846-54, San Vicente, 9 July 1957, native for A. Schwartz; AMNH 77855-62, San Vicente, 10 July 1957, native for A. Schwartz; AMNH 77863, San Vicente, 11 July 1957, native for A. Schwartz; AMNH 77929-33, San Vicente, 10 July 1957, native for A. Schwartz; AMNH 77929-33, San Vicente, 10 July 1957, native for A. Schwartz.

Specimens examined and not designated as paratypes: (all from Pinar del Río Province, Cuba): AMNH 81120 (6), 0.5 miles north of San Vicente; AMNH 81121 (3), 81122 (9), San Vicente; AMNH 81124, 1.6 miles east of Viñales; AMNH 81125 (26), 1 mile northwest of Cayuco; AMNH 77922-26, 3 kilometers west of Bartoli sawmill village (La Majagua), 10 kilometers southwest of Cayuco; AMNH 77934-37,

7.6 miles east of Isabel Rubio (Mendoza); AMNH 81123 (3), 1 kilometer north of Las Canas; MCZ 7943, Herradura; AMNH 81251, 3 kilometers west, 4 kilometers south of Las Pozas.

DISTRIBUTION: known from the western edge of Cabo Corrientes east throughout the mountains and north coast of Pinar del Río Province to the vicinity of Las Pozas (fig. 2).

Diagnosis: A subspecies of *L. stictigaster* characterized by dark brown dorsal coloration, bright orange sides, and the yellow ventral surface of males spotted with black dots.

Description of Type: An adult male with the following measurements and counts: snout-vent length 75, tail distal half regenerated 116, snout to anterior border of tympanic opening 16.0, head width 13.5, supraocular scales 6/6, loreals 4, temporals 12, enlarged auricular scales 4/4, median head scales 4, prefrontal row complete 3 scales, frontoparietal row incomplete 3 scales, parietals in contact, semicircles incomplete, dorsal crest scales occiput to vent 55, dorsal crest scales occiput to axilla 20, scales around one half of body at midbody 24, fourth toe subdigital tricarinate scales 23/24.

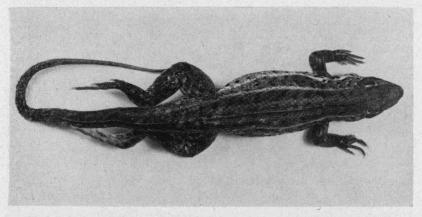


Figure 8.—Leiocephalus s. sierrae, dorsal view, type (AMNH 77813); snout-vent length 75 mm.

Coloration: The dorsal color is dark brown. Zone 1 is medium brown with small, poorly defined, alternating black blotches. Zone 2 is paler brown. Zone 3 is dark brown with 12 opposite, paired blotches on either side to above vent. Zone 4 is almost white, boldly separating zone 5 above, as zone 6 does below. Zone 5 is dark brown with extensive bright orange suffusion. Zone 6 is boldly white (fig.

8). The sides, beginning posterior to the temporals, are spotted with discrete black spots which in the lateral field tend to form vertical bars between the insertions of the fore- and hindlimbs. The dorsal and ventral surfaces of the limbs and the sides of the proximal portion of the tail have scattered discrete brown dots. The venter is pale yellow with an orange suffusion on the sides. The throat is pale yellow with black scales arranged in blotches anteriorly and in longitudinal lines posteriorly. The immaculate head shields are unicolor with the dorsum. The postorbital blotch is absent, its area marked by a dorsal and ventral black longitudinal stripe separated by tan pigment. The tail has indistinct dusky dorsal chevrons, their apices pointed posteriorly, on the tan ground color.

Variation: In snout-vent length 30 male paratypes average 73.2 (60-81), 30 female paratypes average 62.8 (57-67). Dorsal crest scales in occiput-vent length (combined data for both sexes) average 49.9 (45-55), and dorsal crest scales in occiput-axilla length average 19.3 (16-24). One half scales at midbody average 24.8 (21-32), loreals 4.8 (3-10), temporals 12.5 (10-16), subdigital fourth toe tricarinate scales 23.8 (21-28). The parietals are in contact in 78% of the individuals; the supraorbital semicircles are more often (66%) complete than incomplete.

