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THE *LEIOCEPHALUS* (LACERTILIA, IGUANIDAE) OF HISPANIOLA.
II. THE *LEIOCEPHALUS PERSONATUS* COMPLEX.

ALBERT SCHWARTZ

10000 SW 84 St., Miami, Florida



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 II. THE *LEIOCEPHALUS PERSONATUS* COMPLEX.

ALBERT SCHWARTZ

10000 SW 84 St., Miami, Florida

ABSTRACT

Examination of 1240 specimens of *Leiocephalus* from Hispaniola revealed that the species *L. personatus* Cope is actually composed of four species: 1) *L. personatus*, with its subspecies *personatus* (north shore of the Tiburon Peninsula), *trujilloensis* (vicinity of Santo Domingo), *mentalis* (extreme eastern República Dominicana), *tarachodes* (north and south of the Bahía de Samaná and including the Peninsula de Samaná), *aetites* (northern coast of República Dominicana), *scularis* (northern Hispaniola, from Cap-Haïtien in Haiti east through the Valle de Cibao in República Dominicana), *budeni* (northern slope of Cordillera Central at intermediate elevations), and *agrutus* (uplands of Cordillera Central near Constanza and southern slopes of same range); 2) *L. lunatus*, with its subspecies *lunatus* (southeastern Dominican coast near Santo Domingo), *arenicolor* (southeastern Dominican coast from San Pedro de Macoris to Boca Chavón), *thomasi* (vicinity of Boca de Yuma), *meluenaecelis* (Isla Catalina), *louisae* (Isla Saona); 3) *L. barahonensis* with its subspecies *barahonensis* (northern and eastern foothills of Sierra de Baoruco), *orygaster* (Península de Barahona), *aureus* (southern Haiti from Jacmel east into southern República Dominicana near Pedernales), *beatanus* (Isla Beata); 4) *L. vinculum* with its subspecies *vinculum* (Ile de la Gonâve), *endomychus* (interior Haiti), *altavelensis* (Isla Alto Velo). The status of *L. cremitus* (Navassa Island) is discussed and this species is considered distinct from any Hispaniolan species. A history of the *personatus* complex is pre-

sented and comparisons of the *Leiocephalus* faunas of the Antilles are made; Hispaniola is shown to have the greatest diversity of species, none of which shows any obvious relationship to the Cuban *Leiocephalus*.

INTRODUCTION

Of the five species of the lizard genus *Leiocephalus* occurring on Hispaniola, *L. personatus* Cope, 1862, is the most widely distributed. The description was based upon two syntypes from near Jérémie, Département du Sud, Haiti, near the tip of the Tiburon Peninsula. In the same paper, Cope also described "*Liocephalus trigeminatus*", also from near Jérémie; presumably (the type cannot presently be found) this description was based upon a female of *L. personatus*, since the description includes notes on the dorsal pattern and coloration which agree with females rather than with males of that species. No further names were proposed for this group of lizards until *barahonensis* Schmidt, 1921, from the western portion of the República Dominicana, and this was followed by *beatanus* Noble, 1923, from Isla Beata and *vinculum* Cochran, 1928, from Ile de la Gonâve. During the next decade, the populations from the northern portion of Hispaniola (*scularis* Cochran and *mentalis* Cochran, 1932), from Isla Alto Velo (*altavelensis* Noble and Hassler, 1933), southern Haiti (*aureus* Cochran, 1934), southern República Dominicana (*lunatus* Cochran, 1934) and Isla Saona

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(*louisae* Cochran, 1934) were named. Finally, two southern coastal Dominican populations (*trujilloensis* Mertens, and *avenicolor* Mertens, 1939) and a northern Dominican subspecies (*pulcherrimus* Mertens, 1939) were described—a total of thirteen named subspecies. Cochran (1941:217) also included *L. semilineatus* Dunn as a subspecies of *L. personatus*, but this form is a distinct species.

My collecting efforts in Hispaniola between 1962 and 1964 showed that, as Cochran (*op. cit.*: 202) had surmised, there were several additional distinct subspecies. Inasmuch as there were also fourteen lizards which Dr. Cochran was unable to place in any category known at that time, and since several subspecies had been described and were known from only single localities, or at best were very poorly represented in collections in the past, it seemed appropriate to discuss this species as a whole in the light of the large body of recently acquired material.

I have had the very capable assistance in the field in Hispaniola from the following: Miss Patricia A. Heinlein, and Messrs. Donald W. Buden, Ronald F. Kliniowski, David C. Leber, and Richard Thomas. I am very grateful for their efforts in securing these lizards, and I am especially in the debt of Messrs. Leber and Thomas for their visit to Isla Beata and to Mr. Thomas for his visit to Isla Saona. Except for typical material of new forms, all specimens collected by us are in the Albert Schwartz Field Series (ASFS) or the collection of Richard Thomas (RT). The collections of the Museum of Comparative Zoology (MCZ) at Harvard University, assembled through the efforts of Dr. Ernest E. Williams, have been indispensable; the fresh and well preserved specimens from Haiti have aided immeasurably in the study of the *L. personatus* complex in that country. I have also used specimens in the following collections, and wish to extend my thanks to the respective curators for the loan of interesting and significant material: American Museum of Natural History (AMNH), Charles M. Bogert and George W. Foley; Carnegie Museum (CM), Neil D. Richmond and Clarence J. McCoy; Natur-Museum and Forschungs-Institut Senckenberg

(SMF), Konrad Klemmer; United States National Museum (USNM), Doris M. Cochran and James A. Peters. Paratypes of new forms have been placed in the University of Florida Collections (UF), the University of Illinois Museum of Natural History (UIMNH), and the Museum of Natural History, University of Kansas (KU), as well as in the above collections. I wish especially to thank Dr. Wayne King for his delineations of the lateral and ventral views of various subspecies in the *L. personatus* complex. His careful work has aided immeasurably in the visualization of the descriptions.

THE PROBLEM

I have had 1240 specimens available for study. Of these, 552 were collected by myself and parties, and are carefully documented as to locality, coloration, and pattern. The number of specimens examined far exceeds the 224 lizards available to Dr. Cochran at the time of her study of Hispaniolan herpetology, and amplifies both her conclusions and those reached by Mertens (1939).

It early became evident in our Hispaniolan collecting that the lizards assigned to *L. personatus* were an unusually variable lot. Specimens from the Península de Barahona, for example, are quite different in aspect, coloration, and pattern from lizards from the Valle de Cibao in the northern República Dominicana. It seemed likely that several distinct species were confused under the name *L. personatus*. In studying these lizards in the laboratory, the above suspicion was rapidly confirmed; there are four distinct species presently grouped under the name *L. personatus* Cope. Not only are there radically different features of pigmentation and pattern, but also striking differences in scalation, involving the dorsal crest scales, the size of the preauricular scale, and the completion of the supraorbital semicircles. Additionally, in at least one case, the ranges of two "subspecies" overlap along the southeastern Dominican coast. The traditional counts of dorsal crest scales in occiput-vent distance and in occiput-axilla distance, the number of trunk dorsals, subdigital fourth toe tricarinate scales, loreals and temporals overlap broadly between the four species herein recognized; these counts do, however, have some effectiveness in

separating subspecies, as do also details of pattern and coloration. Details of head scale terminology used in this paper are shown in Figs. 1, 2 and 9.

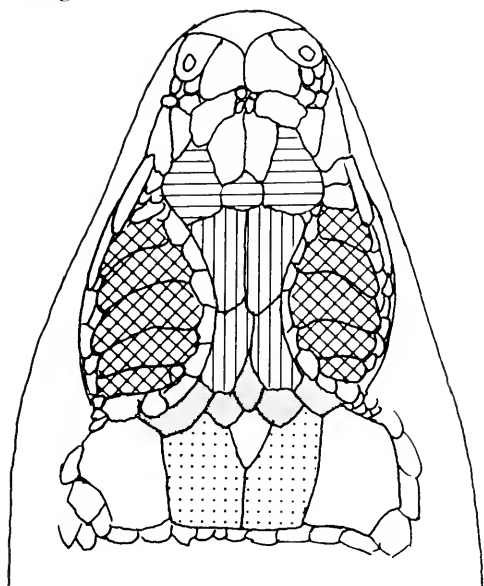


Figure 1. Stylized dorsal view of *Leiocephalus* (based on Schmidt, 1921, Bull. Amer. Mus. Nat. Hist., 44(2), fig. 11) to show head scale terminology employed in the present paper, as follows: prefrontal row, horizontal lines; median head scales, vertical lines; frontoparietal row, dense stippling; parietals, open stippling; supraoculars, crosshatching. Counts on this specimen are: prefrontal row complete, 3 scales; median head scales 4; frontoparietal row complete, 5 scales; supraoculars 5/5; supraorbital semicircles complete; parietal scales in contact.