The variation in color and pattern among the paratypes of L. s. sierrae is relatively small. All specimens are dark colored. Males are essentially like the type, although one adult specimen lacks any ventral dots. In some males the degree of ventral dotting is less than that of the type, and in a very few the central region of the belly lacks spotting, though dots appear about the periphery of the belly. The fusion of the dots in the lateral fields into vertical bars occurs regularly, but some individuals do not have this character well expressed. The postorbital blotch is uniformly absent or represented by a dorsal and ventral black longitudinal stripe. The amount of black blotching in the dorsal field varies from none to relatively large blotches; when present, there are always more pairs of blotches in the lateral fields than in s. stictigaster.

Females are usually distinctly lined dorsally. The black blotches in the dorsal fields are prominent, and in some individuals these black blotches fuse to form a longitudinal black band. The belly is either immaculate yellowish gray or spotted with diffuse, poorly defined, gray spots. As black lateral dots are absent, the lateral fields show no vertical barring, though diffuse dark brown or black pigment may form ill-defined bars comparable to those of the males. The head

shields are usually immaculate, although a few individuals show widely scattered fine dark brown dots. The throat is yellowish gray with longitudinal darker gray lines, including a pair of paramedian lines; anteriorly the throat may have gray dashes arranged obliquely to the median region of the throat, or these may be coalesced into diagonal gray lines extending toward the region of the tympanic opening from the chin and adjoining area of the throat. The postorbital spot is absent.

Comparisons: L. s. sierrae differs from L. s. stictigaster in dark brown rather than pale tan coloration, presence in males of vertical black bars in the lateral fields, less prominent postorbital blotch, and orange rather than pink lateral suffusion. Scale counts show no significant differences, though sierrae averages less in dorsal crest scales, counted both from occiput to vent and occiput to axilla. L. c. stictigaster reaches a higher dorsal crest count than sierrae. In size both are small; both sexes of sierrae average larger than males and females of stictigaster, but the higher extremes in both sexes are comparable. The difference between the percentage of individuals with complete semicircles (40% in stictigaster, 66% in sierrae) tested by chi square is significant (P = < .01). Though sierrae has a higher percentage (78%) of individuals with parietals in contact than stictigaster (59%), the difference is not significant.

REMARKS: The specimens from Isabel Rubio, Herradura, Las Canas, and Las Pozas are identical with the series from San Vicente. A few specimens of the series from the Cayuco area are paler than average for sierrae, but judging on the entire series I regard them as sierrae. From Cayuco to the west shore of the Cabo Corrientes sierrae occupies the mesic forest; at the edge of the dry and sandy beach there is an abrupt transition from this form to stictigaster. Apparently sierrae occupies the mountains and mesic lowlands, stictigaster the xeric Península de Guanahacabibes.

L. s. sierrae is abundant in the vicinity of the type locality, which lies at an elevation of about 1000 feet in the Sierra de los Organos. The lizards occur along abandoned roadways, at the edges of cane fields, and in clearings in the tropical forest, all on more or less gravelly soil. The specimens from Isabel Rubio were collected along the edge of a lowland stream in dense riparian shrubby growth and in associated pastures nearby; those from Cayuco in a grove of oaks.

The range of L. s. sierrae encompasses the most humid area in Cuba—the Sierra de los Organos. Marrero (1951: 80-81) places the average annual rainfall in this mountain range at more than 178 cm.

These mesic conditions may well be reflected in the dark coloration of *sierrae*, in contrast to that of the adjacent *stictigaster*.

The easternmost locality for L. s. sierrae (vicinity of Las Pozas, Pinar del Río Province) is about 72 kilometers from the westernmost locality for L. c. cubensis (Caimito, Habana Province). No specimens of either species of this complex are known from the intervening area. I suspect that sierrae will be encountered as far east as the foothills of the Sierra del Rosario, in the vicinity of Candelaria, and that cubensis occurs as far west as Guanajay and Artemisa. It may well be that in this intermediate region both species occur together although ecologically separated, sierrae possibly occupying stream bottoms and associated "monte", and cubensis inhabiting fields and pastures.

Comment has already been made under the discussion of L. c. gigas on the differences between the northern and southern specimens collected in December 1957 and 9 taken the summer of 1958, all from various north coast localities, as well as 19 old specimens from the Link collection with the locality data "Isle of Pines". All represent an insular population of L. stictigaster which may be called

Leiocephalus stictigaster exotheotus, new subspecies

Type: AMNH 81088, adult male, from 1.5 miles west of Santa Fé, Isla de Pinos, Habana Province, Cuba, taken 1 July 1958, by Albert Schwartz. Original number 5477.

PARATYPES: (all from Isla de Pinos), AMNH 81086-87, same data as type; AMNH 78567, same locality as type, 25 December 1957, A. Schwartz; AMNH 81091, 2 kilometers north, 13 kilometers west of Santa Fé, 6 July 1958, A. Schwartz; AMNH 78569-73, 5 miles northeast of Siguanea, 27 December 1957, E. B. Erickson, W. M. Stitzell, G. R. Zug.

Specimens examined and not designated as paratypes (all from Isla de Pinos): AMNH 81089-90, just west of Nueva Gerona, east base of the Sierra de las Casas; AMNH 78574-75, 81092-94, east shore of Ensenada de la Siguanea; CM 671-78, 681-88, 690-92, "Isle of Pines"; CM 1081-82, "Isle of Pines?" (see comments below).

DISTRIBUTION: the north coast of the Isla de Pinos (fig. 2).

DIACNOSIS: A subspecies of *L. stictigaster* characterized by dirty brown dorsal coloration, zones 4 and 6 yellow and prominent, sides red with scattered green dots, and yellow ventral surface of males either immaculate or spotted with black dots.

Description of Type: An adult male with the following measurements and counts: snout-vent length 70, tail broken 52 millimeters from body and distal quarter regenerated 110, snout to anterior border of tympanic opening 15.8, head width 13.2, supraocular series 6/6, loreals 4, temporals 12, enlarged auricular scales 5/4, median head scales 4, prefrontal row complete 3 scales, frontoparietal row complete 5 scales, parietals in contact, semicircles incomplete, dorsal crest scales occiput to vent 47, dorsal crest scales occiput to axilla 20, scales around one half of body at midbody 24, fourth toe subdigital tricarinate scales 23/21.

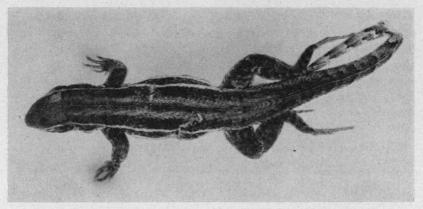


Figure 9.—Leiocephalus s. exotheotus, dorsal view, type (AMNH 81088); snout-vent length 70 mm.

Coloration: The dorsum is dirty tan. Zonation is not especially prominent on the back itself; zone 1 is a dull brownish tan mid-dorsal line three scales in width bounded on each side by a dirty tan zone 2. Zone 3 is dark brown without any black markings and is set off sharply from zone 2 above and a prominent yellow narrow zone 4 below which begins above the eye and continues to above the hindlimb insertion (see fig. 9). The lateral fields (zone 5) are red and green in life, the green pigment not extending onto the sides of the venter. Zone 6 is yellow, especially anteriorly where it begins at the tympanic opening, and continues to the hindlimb insertion. Below zone 6 additional red and green pigment is separated from the belly by another longitudinal yellow line which arises as a pale yellow axillary spot and continues to the groin. Below this line are still more red and green scales before the pale yellow venter is reached. The lateral fields lack black spots, and the postorbital spot is absent. The

head scales are very dark brown and all head markings are pale yellow. The chin and throat are pale yellow unicolor with the venter, and the throat pattern is a group of isolated black spots anteriorly, and posteriorly about six longitudinal black lines extending to the chest. The chest itself and the abdomen are dotted with brown dots, a bit smaller centrally than peripherally where they have a distinct orange hue, and the undersurface of the fore- and hindlimbs are immaculate pale yellow. The hindlimbs are brown with scattered black dots. The ventrolateral portions of the tail are likewise spotted with brown, and the dorsal surface of the tail is brown with about seven darker chevrons, their apices pointed posteriorly.