In general, the four species (whose characters are shown in Table I on p. 49) show cogent geographical distributions. *L. personatus* is widespread, occurring along the northern coast of the Tiburon Peninsula, and throughout much of the República Dominicana except along the southeastern coast. This latter area (as well as Isla Saona and Isla Catalina) is occupied by *L. lunatus* Cochran. The southeastern portion of the Tiburon Peninsula and the Península de Barahona (including Isla Beata) is inhabited by *L. barahonensis* Schmidt. The fourth species, *L. vinculum* Cochran, has a split distribution, including the central Haitian mainland, Ile de la Gonâve, and Isla Alto Velo to the south of Isla Beata. These

distributions will be discussed in detail later in the present paper.

I cannot distinguish any differences between the hemipenes of the four species in the *personatus* complex, and in fact these organs do not differ strongly from the he-

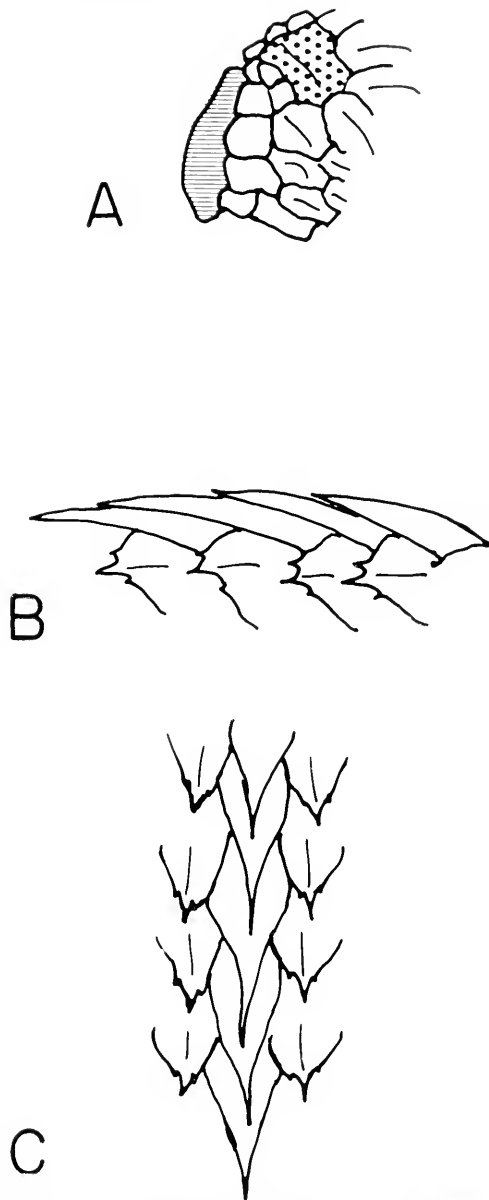


Figure 2. Scale features of *L. personatus* and *L. lunatus*, showing a) auricular opening (horizontal lines) and preauricular scale (stippled); b) lateral view of median dorsal crest scales; and c) dorsal view of median dorsal crest scales.

mipenis of *L. melanochlorus* (see Schwartz, 1966). The hemipenis in *L. limatus* (based upon ASFS X7764) is typical of these organs for the entire complex. The hemipenis is moderately large, extending the length of about six subcaudal scales. The sulcus is deep and prominent and is formed laterally by an extensive membranous flap from the base of the organ to near the tip. The non-sulcate surface has a series of about four flounces (which extend around the organ to near the sulcus) which rather abruptly merge into a series of about six rows of calyces. The tip of the hemipenis is smooth, weakly bifurcate and much crenulated, the sulcus extending into a cordate terminal area which includes a very weak pair of papillae. From these papillae, a raised area continues down the non-sulcate surface, expands on its proximal half, and ends at the level of the flounces on the non-sulcate surface. In the other species, the number of basal flounces may be more numerous and extend more clearly into the calyculate region, but these characteristics are variable and there are no prominent hemipenial differences among the four species.

SYSTEMATIC ACCOUNT

Leiocephalus personatus Cope, 1862

Leiocephalus personatus Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, 14:182 (type locality—near Jérémie, Dépt. du Sud, Haiti).

Leiocephalus trigeminatus Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, 14:183 (type locality—near Jérémie, Dépt. du Sud, Haiti).

Definition: A species of *Leiocephalus* characterized by a combination of 1) moderate size (males to 86 mm, females to 63 mm snout-vent length), 2) distinctly sexually dichromatic, and males with a prominent pair of enlarged postanal scales, 3) absence of a lateral fold, 4) dorsal scales imbricate, weakly tricuspid or denticulate, and keeled, ventral scales imbricate, smooth, and weakly denticulate, 5) median dorsal crest scales enlarged (Fig. 2b and c), greatly attenuate and strongly overlapping, much lower than median dorsal caudal scales, 41 to 64 in occiput to vent distance, 6) one half midbody scales 18 to 28, 7) supraoculars usually 6/6, 8) loreals 2-10, 9) temporals 7-14, 10) supraorbital semi-

circles usually complete (in all but one subspecies), 11) parietals usually in contact, 12) median head scales varying between 4 and 6 (mode 4), 13) preauricular scale small,¹ 14) throat in males varying from solid black to immaculate yellow, in some races with a few scattered and diffuse dusky spots but never heavily, regularly and discretely dotted, in females with heavy black to dark gray dots, 15) ventral color some shade of bright to deep green, yellow-green, or yellow, 16) ventral pattern absent in males, venter heavily dotted with dark gray to black dots in females, 17) a dark brown to black mask in males, and 18) black neck and shoulder blotches absent.

Leiocephalus personatus personatus Cope, 1862

Type locality: near Jérémie, Dépt. du Sud, Haiti.

Syntypes: MCZ 3615, two males with snout-vent lengths of 73 and 77 mm.

Diagnosis: A subspecies of *L. personatus* characterized in males by a combination of solid black throat confluent with a black loreal-temporal-lateronuchal area (Figs. 4a, 5a), three to five transverse dark dorsal bars on the neck and shoulders, a broad dorsal zone bounded by wide pale dorsolateral longitudinal lines; size large (males to 79 mm, females to 62 mm snout-vent length) high number of loreals (mean 5.6) and temporals (mean 11.1), and median head shields modally 5, frontoparietals modally 4.

Distribution: The northern portion of the Tiburon Peninsula in Haiti, from near Jérémie in the west, east or least to Leogâne; records from Furcy considered doubtful and "Bellevue" unlocatable but possibly farther east than Leogâne (see discussion); a single specimen from Aquin, Dépt. du Sud (Fig. 3).

Variation and discussion: The series of 55 *L. p. personatus* has the following scale counts: dorsal crest scales occiput-vent 47-

¹ The term "preauricular" scale requires definition. I use this name for an upper temporal scute which lies just above and anterior to the auricular opening (Fig. 2a). It is the largest of the temporals and in *L. barahonensis* is greatly enlarged, whereas in the remaining three species, it is considerably smaller and not especially enlarged in comparison with the temporals ventrad to it.

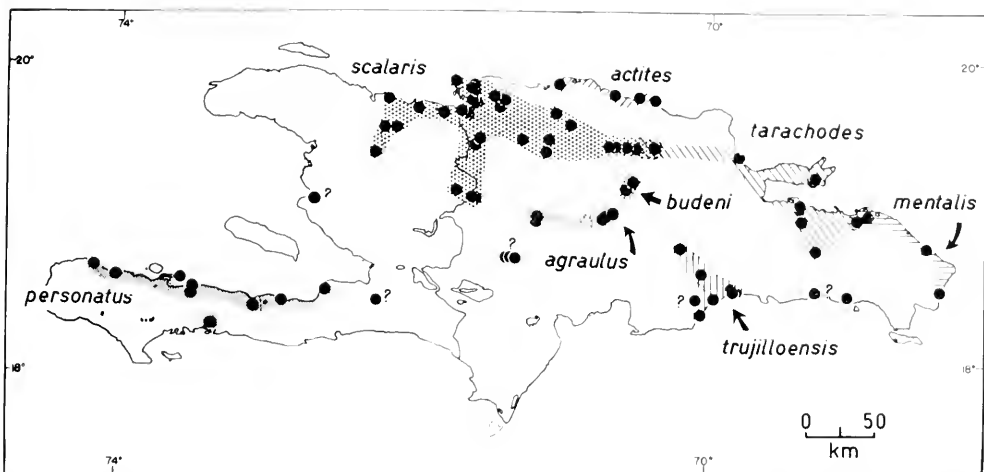


Figure 3. Hispaniola, showing the known distributions of the subspecies of *L. personatus*, as follows: *personatus*, fine stippling; *trujilloensis*, widely spaced vertical lines; *mentalis*, horizontal lines; *tarachodes*, diagonal lines, upper left to lower right; *actites*, diagonal lines, upper right to lower left; *scalaris*, coarse stippling; *budeni*, crosshatching; *agraulus*, fine vertical lines. Overlap of symbols of *tarachodes* and *mentalis* indicates genetic influence of the former in the topotypical population of the latter. Overlap of symbols of *tarachodes* and *scalaris* shows areas of intergradation. Note disjunct range of *L. p. personatus* from the balance of the species. Questioned symbols indicate either dubious record (Furcy) or small samples presently not assignable to subspecies.

61 (mean 53.5), dorsal crest scales occiput-axilla 16-27 (mean 21.1), dorsal crest scales on trunk 24-40 (mean 32.4), one half midbody scales 20-26 (mean 22.9), subdigital fourth toe tricarinate scales 20-25 (mean 22.9), loreals 3-9 (mean 5.6), temporals 7-13 (mean 11.1), supraoculars 6-6 (26 specimens, 5 5 (1), 5 6 (4), 6/7 (12), 7 7 (11), 7 8 (3), 8 8 (1), semi-circles usually complete (90.0 percent), and parietals usually in contact (94.9 percent). The prefrontal row consists of 2 to 5 scales (mode 3), the median head shields vary between 2 and 9 (mode 5), and the frontoparietal row has 0 to 5 scales (mode 4); the prefrontal row is always complete (61 specimens) and the frontoparietal row is usually complete (51 of 59 specimens). The largest male has a snout-vent length of 79 mm, the largest female 62 mm; the male is from Grand Boucan and the female from L'Acul.

Although I have collected within the range of *L. p. personatus*, I have not seen this subspecies in life; consequently the discussion of coloration and pattern is much abbreviated. Adult and subadult males (with snout-vent lengths in excess of about 65 mm) have the throat solid black, this color continuing

dorsally onto the sides of the neck and the temporal region. A male with a snout-vent length of 65 mm shows an intermediate condition wherein the black throat pigment is limited to a few dark and diffuse throat

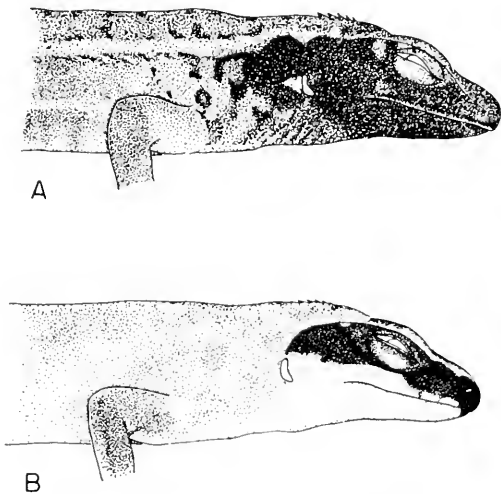


Figure 4. a) *L. p. personatus*, lateral view of head and neck, MCZ 74636, adult male, from Roseaux, Dépt. du Sud, Haiti. b) *L. p. mentalis*, lateral view of head and neck, MCZ 75131, adult male, from Juanillo, La Romana Province, República Dominicana.

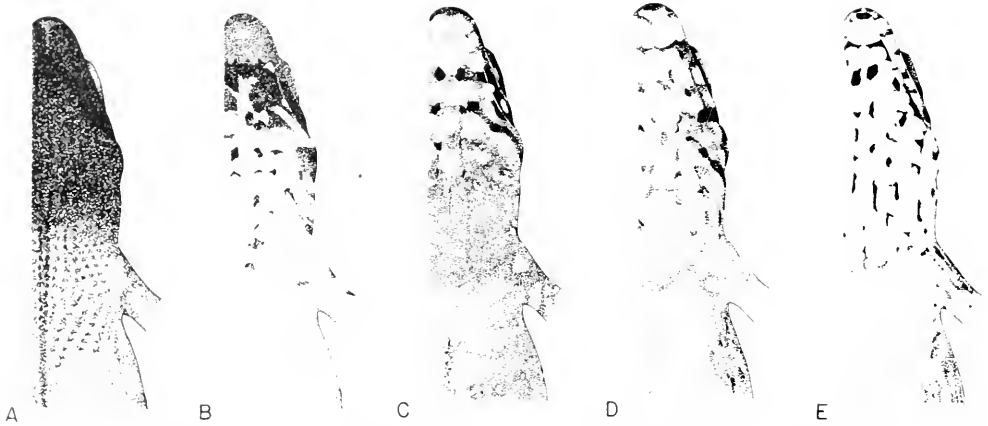


Figure 5. Ventral view of throat of male of five subspecies of *L. personatus*, as follows: a) *L. p. personatus*, MCZ 74636, Roseaux, Dépt. du Sud, Haiti; b) *L. p. trujilloensis*, ASFS X7734, 2.2 km SW Río Ozama, Santo Domingo, Distrito Nacional, República Dominicana; c) *L. p. tarachodes*, MCZ 81087, holotype, 6 km SE Nagua, María Trinidad Sánchez Province, República Dominicana; d) *L. p. actites*, MCZ 81088, holotype, Sosúa, Puerto Plata Province, República Dominicana; e) *L. p. budeni*, MCZ 81089, holotype, 12 km NE Jarabacoa, 2000 feet, La Vega Province, República Dominicana.

spots, some heavy and irregular blotching along the sides of the lower jaw, and a prominent black mask. Two younger males (snout-vent lengths 40 mm and 52 mm) show the throats dotted with dark in the fashion of females. The neck and shoulders are crossed by three to five transverse dark bars, and at times these bars are expanded medially to give an irregular black median dorsal nuchal figure (USNM 80776). In other lizards, the transverse bars are somewhat reduced but always there is at least a scapular transverse bar present. The dorsal pattern consists of a median wide brown zone, bounded laterally by broad dorsolateral pale lines; there is a pale lateral line between the limbs and both above and below this line the sides are tannish to gray; considering the bright lateral colors of other races of *L. personatus*, doubtless these lateral areas have an admixture of green and reddish scales in life. The ventral color is presently grayish-blue to tan, but Cochran (1941: 214) who had seen some of this material when it was more fresh, called the ventral coloration "china blue". I suspect that originally the coloration was some shade of green, the typical ventral color of the species *personatus*. The tail is rather weakly chevronate with dark pigment, and the ground color is brown. A sacral transverse bar is sometimes manifested

The females lack the dark throat and head coloration of the males, and the dorsal zone has a series of complete or incomplete chevrons. The lateral fields are tan with dark vertical brown bars especially on the neck and above the forelimbs. The mask is restricted to a dark-edged temporal rectangle, and both the dorsolateral and lateral pale lines are usually prominent. The throat is heavily spotted with dark gray to black spots, and this pattern continues onto the venter, although the dots may be reduced centrally on the latter region. In some (MCZ 74630) the pale interspaces on the throats have additional dark pigmentation, thereby giving the throat a very densely pigmented appearance.

In general, the pigmentation of young males and adult females is comparable, although young males lack the very heavy ventral spotting that females usually possess.

L. p. personatus is known from the northern shore of the Tiburon Peninsula in Haiti (Fig. 3). This subspecies occurs from near Jérémie (the syntypes) east of Leogâne, and inland to 6 miles (9.7 km) southwest of Miragoâne. The single isolated female (USNM 72613) from Aquin near the south coast, with a snout-vent length of 54 mm, resembles females of *personatus* in all ways. Since females are seldom diagnostic of the subspecies of *L. personatus*, this individual

does not allow complete assurance that *personatus* is the subspecies in this more southern region. There is no justification for considering otherwise, however.

Five specimens (MCZ 8720, 8722-25) from Furcy are clearly *L. p. personatus*; the two males have the typical black throats and heads. However, since neither ourselves nor others have taken any specimens of this lizard at Furcy, despite intensive collecting in that region on the Montagne Noire, I consider the locality dubious. Another specimen (MCZ 25434) from 3 miles (4.8 km) north of Bellevue, Haiti, is also presumably *L. p. personatus* (the specimen is a female). The name Bellevue is a commonplace in Haiti, and although there is a district by this name to the immediate south of Carrefour and west of Port-au-Prince, there is no certainty that this is the locality referred to; it is possible that *L. p. personatus* occurs east of Leogâne, the presently easternmost locality whence it has been definitely recorded.