Variation: In snout-vent length 9 males average 59.9 (46-70), 16 females average 49.9 (43-57). Dorsal crest scales in occiput-vent length (combined data for both sexes) average 48.7 (43-53), and dorsal crest scales in occiput-axilla length average 21.1 (15-26). One half scales at midbody average 22.3 (19-26); loreals 4.5 (2-7), temporals 11.4 (8-15), subdigital fourth toe tricarinate scales 22.2 (19-27). The parietals are not in contact in 53% of the individuals; the supraorbital semicircles are more often (55%) complete than incomplete.

The basic color and pattern of males is similar to that described for the type. The longitudinally lined dorsal pattern, with zones 4 and 6 yellow and prominent and the dirty tan and brown dorsum with red and green mottled lateral fields, are constant in all specimens. Only one recent specimen other than the type has the prominent accessory lateral longitudinal yellow stripe, and one other shows it faintly. The dorsal fields vary from immaculate to dotted or spotted, the dots or spots arranged in two parallel series. The greatest variation is in the ventral spotting of males. Of the Link specimens all but one have the venters with discrete brown dots; in the recently collected males these dots are absent in four and present to varying degrees in five. The dots on the dorsal surface of the legs are likewise variable; they occur in 16 males and are absent in 2. As specimens of equal size collected at a single place may show variation from immaculate to dotted venters, these differences are neither ontogenetic nor associated with locality. Apparently the spotted venter characteristic of males of the Cuban subspecies of L. stictigaster is a variable character in the populations of the north coast of the Isla de Pinos.

Females are distinctly lined longitudinally as is usual in this species. The dorsal fields are much mottled with black, and zones 4 and 6 are prominent and pale yellow in life. The median zone 1 is

usually delineated by irregular black blotches which encroach into zone 2. The venters are pale cream dotted peripherally with gray dots. The throat pattern involves gray blotches near the chin and longitudinal gray lines extending from the throat onto the chest; these lines are a pair of paramedian lines and three or four diagonal lines directed toward the region between the tympanic opening and the forelimb insertion.

Comparisons: L. s. exotheotus differs from s. stictigaster in the dark dirty tan and brown rather than pale sandy dorsal color, yellow rather than pale tan zones 4 and 6, red and green rather than pink lateral fields, slightly smaller adult size, and absence of black dots in the lateral fields. From sierrae, exotheotus differs in red and green rather than bright orange lateral fields, absence of black spots or vertical bars in the lateral fields, and smaller adult size. These two races resemble each other in dorsal color, but exotheotus is in general darker than sierrae. No significant differences in scalation are apparent between exotheotus and the two mainland forms, though exotheotus averages slightly less in all counts taken than either sierrae or stictigaster, and both Cuban races are represented by higher counts of scales in the occiput-vent length (62 in stictigaster, 55 in sierrae, 53 in exotheotus).

REMARKS: Two specimens (a male and a female) listed above (CM 1081-82) are recorded in the Carnegie Museum register as questionably from the Isla de Pinos and questionably collected by Link. They may well have originated on the Isla as their venters are dotted; the female is slightly larger (61) than other female exotheotus examined, and the male appears to be a stouter lizard than other male exotheotus. I suspect that they may actually be somewhat faded specimens of sierrae, or perhaps stictigaster. Link collected in Cuba in the vicinity of La Habana, and he may have collected these lizards in eastern Pinar del Río; on the other hand they may well be Isla de Pinos specimens. I refer them provisionally to exotheotus with these reservations.

L. s. exotheotus occurs sparingly over the north coast of the Isla de Pinos. It is found on gravelly soils (Mal Pais gravel) in pine woods, especially in the vicinity of the lush tropical "arroyos" along the margins of the streams that course through the pineland. The lizard also occurs occasionally in dense grass and along sandy beaches in a halophytic shrubby growth. Along the northern shore of the Ciénega de Lanier at least, exotheotus is replaced by L. c. gigas, which is typically a dweller in broadleaf forest. I have seen no specimens

that are intermediate between the species; in fact, it was the lack of intergrades here and on the south coast of the Isla de Pinos which first suggested the possibility that two species were involved both here and on Cuba. L. c. gigas and L. s. exotheotus occur within 15 kilometers of each other, gigas at Paso de Piedras, exotheotus 5 miles northeast of Siguanea, and I am certain that exotheotus occupies suitable areas much closer to the Paso and the Ciénega de Lanier. The ecological preferences of the two species in this region are very marked.

Leiocephalus stictigaster astictus, new subspecies

Type: AMNH 81095, from Caleta de Carapachibey, Isla de Pinos, Habana Province, Cuba, taken 18 July 1958, by Albert Schwartz and George R. Zug. Original number 5924.

PARATYPES: AMNH 81096-81119, same data as type.

DISTRIBUTION: known only from the type locality on the south coast of the Isla de Pinos (fig. 2).

DIAGNOSIS: A subspecies of *L. stictigaster* characterized by prominently lined brown dorsum with zones 4 and 6 very broad and white, absence of ventral dots, and sides red with scattered green dots.

Description of Type: Adult male, with the following measurements and counts: snout-vent length 74, tail 108, snout to anterior border of tympanic opening 16.0, head width 12.5, supraocular scales 6/5, loreals 5, temporals 12, enlarged auricular scales 4/5, median head scales 4, prefrontal row complete 3 scales, frontoparietal row complete 4 scales, parietals not in contact, semicircles complete, dorsal crest scales occiput to vent 50, dorsal crest scales occiput to axilla 23, scales around one half of body at midbody 23, fourth toe subdigital tricarinate scales 24/23.

Coloration: The dorsum shows the maximum expression of zonation, with the exception of zone 1. Zones 1 and 2 are uniform metallic tan bounded laterally by zone 3 which is dark brown. Zone 4 is white and broad, encompassing one longitudinal scale row and parts of two adjacent scale rows (see fig. 10). Zone 5 is likewise dark brown, sharply delineated above and below by zones 4 and 6, and has a few greenish scales scattered throughout. Zone 6 is white and broad, extends from the tympanic opening to the groin, and is more prominent anterior than posteriorly. Below zone 6 on the sides of the venter the lateral coloration continues in red and green scales sharply set off from the pale yellow belly. The postorbital spot is represented by an obscure black-edged hollow

spot, not distinct from the lateral fields which also lack any black barring or spots. Zone 6 is continued on the head as a broad pale supralabial line from the naris to the anterior margin of the tympanic opening. The hindlimbs lack dorsal spots or dots. The ground color of the chin and throat is grayish white, with black pigment aligned into two pairs of diagonal lines, their apices directed toward the chin, and a group of more posterior longitudinal short black or gray dashes extending in fragments onto the chest. The belly and underside of the limbs are immaculate. The tail is brown with a series of poorly defined blackish crossbands.

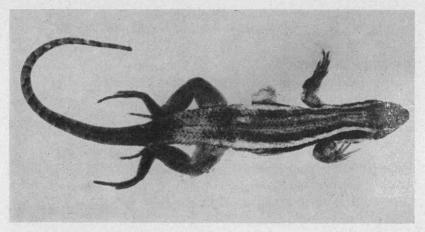


Figure 10.—Leiocephalus s. astictus, dorsal view, type (AMNH 81095); snout-vent length 74 mm.

Variation: In snout-vent length 15 male paratypes average 69.2 (58-79), 10 female paratypes average 58.7 (55-62). Dorsal crest scales in occiput-vent length (combined data for both sexes) average 49.2 (45-54), and dorsal crest scales in occiput-axilla length average 21.5 (17-26). One half scales at midbody average 22.0 (20-25), loreals 5.0 (3-7), temporals 11.0 (9-12), subdigital tricarinate scales on the fourth toe 22.8 (20-25). The parietals are usually (73%) not in contact; the supraorbital semicircles are more often complete (86%).

In astictus both males and females are remarkably similar in dorsal pattern and color. Most specimens resemble the type in color, even to the presence of green dots in the red sides. All are prominently lined longitudinally, and zones 4 and 6 are always broad and usually white, although in one male (snout-vent 70, and thus not the largest specimen) these lines are tan and like zone 2. The dorsal fields

may be unmarked as in the type, or may have obscure dark brown to blackish mottling or shading; this is especially true of females, but occurs in some males as well. The broad supralabial extension of zone 6 is very bold in most individuals. Ventrally the females have the customary lateral diffuse gray dots, a spotted gray chest, and a distinctly lined throat, usually with two anterior V's, their apices directed forward, and a pair of paramedian posterior black lines with more lateral black dashes. The males have this same basic pattern, except that all throat markings show a tendency toward fragmentation. The bellies of males are unspotted. Only one specimen shows any indication of spotting on the dorsal surface of the hindlimbs.