Another specimen (USNM 75906) requires mention here; it will be discussed in detail later. This lizard is from "Bayeux, near Port-au-Prince" and might be assumed to represent *L. p. personatus*. The lizard is, however, *L. barabonensis*. I cannot locate "Bayeux" on any modern map. As will be shown later, this specimen likely did not originate in this region since it is referable to *L. b. aureus*.

L. p. personatus is primarily coastal. Other than the specimen from 6 miles southwest of Miragoâne, all records are from near the coast. The highlands of the Massif de la Hotte and Massif de la Selle must act as a southern barrier for this species (although the specimen from Aquin indicates that *L. personatus* has crossed these mountains somewhere). Other than the syntypes, there is only one series (14 specimens) from Roseaux, about 15 kilometers southeast of Jérémie, from this general region. Considering the abundant material of *L. melanochlorus* from the same area (but none of this latter species from Roseaux), it is probable that *personatus* greatly outnumbered *melanochlorus* near the type locality of both species. *L. p. personatus* is known to be sympatric (but likely not syntopic) only with *L. melanochlorus* and only in the Jérémie

region. If the *personatus* from Furcy are correctly labelled, sympatry between *personatus* and *melanochlorus* occurs there as well. I have given detailed reasons elsewhere (Schwartz, 1966) for considering that the two species do not occur there.

Specimens examined: Haiti, *Dépt. du Sud*, near Jérémie, 2 (MCZ 3615, syntypes); Roseaux, 14 (MCZ 74626-39); Grand Boucan, 14 (USNM 80774-87); 10 mi. (16.1 km) E Baradères, 4 (USNM 80763-66); Petit Trou de Nippes, 9 (USNM 80788-89, 80791-92, 80794-98); Aquin, 1 (USNM 72613); 6 mi. (9.7 km) SW Miragoane, 1 (MCZ 25433); *Dépt. de l'Ouest*, L'Acul, 6 (USNM 72607-12); Leogane, 4 (MCZ 13834-37); 3 mi. (4.8 km) N Bellevue (not mapped), 1 (MCZ 25434); "Furcy", 5 (MCZ 8720, 8722-25).

Leiocephalus personatus trujilloensis

Mertens, 1939

Leiocephalus personatus trujilloensis Mertens, 1939, *Abh. Senckenberg. Naturf. Ges.*, 449:45.

Type locality: coast at the German-Dominican Tropical Research Institute in Ciudad Trujillo (= Santo Domingo), about 4 km west of the mouth of the Río Ozama, Distrito Nacional, República Dominicana.

Holotype: SMF 26213, an adult male with a snout-vent length of 78 mm (*vide* Mertens, *loc. cit.*).

Diagnosis: A subspecies of *L. personatus* characterized in males by a combination of greenish-orange throat with black smudges (Fig. 5b), confluent on sides of head and neck with a black mask, transverse neck bars reduced or absent, a broad dark brown to rich reddish-brown dorsal zone, in fully adult males not bordered by pale dorso-lateral lines, and dotted with bright yellow; size moderate (males to 78 mm, females to 60 mm snout-vent length), low number of loreals (3.7), median head shields modally 4, frontoparietals modally 5.

Distribution: South central República Dominicana, from coastal San Cristóbal Province (Sabana Grande de Palenque) east to the Río Ozama (Santo Domingo), and into the interior as far as the vicinity of Villa Altagracia, San Cristóbal Province (Fig. 3); specimens from the city of San

Cristobal and east at the Río Cumayasa atypical (see discussion).

Variation and discussion: The series of 23 *L. p. trujilloensis* has the following scale counts: dorsal crest scales occiput-vent 47-57 (mean 52.3), dorsal crest scales occiput-axilla 15-21 (mean 19.1), dorsal crest scales on trunk 28-42 (mean 33.1), one half midbody scales 19-25 (mean 21.7), subdigital fourth toe tricarinate scales 19-24 (mean 21.4), loreals 3-10 (mean 3.7), temporals 7-12 (mean 9.1), supraoculars 6-6 (9 specimens), 4-4 (1), 5-5 (8), semicircles usually complete (72.7 percent), and parietals always in contact (100 percent). The prefrontal row consists of 3 scales in all specimens, the median head shields vary between 4 and 5 (mode 4), and the frontoparietal row has 2 to 5 scales (mode 5); the prefrontal row is always complete (24 specimens) and the frontoparietal row is usually complete (16 of 20 specimens). The largest male examined by me (UIMNH 44700, a paratype) has a snout-vent length of 75 mm, but Mertens (*op. cit.*:46) gave the snout-vent length of the type as 78 mm. The largest female has a snout-vent length of 60 mm and is from the city of Santo Domingo.

The coloration of freshly collected males may be seen from the following notes on a specimen from Santo Domingo. The dorsum is rich reddish-brown, without dorsolateral pale longitudinal lines; each scale has a yellow dot, thus giving a flecked appearance dorsally. There are about five very diffuse black nuchal and scapular transverse bars, but these are barely visible. The top of the head is brown, with black pigment in the sulci between the scales, and the sides of the head and the chin are deep brown, forming a conspicuous mask. The throat is greenish-orange; anteriorly this color is completely obscured by the dark brown chin pigment, and posteriorly the throat has many fairly large and irregular dark brown smudges. The ventral ground color is greenish-orange, the orange pigmentation due to the deposition of red earth in the epidermis. The underside of the tail is deep reddish (brick) and the underside of the hindlimbs greenish-yellow.

In younger males, the dark brown dorsal band is outlined by buffy dorsolateral lines, and the sides are tan to buffy with mixed

red and yellow-green scales. The ventral ground color is pale yellow-green; the chin is bright to pale yellow and heavily smudged with black to dark brown. The underside of the tail is brick to orange, and the sides of the head have creamy to dull orange markings (these head markings are completely obscured by the dark brown mask in fully adult males). The hindlimbs are green to yellowish-green above. The tail is brown, with faint chevrons distally.

Females are like males in dorsal coloration, but have the dorsolateral lines buffy and prominent, and the dorsal zone in young females has about 7 or 8 transverse bars anterior to the hindlimbs. The ventral ground color is dirty yellow, and both the throat and venter are heavily spotted with dark gray to black. Three very young males (snout-vent lengths 47 mm and less) have the female pattern, but this is quickly lost in *trujilloensis*, since two young males with snout-vent lengths of only 42 and 48 mm already show the adult male throat and head pattern, and the reduction of the young male belly dotting.

Four specimens require separate comment; MCZ 75138 from San Cristóbal, San Cristóbal Province, AMNH 7556 from San Pedro de Marcorís, San Pedro de Marcorís Province, and ASFS X8231-32, from the Río Cumayasa, 17 km W La Romana, La Romana Province. The first of these is a large adult male (73 mm) which theoretically should be assignable to the race *trujilloensis*. However, it is pale in color, and has the throat with only vague dusky smudges and no indication of a black face and chin. It may represent another subspecies of *L. personatus*, although I consider this unlikely since specimens from nearby (Sabana Grande de Palenque) are typical *trujilloensis*.

The lizard from San Pedro de Marcorís (a young male, snout-vent length 60 mm), and the two specimens from the Río Cumayasa (two males, snout-vent lengths 62 mm and 52 mm) are all much like the San Cristóbal specimen. Despite the fairly large size of the one male from the Cumayasa, it too lacks any extensive dark chin and face pigmentation. In life, these Cumayasa specimens were grayish-tan dorsally with distinct grayish-buffy dorsolateral lines, and had the sides dotted orange and green.

The throat of the adult has only a few very pale dusky smudges, whereas that of the smaller male has fairly conspicuous dusky markings.

These four specimens are all close to one another in throat pattern. I cannot reconcile them with the much more heavily marked and brightly colored males from the type locality. The status of these four specimens must await further material.

Little need be said concerning comparisons of the races *personatus* and *trujilloensis*. Males are easily distinguished in that the former has a black face and throat, with no indications of dusky throat spotting, whereas the face and throat in *trujilloensis* are dark brown, and the throat always has some indication of dusky smudging. In *personatus*, there is usually a dorsal zone set off by dorsolateral pale lines, whereas adult *trujilloensis* males lack dorsolateral lines. Females of the two races are not distinguishable.

The type localities of both *L. p. trujilloensis* and "*L. p. lunatus*" Cochran are Santo Domingo. Mertens (*loc. cit.*) had considered (and his material confirmed this assumption) that *trujilloensis* was the subspecies to the west of the Río Ozama and *lunatus* the race to the east of that river. Our data indicate that such is not the case; aside from the fact that present collections show the occurrence of *L. personatus* (but apparently not *trujilloensis*) to the east of the Ozama, we also have specimens of *lunatus* from the west of that river. As has been pointed out, I regard *personatus* and *lunatus* as distinct species. They are not easily confounded, and examples of *L. lunatus* are quickly separable from *L. personatus* where the two species occur together.