Comparisons: L. s. astictus is distinguishable at once from stictigaster and sierrae by the absence of ventral dots. Some specimens of exotheotus likewise lack ventral dotting; from these astictus can be distinguished by the configuration and color of zones 4 and 6, which are white and broad in astictus and yellow and narrow in exotheotus.

Of the four races of *L. stictigaster*, astictus shows the lowest percentage of parietal contact (27%), as well as the highest percentage of completeness of semicircles (86%). In no other scale counts taken does the southern subspecies differ significantly. In size astictus is larger than exotheotus and equal to stictigaster and sierrae.

REMARKS: L. s. astictus is a well defined subspecies restricted. as presently known, to a limited area on the south coast of the Isla of Pinos. L. c. gigas occurs west of its range at 7 miles east of Jacksonville, east of it at Punta del Este, and north of it at Paso de Piedras. Thus gigas is found within 14 kilometers of astictus. The range of astictus appears to be completely separated from that of its northern ally, exotheotus, by the intervening range of gigas and the Ciénega de Lanier. The ecological preferences of gigas and astictus are distinct; gigas inhabits mesic hardwood forest, astictus occurs at the type locality only near the shore on sandy and rocky ground with scattered and stunted littoral growth. Although gigas occurs near beaches at Caleta Grande and Puerto Francés, for example, these beach areas are close to deciduous forest. At Caleta de Carapachibey the wooded areas are mangrove forest, and gigas does not occur. It is possible, even probable, that astictus has a wider range than now known, but we encountered it only at this one locality on the southern coast. It may well exist at other scattered localities in this area.

Discussion

It has been shown that those lizards formerly regarded as Leiocephalus cubensis represent two distinct species, each of which in turn is represented by four subspecies as follows: Leiocephalus cubensis cubensis from western Habana Province to western Oriente Province, L. c. paraphrus on the Doce Leguas keys off southern Camagüey Province, L. c. gigas in central and southern Isla de Pinos, L. c. pambasileus on parts of the Archipiélago de los Canarreos east of the Isla de Pinos; Leiocephalus stictigaster stictigaster on the Península de Guanahacabibes, Pinar del Río Province, L. s. sierrae in central and eastern Pinar del Río Province, L. s. exotheotus on northern Isla de Pinos, L. s. astictus isolated on the south coast of the Isla de Pinos.

The two species of the cubensis complex, cubensis and stictigaster, are closely related. They differ in details of color, pattern, size, and hemipenial characters. All populations examined can be assigned without difficulty to one or the other species, and I have seen no specimens that show intergradation between the two. While the precise situation in Oriente is at present unknown, it is to be expected that L. cubensis will be found there. Although some populations of cubensis are close geographically to some populations of stictigaster (for example, s. sierrae and c. cubensis; s. exotheotus, c. gigas, and s. astictus) the habitat requirements of the species are distinct and no interbreeding is known to take place.

Leiocephalus cubensis is a lizard of the grasslands, sandy beaches, and scrub growth. It does not occur in broadleaf forest in Cuba, but is found along roadways and in clearings in forested regions. the Isla de Pinos this species is restricted to broadleaf forest and associated scrub. It reaches maximum abundance in areas of sandy soils, but is at times locally plentiful in extremely rocky environments. Altitude appears to play little part in its distribution. Specimens have been taken near sea level on the Doce Leguas keys in Camaguey Province and along the north coast in Habana Province, and one individual was taken in tall grass beside a paved road at an elevation of 1200 feet in the Sierra de Trinidad, Las Villas Province. diurnal, these lizards are common in suitable areas along roadways and are often seen either crossing the roads or resting on the pavement in the shade of shrubs or tall grass. They are wary, but not so easily frightened as L. carinatus, and when disturbed they flee without a pronounced curling of the tail. Occasional individuals curl the

distal third of the tail slightly while running, but L. cubensis never holds the tail in the tight watch-spring coil typical of L. carinatus.

L. stictigaster is an inhabitant of gravelly soils and beaches. In Pinar del Río it is common on the Península de Guanahacabibes and throughout much of the province, and equally abundant in lowland scrub and in montane forest. Altitudinally it ranges from sea level to at least 1000 feet, as at San Vicente. On the Isla de Pinos it occurs on the northern and southern "coasts"; it occupies the northern section of the island exclusively, and another population is apparently isolated on the south coast at Caleta de Carpachibey. The northern section of the Isla is typically pineland on gravelly soil; on the south coast the inhabited area is wave-washed "diente de perro" (limestone) with pockets and ridges of white sand, and covered by scattered and stunted plant growth. Its habits are comparable to those of L. cubensis; it is equally shy and at times holds the distal third of the tail curled while running.

L. stictigaster apparently occurs only in western Cuba and the Isla de Pinos. The close affinity of the faunae of these two regions is well known. Among Cuban birds several species (Gymnoglaux lawrencii, Myadestes elisabeth, Teretistris fernandinae, Quiscalus niger, Agelaius phoeniceus) either occur in western Cuba and the Isla de Pinos, or have two Cuban subspecies, the western one of which occurs in Cuba and the Isla (Bond: 1956). Among amphibians and reptiles Cadea comes to mind at once. The occurrence of L. stictigaster in these two areas emphasizes the closeness of this geographic relationship.

L. cubensis is widespread throughout Cuba, ranging from Habana to Oriente provinces. L. c. gigas on the Isla de Pinos is closely related to the mainland form and differs but little from it. The two remaining races of cubensis, paraphrus and pambasileus, are both insular forms, both differ from their respective parent stocks, cubensis and gigas, in the same fashion and consequently resemble each other closely in size and color. The complete distribution of paraphrus is not known, but it presumably occurs throughout the Doce Leguas chain of keys; pambasileus is known from two keys close to the Isla de Pinos, and its distribution has been discussed in detail above. I believe these two insular subspecies have evolved directly from their adjacent mainland populations, and the resemblances between them are due to convergence in similar habitats rather than to any direct genetic connection between the races themselves.

The habitat of *L. cubensis* varies with locality. In Cuba it is primarily an inhabitant of grasslands and cultivated areas, especially along fence rows and in shrubby growth. Rarely is it found in woodlands and then only along cleared roadways. On the Isla de Pinos the reverse is true; here it is strictly an inhabitant of mesic forest and associated beach growth, and it does not occur in grasslands. On the Doce Leguas and keys of the Archipiélago de los Canarreos it occurs primarily on sandy and rocky beaches, occasionally in open palm forest. *L. stictigaster* in Cuba occupies grassland, forest, clearings, and sandy beaches, areas which typically have a shrubby flora and little or no arboreal cover. On the Isla de Pinos, this species occurs strictly on gravelly soils in pinelands in scattered grass on the north coast, and the range of the south coast subspecies is restricted to a beach and rocky coast near mangrove forest.

It is possible to rationalize these peculiarities historically. I believe that stictigaster and cubensis arose from a common stock through isolation on western and central island masses during the Ogliocene and Lower Miocene. With the reestablishment of the island to approximately its present outline between the Lower and Middle Miocene, these two species extended their ranges gradually from the regions of differentiation. I think that the typical habitat of both species originally was open grassland. From modern distribution it appears that the gap between western stictigaster and eastern cubensis may not yet be closed. L. cubensis also has spread to the east into Oriente as well as to the west into Matanzas and Habana.