In Santo Domingo itself, *L. p. trujilloensis* occurs with some abundance in abandoned lots and even on lawns and along sidewalks. At Sabana Grande we took specimens in a coastal *Cocos* grove where the lizards were not particularly common. The specimens from the Río Cumayasa were taken on rocks near the bluff of the river valley. There is no information on the precise difference in habitat between *lunatus* and *personatus* in this region of overlap, although I have the impression that *L. lunatus* prefers more xeric habitats such as beaches.

Aside from the coastal localities, *L. p. trujilloensis* has been taken inland near Villa Altagracia, and Mertens (*loc. cit.*) mentioned a specimen taken at kilometer 37 on the road between Santo Domingo and La Vega; this individual also came from the vicinity of Villa Altagracia and doubtless is assignable to *trujilloensis*.

The closest approximation of *L. p. personatus* and *L. p. trujilloensis* is about 275 km airline (Villa Altagracia and Leogâne). However, there are specimens of *L. personatus* more or less from the intervening area which will be discussed later. Much of the region between these two localities is extremely arid (Llanos de Azua, Valle de Neiba, Cul de Sac Plain), and these dry regions are inhabited by two other species of *Leiocephalus* (*semilineatus* and *schreibersi*), as well as in part (marginally) by *L. barabonensis*. Probably the distribution of *L. personatus* in the east will be found to approach closely to the city of Bani, Azua Province; this town lies about on the borderline between the arid Llanos de Azua and the more mesic eastern coastal regions.

Specimens examined: República Dominicana, San Cristóbal Province. "on Santiago road, 30 miles (48 km) N Santo Domingo" (= vicinity of Villa Altagracia), 6 (AMNH 49886-91); 4.2 mi. (6.8 km) NE Sabana Grande de Palenque, 3 (ASFS X8138-40); *Distrito Nacional*, 5 km SW Madrigal, 2 (MCZ 58083-84); mouth of Río Jaina, 1 (UIMNH 44700 - paratype); Santo Domingo, 3 (MCZ 53919 - paratype of *L. p. lunatus*, MCZ 57984, MCZ 58082); Santo Domingo, 2.2 km SW Río Ozama, 1 (ASFS X7734); Santo Domingo, old airport, 12 (ASFS X9243-53, RT 703). *L. p. subsp.: San Cristóbal Province.* San Cristóbal, 1 (MCZ 75138); *San Pedro de Macorís Province.* San Pedro de Macorís, 1 (AMNH 7556); *La Romana Province.* Río Cumayasa, 17 km W La Romana, 2 (ASFS X8231-32).

Leiocephalus personatus mentalis

Cochran, 1932

Leiocephalus personatus mentalis Cochran

1932, Proc. Biol. Soc. Washington, 45:178.

Type locality: Jovero, El Seibo Province,

República Dominicana.

Holotype: USNM 65772, an adult male with

a snout-vent length of 64 mm (*vide* Cochran, 1941:228).

Diagnosis: A subspecies of *L. personatus* characterized in males by a combination of bright yellow and completely immaculate throat, mental scale dark brown, dark brown face mask extremely bold and prominent against brown to tan dorsal and head coloration (Fig. 4b), dorsolateral lines tan and fairly prominent to absent depending on the shade of dorsal coloration, no nuchal or scapular transverse bars but median crest scales tipped with dark brown to black on the neck and shoulders giving a median series of dark dots; size small (males to 72 mm, females to 58 mm snout-vent length), low number of loreals (4.0), median head shields modally 5, frontoparietals modally 5.

Distribution: República Dominicana, from the type locality eastward to Juanillo (Fig. 3) south of Cabo Engaño (see, however, the discussion of the following subspecies).

Variation and discussion: The series of 36 *L. p. mentalis* has the following scale counts: dorsal crest scales occiput-vent 44-54 (mean 50.0), dorsal crest scales occiput-axilla 14-22 (mean 17.9), dorsal crest scales on trunk 22-37 (mean 32.7), one half midbody scales 19-26 (mean 22.2), subdigital fourth toe tricarinate scales 21-27 (mean 24.0), loreals 2-8 (mean 4.0), temporals 8-12 (mean 9.9), supraoculars 6/6 (32 specimens), 5/6 (5), 6/7 (5), 7/7 (2), 7/8 (1), 10/11 (1), semicircles usually complete (69.6 percent), and parietals almost always in contact (95.6 percent). The prefrontal row consists of 2 to 4 (mode 3) scales, the median head shields vary between 4 and 6 (mode 4) scales, and the frontoparietal row has 3 to 6 scales (mode 5); the prefrontal row is almost always complete (45 of 47 specimens) and the frontoparietal row is usually complete (38 of 46 specimens). The largest male has a snout-vent length of 76 mm, the largest female 58 mm; the male is from "Península de Samaná" and the female is a topotype.

L. personatus is presently represented by fairly adequate material from the northern portion of the República Dominicana, from Juanillo in the extreme east to Monte Cristi in the northwest. Cochran (1941:231) as-

signed specimens from Jovero and Guarabo on the east to Puerto Plata and Sosúa in the north to *mentalis*. In actuality, the specimens from the extreme eastern portion of this area are quite distinct from lizards to the north and west—one of the major differences being the smudged throats of the more northern lizards. I have seen four male topotypes of *mentalis*, and of them only one, a large adult with a snout-vent maculate throat, a character which I consider diagnostic of *mentalis*. Three have a distinct dark brown mask, and this feature is obsolete in the fourth. The dorsa are in general pale at present. I consider the population at Jovero to be somewhat intermediate between *mentalis* and the race next to the west, but the available material indicates that the topotypical population is closer to the lizards to the east than to the west. Accordingly, I employ the name *mentalis* for the more eastern lizards.

Two males from El Macao were described in life as follows. The dorsal ground color is light brown to tan with tan dorsolateral lines. The sides are tan with scattered brick scales. The mask is dark brown and extremely prominent and sharp-edged, bordered below by a bright yellow supralabial line. The head scales are brown with some scattered dark brown punctations, and some of the median crest scales on the neck and shoulders are dark brown, giving a median dorsal row of dark dots. The throats are immaculate bright yellow. The ventral ground color is pale yellow and there are brick lines extending onto the venter along its posterior sides. The sides of the tail are brown with some brick scales, and the underside of the tail is tan and creamy, not orange. The tail is brown above and lacks chevrons. The hindlimbs are dull brownish-green above.

The females from El Macao are tan to brown dorsally with prominent pale buffy dorsolateral lines. The lateral lines between the limbs are dull buffy and not especially prominent. The median zone has a series of about six complete or incomplete chevrons anterior to the hindlimbs. The ventral ground color is white, with heavy black throat spotting and dark gray belly dotting.

The above descriptions agree in pattern length of 70 mm, has a completely im-

details with specimens from Juanillo, although females from that locality have the throat spots somewhat more reduced than more northern specimens. Males from Juanillo have the head scales irregularly suffused with very dark brown and tan, giving a peculiarly frosted appearance; the same condition occurs in males from El Macao, but not to so conspicuous a degree. Young males from all localities as usual resemble females in having darkly spotted throats and venters.

L. p. mentalis surely is one of the most easily recognized subspecies of *L. personatus*. It stands directly opposed to *L. p. personatus* in throat coloration, the latter having a solid black throat, and *mentalis* having a completely immaculate yellow throat. Although the throat of *trujilloensis* is not so extensively dark as that of *personatus*, the dark throat of the former also distinguishes it from *mentalis*. The yellow throat of *mentalis* and the yellow supralabial line make the dark brown mask in this subspecies very bold and distinct in comparison to the almost obliterated masks of *personatus* and *trujilloensis*. The brown-tipped mental scale in *mentalis* is likewise diagnostic; this brown pigment is placed in bold contrast to the otherwise yellow throat. The pale yellow ventral coloration of *mentalis* contrasts with the shades of green of the venters of *personatus* and *trujilloensis*, *mentalis* being the only subspecies of *L. personatus* with a yellow belly.

L. p. mentalis occurs in more or less coastal localities in extreme northeastern Hispaniola (but see the discussion of the following subspecies). Although I have visited Jovero on several occasions I have never seen the lizard there. Our single series was obtained in a sandy coconut grove immediately adjacent to the beach near El Macao. The lizards were extremely abundant at this locality, but were not in evidence until about 1430 hours, after the heat of the day was past. They became increasingly evident as the afternoon cooled.