The Isla de Piños was probably connected to western Cuba until the Pleistocene. It lies on the same insular platform as does Cuba, and the intervening Golfo de Batabanó has a maximum depth of 6.5 fathoms. If we assume that stictigaster originated in western Cuba, it is only logical that it may well have occurred as well on the part of the land mass which is now the Isla de Pinos. If it arrived on the Isla via overseas transport, the currents between Cuba and the Isla certainly favor transport from western rather than from In any event, I think that stictigaster eastern or central Cuba. occurred on the Isla before the arrival of *cubensis*. It is possible as well that the north and south coasts have at times been two separate islands, divided by what is now the Cienega de Lanier. Under these circumstances differentiation of a parent stock into exotheotus on the north coast and astictus on the south coast is reasonable. That the two Isla races of stictigaster are more closely related to each other than to stictigaster and sierrae on Cuba is shown by the similarity

of coloration and pattern, as well as the tendency in exotheotus to lose ventral dots, and their complete loss in astictus. The close resemblance of sierrae and stictigaster to each other indicates a shorter period of differentiation between these two forms. Of the two I think that sierrae is the more primitive and closer to the basic stock, and that stictigaster represents a more recent offshoot on the Península de Guanahacabibes.

Prior to the arrival of L. cubensis on the Isla de Pinos, there were thus probably two races of stictigaster, one on the north coast and one on the south. The similarity between the races cubensis and gigas suggests to me that the invasion of the Isla by this species has been recent, and probably by overseas transport from Cuba, not across a land connection at the same time as L. stictigaster. On its arrival L. cubensis had to compete with the established L. stictigaster. Both species being grassland dwellers, competition for this habitat must have begun at once. I think that, by virtue of its earlier arrival and greater numbers, and possibly because of its smaller size, L. stictigaster was the more successful, and the invading L. cubensis was forced to occupy mesic forests to the south in the area of the Ciénega and the south coast, a habitat it shuns in Cuba where it need not compete with L. stictigaster. Once so established on the Isla, or possibly before, this stock became slightly modified toward the present gigas. At the same time the southern coast form of L. stictigaster was crowded out of its much smaller range by the invading gigas. If gigas is typically a forest form, it is capable of spreading throughout the forests of the Ciénega and associated forests on the south coast. Competition with astictus may well have been primarily a marginal situation, with both species occupying fringes of forest and associated With increasing numbers and increasing adaptation for a forest dwelling existence, gigas became the dominant form. Unable to expand to the north because of lack of suitable habitat, it expanded to the south into marginal habitats already occupied by astictus, and the latter has had its range increasingly contracted by invasion of gigas. In support of this theory, gigas occurs throughout the south coast in woods and in associated marginal scrub, whereas astictus occupies similar marginal scrub only where mesic forest does not occur immediately behind the beach.

On the keys apparently only cubensis has occurred. Arrival of this species on the Doce Leguas from the southern Cuban coast and on the Archipiélago from Punta del Este (or at least the eastern portion of the Ciénega de Lanier) is favored by oceanic currents. With-

out competition from L. stictigaster in either locality, these lizards were able to survive in what elsewhere would be marginal habitats for this species—rocky beaches and sandy areas. No other Leiocephalus occurs on the keys of the Archipiélago; on the Doce Leguas, L. cubensis shares its habitat with L. carinatus, but the two species have dissimilar habitat requiréments. L. carinatus dwells principally among exposed broken rocks and rocky cairns, whereas cubensis occupies rocks when they are less massive and lie on and in sandy soils. This difference is manifested as well at Punta del Este on the Isla; here, however, both species occur together only where their habitats overlap. Since the two key chains involved present similar edaphic conditions, it is not surprising that on both chains differentiation has been rapid and along the same general lines—smaller size and pale coloration.

The major fault with this explanation lies, I think, in the alternating role of the L. stictigaster populations on the Isla de Pinos, first as a dominant form on the north coast with which the invading L. cubensis is unable to compete, and later as an incompetent form on the south coast, unable to compete with the expanding L. cubensis. It is possible that this alternation depends on the area involved. Upon its arrival, L. cubensis was unable to compete with a wide ranging and established north coast L. stictigaster population and was forced to occupy forests near the Ciénega to survive. Once modified for this type of existence, it was able to push out into adjacent less suitable habitats. Such expansion did not put it into direct competition with the northern exotheotus, which it could conceivably have restricted, because the forest habitat lacks extensive continuity or soon ceases to the north. Instead it was able to expand southward in competition with astictus, which originally had a much smaller and more restricted distribution than its northern ally exotheotus, and forced astictus into more and more restricted areas, as at present at Caleta de Carapachibey. There may well be other explanations for the present distribution of the complex, but the one here given seems logical and is formulated on the basis of known facts of distribution, ecology, and historical geology.

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