Specimens examined: República Dominicana, El Seibo Province, Jovero, 10 (USNM 65770-71, 65775-79, 66708-09, 66712,—paratypes); Guarabo, 2 (USNM 66710-11—paratypes); La Romana Province, 0.9 mi. (1.4 km) SE El Macao, 20 (ASFS V887-

906); Juanillo, 14 (MCZ 75124-37); *Samaná Province, "Península de Samaná" (not mapped), 1 (USNM 66764—paratype); "Samaná and Laguna" (not mapped), 1 (USNM 65774—paratype); see discussion of following subspecies for comments on these two specimens. (USNM 65774—paratype); see discussion of following subspecies for comments on these two specimens).*

Leiocephalus personatus tarachodes,
new subspecies

Holotype: MCZ, 81087, an adult male, from 6 km SE Nagua, María Trinidad Sánchez Province, República Dominicana, one of a series collected 26 October 1963 by Albert Schwartz and Richard Thomas. Original number V1804.

Paratypes: ASFS V1802-03, V1805-06, V1813-16, UIMNH 61616-19, UF 21325-27, CM 40564-65, RT 837-38, same data as holotype.

Associated specimens: República Dominicana, Samaná Province, Samaná, 4 (AMNH 63105-08); Chico Puerto Francés (not mapped), 1 (AMNH 42314); El Seibo Province, Sabana de la Mar, 52 (MCZ 57139-43, 58052-58, 58060-63, SMF 26033-47, 26288, AMNH 50047, 50049-56, 50060-61, 50063-67, 50125); 0.5 mi. (0.8 km) S Sabana de la Mar, 2 (MCZ 57144, AMNH 41988); 15 km S Sabana de la Mar, 1 (MCZ 58064); Hato Mayor, 2 (AMNH 49804-05).

Diagnosis: A subspecies of *L. personatus* characterized in males by a combination of green or gray throat with two rather bold transverse lines composed of black smudges at the level of the fourth and sixth chin shields (Fig. 5c), bright green ventral color, mask present but not especially conspicuous because of dark brown head coloration, bordered below by two or three bright yellow to cream subocular and temporal spots, dorsal ground color tan with transverse nuchal and scapular bars rarely present and usually reduced to a series of black median dots on the dorsal crest scales; size moderate (males to 75 mm, females to 63 mm snout-vent length), low number of loreals (3.8), median head shields modally 4, frontoparietals modally 4, and supraorbital semicircles more often incomplete (63.2 percent) than complete.

Distribution: República Dominicana, from the vicinity of Nagua southeastward to Sabana de la Mar and Hato Mayor, west to near Moca and Salcedo, and presumed to include the Peninsula de Samaná (but see discussion) (Fig. 3).

Description of holotype: An adult male with the following measurements and counts: snout-vent length 75 mm, tail broken; dorsal crest scales occiput-vent 48, dorsal crest scales occiput-axilla 21, dorsal crest scales on trunk 27, one half midbody scales 22, subdigital fourth toe tricarinate scales 21-22, loreals 4, temporals 11, enlarged auriculars 4-5; 3 prefrontal scales, row complete; 4 median head shields; 5 frontoparietal scales, row complete; 5/5 supraocular scales; supraorbital semicircles incomplete; parietal scales in contact.

Dorsal ground color tan, each scale with a golden fleck; dorsolateral pale longitudinal lines absent; sides tan with some brick scales admixed. Mask dark brown, involving the loreal and temporal regions, not especially conspicuous because of brown dorsal cephalic coloration; three yellow spots below mask, two on supralabials and one on temporals. Three transverse nuchal and scapular bars indicated but not prominent. Top of head brown with a series of dark brown dots outlining the median curve of the supraoculars and a single spot on the snout; a series of pale dots more medial to the dark dots outlining the supraoculars, thus giving a double series of dark and light dots in this region. Upper surface of hindlimbs green, of forelimbs tan. Throat green, chin yellowish, with two transverse black bars across the throat at the levels of the fourth and sixth chin shields, followed by a series of both pale (yellow-green) and dark scales rather randomly smudging the balance of the throat. Ventral ground color bright green. Tail brown above, rather indistinctly chevronate basally and more prominently distally.

Variation: The series of 58 specimens of *L. p. tarachodes* has the following scale counts: dorsal crest scales occiput-vent 44-57 (mean 49.8), dorsal crest scales occiput-axilla 14-23 (mean 17.9), dorsal crest scales on trunk 23-38 (mean 31.2), one half midbody scales 18-24 (mean 20.9), subdigital fourth toe tricarinate scales 18-25 (mean 20.8), loreals 2-6 (mean

3.9), temporals 8-14 (mean 9.8), supraoculars 6-6 (36 specimens), 4-5 (1), 4-6 (1), 5-5 (18), 5-6 (19), 6-7 (1), semicircles more often incomplete (63.2 percent), and parietals usually in contact (98.7 percent). The prefrontal row consists of either 3 or 4 scales (mode 3), the median head shields vary between 4 and 6 (mode 4), and the frontoparietal row has 2 to 5 scales (mode 4); the prefrontal row is almost always complete (76 of 77 specimens) and the frontoparietal row is more often complete than not (65 of 78 specimens). The largest males have snout-vent lengths of 75 mm and are topotypes, and the largest female measures 63 mm and is from Sabana de la Mar.

The series of topoparatypes was described in life as follows. Males have the dorsal ground color tan, at times flecked with golden (the type is in this latter condition). The pale dorsolateral lines may be either present or absent, the latter situation being typical of fully adult individuals. The sides are usually tan with brick and green scales admixed, but at times there is no green (even in large adults like the type) and very little brick. The mask is dark brown and has two or three cream to yellow spots along its lower border. The ventral ground color is always bright green, and the throats are green to gray, the brighter color in full adults. There are usually one or two transverse bands across the throat, at the levels of the fourth and sixth chin shields, but in some (not necessarily small) males these may be somewhat reduced (UF 21326, SMF 26033) or even almost completely absent (ASFS V1803, SMF 26036). In a male from Sabana de la Mar (MCZ 58063) the chin is heavily dotted with dark brown and only the anteriormost band is indicated, with additional heavy pigment anterior to it. There may be a few bright yellow scales on the lower jaw near the angle of the mouth.

Females are dark brown dorsally, with tan dorsolateral lines more or less distinct. Many larger females lack any obvious chevronate pattern and the dorsal zone may be flecked with tan. Other females show about eight dorsal chevrons before the hindlimbs. The ventral ground color is pale green as are also the throats, and there is exception-

ally heavy black throat dotting, the dots at times coalescing into short bars or dashes. The venters are dotted with dark gray, often to the ventral midline.

Juvenile males resemble females in dorsal and ventral patterns, but have the belly spotting somewhat less obvious than do young females.

Comparisons: Male *L. p. tarachodes* may be differentiated from *mentalis* in having a green (instead of yellow) throat and venter, in having a patterned (rather than immaculate) throat, and in having a less conspicuous mask and dark mental scale. From both *personatus* and *trujilloensis*, *tarachodes* differs in having the throat less heavily pigmented, and in having the throat crossed by two bars rather than being more or less solidly dark. *L. p. tarachodes* reaches a slightly larger size than *mentalis* and is slightly smaller than *personatus*. The modal head scalation formula (prefrontals-median shields-frontoparietals) in *tarachodes* is 3-4-4; the formulae for the other three races are 3-5-4 (*personatus*) and 3-4-5 (*trujilloensis* and *mentalis*). An interesting similarity between *tarachodes* and *trujilloensis* is that both have high frequencies of 5/5 supraoculars, although this category is relatively more frequent in *trujilloensis* than in *tarachodes*. It occurs but rarely in *personatus* and *mentalis*. *L. p. tarachodes* is the only subspecies of *L. personatus* which has the supraorbital semicircles more often incomplete.

Remarks: The precise situation on the Península de Samaná as far as the races *tarachodes* and *mentalis* are concerned is unknown. There are only seven specimens available from the Samaná; of these, four are adult males and easily distinguishable as to subspecies. Two of the males (AMNH 63105-06), although much desiccated and discolored, clearly show the throat smudging of *tarachodes*. The other two males (USNM 65774 and USNM 66764—both paratypes of *mentalis*) are just as clearly *mentalis*. It is possible that *mentalis* occurs on the Samaná, but such a possibility seems remote, especially since the base of the Samaná is bracketed by *tarachodes* (Nagua and Sabana de la Mar). The Samaná *mentalis* may have been fortuitously introduced near the tip of the Samaná, or *mentalis* may have reached

that peninsula from the mainland across the Bahía de Samaná. Probably the most likely explanation is that these two lizards were originally mislabeled as to locality. Both were collected by W. L. Abbott on his last trip to the República Dominicana in 1923; one specimen has no date other than the year and the other specimen was collected in March. Abbott made two trips to the República Dominicana in 1923 (Wetmore and Swales, 1931:30-31); on the earlier trip (February and March) he collected south of the Bahía de Samaná at Jovero (where he took the holotype of *mentalis*), El Liar and Las Cañitas. In early March he crossed to the city of Samaná and later collected at Sánchez at the base of the peninsula. On his second 1923 visit (November and December) Abbott collected twice at Sánchez and Samaná, and spent the balance of the time on the south side of the Bahía de Samaná. Conceivably the two "Samaná" specimens of *mentalis* originated south of the Bahía de Samaná during one of Abbott's visits to that area, and did not come from the Peninsula. Additional material from the Samaná should confirm the presence or absence of *mentalis* on the peninsula.

The range of *L. p. tarachodes* embraces much of the very mesic northeastern portion of the República Dominicana. To the east, *tarachodes* approaches *mentalis* closely (Hato Mayor and Jovero), and, as has already been pointed out, specimens from Jovero (the type locality of *mentalis*) show some genetic influence of *tarachodes*. Apparently the Cordillera Oriental does not act as a barrier for *tarachodes*, since the two specimens from Hato Mayor are from the south side of that mountain range. These two specimens are both juveniles and in rather bad condition; possibly they are in actuality related to the southern coastal form discussed under *L. p. trujilloensis*.

In the west, *L. p. tarachodes* intergrades with *L. p. scalaris*. A series of eight lizards from Moca, Espaillat Province (SMF 25955, 26118-23, 26318) and a single female from 3 km NW Salcedo, Salcedo Province (ASFS V2941), are clearly *tarachodes* in coloration and pattern. Of the nine specimens, four have the supraorbital semicircles incomplete. The high dorsal crest scale counts of 50 to 61 are closer to the crest counts for

scularis (44-63) than *tarachodes* (44-57). I consider these lizards as being intermediate between *tarachodes* and *scularis*, but much closer to the former.

Much of the range of *L. p. tarachodes* lies within that region of the República Dominicana which has the heaviest rainfall (mean annual precipitation of 2000 mm to 2500 mm or above) in the republic. The rather sharp break in precipitation (and a concomitant change in vegetation) in the region between San Francisco de Macoris and Santiago corresponds in general to the dividing line between the subspecies *tarachodes* and *scularis*.

The type series from near Nagua was taken along beach dunes and among sea-edge driftwood. Very few lizards were seen in an immediately adjacent and sandy *Cocos* grove, although they were extremely abundant along the beach itself. The series from Moca was taken (Mertens, *op. cit.*:50) in pineapple fields, where the lizards were numerous.

Leiocephalus personatus actites,
new subspecies

Holotype: MCZ 81088, an adult male, from Sosúa, Puerto Plata Province, República Dominicana, one of a series collected 15 October 1963 by Albert Schwartz and Richard Thomas. Original number V1636.

Paratypes: ASFS V1633-35, V1637, V1646-48, UF 21338-42, UIMNH 61637-40, KU 93333-36, RT 829-30, same data as type; MCZ 13679-91, same locality as type, J. L. Peters, 1916; MCZ 43671-75, same locality as type, W. J. Clench, 1937; MCZ 5443 (2 specimens), Puerto Plata, Puerto Plata Province, República Dominicana, M. A. Frazar, no date; AMNH 40364-66, Puerto Plata, Puerto Plata Province, República Dominicana, 27 September 1929, W. G. Hassler; AMNH 44846-51, Puerto Plata, Puerto Plata Province, República Dominicana, 1 August 1922, G. K. Noble; ASFS V1671, 10 km NW Sabaneta de Yásica, Puerto Plata Province, República Dominicana, 16 October 1963, R. Thomas; USNM 156731-37, USNM 156750, 9 km N Villa Isabela, Puerto Plata Province, República Dominicana, 14 September 1963, A. Schwartz, R. Thomas.

Diagnosis: A subspecies of *L. personatus*

characterized in males by a combination of pale green throat with usually a pair of transverse black lines at the level of the second and third chin shields (Fig. 5d), pale greenish ventral color, mask present but somewhat faded in older adults with a pair of vertical broad subocular creamy to yellow-orange bars which may in turn be partly or wholly confluent with a horizontal pale temporal bar and its postauricular mate, dorsal ground color from grayish-tan and sandy to practically black, dorsolateral longitudinal lines fairly prominent and bordered medially by a broad ill-defined darker area of the dorsal zone, nuchal and scapular transverse bars absent in adults and only at times indicated by a series of darker (dull brown, rather than dark brown or black) median crest scales; size very large (males to 86 mm, females to 61 mm snout-vent length), moderate number of loreals (4.3), median head shields modally 4, frontoparietals modally 4, and supraorbital semicircles more often complete (58.9 percent).

Distribution: The northern coast of the República Dominicana in Puerto Plata Province, from near Villa Isabela in the west to near Sabaneta de Yásica in the east (Fig. 3).

Description of holotype: An adult male with the following measurements and counts: snout-vent length 76 mm, tail 79 mm, distal half regenerated; dorsal crest scales occiput-vent 48, dorsal crest scales occiput-axilla 17, dorsal crest scales on trunk 31, one half midbody scales 22, subdigital fourth toe tricarinate scales 22/22, loreals 5, temporals 9, enlarged auriculars 3/3; 3 prefrontal scales, row complete; 5 median head shields; 4 frontoparietal scales, row complete; 6/6 supraoculars; supraorbital semicircles complete; parietal scales in contact.

Ground color of dorsal zone tan, somewhat darker laterally, leaving a middorsal longitudinal paler band, the whole back with creamy flecks; dorsolateral longitudinal lines pale sandy and fairly conspicuous; about five darker brown dots on the crest scales in the nuchal and scapular regions; sides deep reddish-orange with some green scales admixed; lateral line between limbs whitish, conspicuous. Top of head brown,

suffused with darker brown and some paler brown, and with a cream line from the canthus over the outer margin of the supraoculars onto the upper temporal region; mask fairly conspicuous, outlined below by a pair of creamy vertical subocular bars and a more diffuse creamy lower temporal region. Upper surface of hindlimbs green, heavily flecked with yellow green; upper surface of forelimbs tan. Throat pale greenish with a prominent transverse bar at the level of the first chin shield and a second bar indicated at the level of the third and fourth chin shield, the latter bar fragmented; remainder of throat with diffuse and scattered dusky smudges. Ventral ground color greenish. Tail brown above with no chevrons.

Variation: The series of 42 specimens of *L. p. actites* has the following scale counts: dorsal crest scales occiput-vent 43-58 (mean 50.3), dorsal crest scale occiput-axilla 16-21 (mean 18.7), dorsal crest scales on trunk 23-39 (mean 31.4), one half midbody scales 21-26 (mean 22.6), subdigital fourth toe tricarinate scales 19-25 (mean 22.3), loreals 3-7 (mean 4.3), temporals 8-11 (mean 9.2), supraoculars 6-6 (44 specimens), 5/6 (4), 6/7 (1), semicircles more often complete (58.9 percent), and parietals always in contact (100 percent). The prefrontal row consists of either 3 or 4 scales (mode 3), the median head shields vary between 3 and 6 (mode 4), and the frontoparietal row has 2 to 5 scales (mode 4); the prefrontal row is always complete (56 specimens) and the frontoparietal row is more often complete (50 of 56 specimens). The largest male has a snout-vent length of 86 mm, the largest female 61 mm; both specimens are topotypes.

The series of living *L. p. actites* from Sosúa and Villa Isabela were described as follows. Males have the dorsal ground color brown, sandy, grayish-tan or even black, overlaid with creamy flecks. The dorso-lateral lines are buffy and usually readily discernible, especially because of a darker dusky suffusion along their median edges. Adult males lack nuchal and scapular transverse bars and may have dark dots on the anterior crest in this region, but the dots are usually not prominent and may be absent completely. The sides are grayish-

tan to sandy with some brick and creamy flecking and without any green lateral dotting; old adults have no red or cream on the sides, which are colored entirely of dusty tans and browns. The mask is variable in extent, and may be bold and prominent and outlined below by the vertical yellow-orange to cream subocular bars, a horizontal bar and a postauricular bar of the same color, or it may be hollowed centrally (Villa Isabela), forming a black-edged tan rectangle. The head is brown, suffused both with paler and darker browns, and there is often a cream canthal-supraocular-temporal line which borders the mask above and renders it more prominent. The ventral ground color is green, usually pale or grayish-green, and the throat is the same shade; there is no yellow on the chin or throat. There are usually two transverse throat bars at the level of the second and third or fourth chin shields. These bars are somewhat variable, but the first is almost always present and the second at least indicated. At times (ASFS V1634) the throat appears to be almost immaculate except for some vague lateral dusky smudges at the level of the second transverse bar. The hindlimbs are dull green with much yellow-green or paler green flecking.

Females are tan to brownish dorsally with usually about four complete and broad chevrons anterior to the hindlimbs; the remainder of the chevrons (alternating between the dark and prominent ones) are suppressed and indistinct. The buffy dorso-lateral and lateral lines are bold and prominent. The sides are often dark brown and strongly contrasting with the pale lines both above and below, and are marked with short diagonal darker brown dashes. The ventral ground color is pale green to opalescent, and the throats are whitish-green. The throats are heavily dotted with black to dark gray, and the anterior dots often are aligned to form the two transverse bars which are characteristic of the males. The venter is dotted with dark gray laterally, but is usually more or less clear centrally.

Juvenile males resemble females in coloration and pattern, and have the same reduction of dorsal chevrons which characterizes females.

Comparisons: *L. p. actites* can be dif-

terrenated from *L. p. mentalis* by having a green rather than yellow venter and having the mask less prominent. From *personatus* and *trujilloensis*, *actites* differs in lacking a black or heavily patterned throat and face. Both geographically and in characteristics, *actites* is closest to *tarachodes*; these two subspecies form part of a complex of three similar races from northern Hispaniola. *L. p. actites* differs from *tarachodes* in the position of the transverse throat bars (on the first and third or fourth chin shields in *actites*, on the fourth and sixth in *tarachodes*), and in having these bars much more bold in *tarachodes* than in *actites*. The lack of green on the sides of *actites* and the creamy (versus golden) dorsal flecks are additional chromatic features which distinguish the two races. In size, *actites* is larger than all other subspecies of *L. personatus*.

In having a head scalation formula of 3-4-4, *actites* is like *tarachodes*, but differs from the other subspecies which have formulae of 3-5-4 and 3-4-5. The high incidence of incomplete semicircles in *tarachodes* differentiates that race from *actites* which has the semicircles more often complete. *Tarachodes* has a high frequency of 5/5 supraoculars (as does also *trujilloensis*); this category has not been observed in *actites*.

Remarks: The distribution of *L. p. actites* as currently known is restricted to the coastline of a single province in northern República Dominicana; the distance between the known extreme localities of *actites* is about 80 kilometers. Between the easternmost locality for *actites* (Sabaneta de Yásica) and the westernmost record for *tarachodes* (Nagua) is about 65 kilometers. Although Thomas, Buden, and I have collected several times in the intervening area, we have not encountered *Leiocephalus* in this intermediate region.

The range of *L. p. actites* is separated from the race to the south by the Cordillera Septentrional which lies between the north coast and the Valle de Cibao. *L. personatus* is not known from this mountain range which reaches a maximum elevation of 1249 meters (Pico Diego de Ocampo) between Santiago and Puerto Plata.

The specimens from Villa Isabela were collected on a low rocky bluff immediately

adjacent to extensive mangrove flats, whereas those from Sosúa were taken along an open beach and about deserted bath houses where the lizards were exceptionally abundant. Here they sought sanctuary from the heat in copses of *Coccoloba* and in the shade of sandy overhangs at the rear of the beach. The specimen from near Sabaneta de Yásica was collected along the roadside in *Psidium* scrub.

Leiocephalus personatus scalaris

Cochran, 1932

Leiocephalus personatus scalaris Cochran, 1932, Proc. Biol. Soc. Washington, 45: 181.

Leiocephalus personatus pulcherrimus Mertens, 1939, Abh. Senckenberg. Naturf. Ges., 449:50 (type locality—2 km S Monción, 450 meters, Santiago Rodríguez Province, República Dominicana; holotype-SMF 25757, an adult male with a snout-vent length of 56 mm, *vide* Mertens, *op. cit.*: 51).

Type locality: Cap-Haïtien, Dépt. du Nord, Haiti.

Holotype: USNM 74054, an adult male with a snout-vent length of 75 mm (*vide* Cochran, 1941:226).

Diagnosis: A subspecies of *L. personatus* characterized in males by a combination of green to yellow-green venter and throat, the latter almost immaculate or with only a few dusky smudges usually not aligned into any discernible transverse bars, dorsal ground color varying from tan to dark brown, often flecked or mottled with yellow, cream or brick even in small individuals, dorsolateral line faint in adults, mask prominent and outlined above by an orange canthal-supraocular-temporal line and below by two or three orange vertical subocular bars, which at times are continuous with an orange bar across the lower temporal region, nuchal and scapular bars faint or usually absent, their positions indicated by dark brown crest scale dots; size large (males to 82 mm, females to 63 mm snout-vent length), low number of loreals (3.9), median head shields modally 1, frontoparietals modally 5.

Distribution: From the vicinity of Cap-Haïtien on the north coast of Haiti, and St. Michel de l'Atalaye, eastward along the coast to Monte Cristi; thence inland in the

Valle de Cibao as far east as the vicinity of Santiago along the Dominico-Haitian border and as far south as Cerca-la-Source in Haiti and Bánica in the República Dominicana; Isla Monte Chico in the Siete Hermanos Islands and Isla Cabras off Monte Cristi (Fig. 3).

Variation and discussion: The series of 131 *L. p. scalaris* has the following scale counts: dorsal crest scales occiput-vent 44-63 (mean 53.3), dorsal crest scales occiput-axilla 14-24 (mean 19.6), dorsal crest scales on trunk 24-44 (mean 33.7), one half midbody scales 19-28 (mean 23.3), subdigital fourth toe tricarinate scales 18-26 (mean 22.1), loreals 2-7 (mean 3.9), temporals 7-13 (mean 9.8), supraoculars 6/6 (166 specimens), 5/5 (9), 5/6 (11), 6/7 (15), 7/7 (4), 8/8 (2), semi-circles usually complete (82.0 percent), and parietals almost always in contact (97.1 percent). The prefrontal row consists of 2 to 5 scales (mode 3), the median head shields vary between 2 and 7 (mode 4), and the frontoparietal row has 1 to 7 scales (mode 5); the prefrontal row is almost always complete (212 of 213 specimens) and the frontoparietal row is usually complete (172 of 204 specimens). The largest male measures 82 mm in snout-vent length, and the largest female 63 mm; both are from Ti Guinin near Cap-Haïtien.

I reluctantly consider *L. p. pulcherrimus* Mertens a junior synonym of *L. p. scalaris* Cochran. I have seen no live specimens from northern Haiti, but I have collected extensively in the Valle de Cibao region in the northern República Dominicana. This latter area is inhabited by "*pulcherrimus*"; although the type locality of *pulcherrimus* is in the lower northern foothills of the Cordillera Central, the thirteen topoparatypes I have examined are indistinguishable from Cibao specimens; additionally Mertens assigned a specimen from Cayo Pablito (= Isla Cabras) to *pulcherrimus*. This islet lies off the coast at Monte Cristi. The intervening mainland area between Monte Cristi and Monción is inhabited by lizards with the same style of coloration and pattern as the specimen from Monción. Specimens from localities in Santiago Rodríguez Province other than Monción (19 km SE Martín García, 3 km S Los Quemados)

are identical with specimens from the Cibao as well. It thus seems certain that all specimens from the Valle de Cibao are identical and belong to "*pulcherrimus*".

The long and well preserved series of near topotypic *L. p. scalaris* in the Museum of Comparative Zoology appears indistinguishable to me in pattern and residual coloration from "*pulcherrimus*." The scale counts of a series of 94 "*pulcherrimus*" and 38 *scalaris* are virtually identical (both in extremes and means) as well. The only difference between the two lots is the larger adult size in both sexes (although more pronounced in the males) in *scalaris*; male *scalaris* reach a maximum snout-vent length of 82 mm and females 63 mm, whereas male "*pulcherrimus*" reach only a snout-vent length of 74 mm and females 60 mm. The difference in size is rather striking when the two series are compared, but no other character will distinguish the two. I therefore consider *pulcherrimus* Mertens a synonym of *scalaris* Cochran.

Color and pattern notes on series from the Valle de Cibao show the following features. Males have the dorsal ground color varying from tan to dark brown, often flecked or mottled with yellow or brick even in subadult specimens. The creamy to sandy dorsolateral lines are faint in full adults but more prominent in subadults. In some adults the dorsal zone is darker laterally, thus effectively reinforcing the appearance of the dorsolateral lines. The sides are brick with admixed green to turquoise scales, and occasionally with some cream scales as well—resulting in a very handsome lizard. The heads are tan to brown with orange to yellow or cream markings including a pair of subocular vertical bars or spots, followed by, or confluent with, a similarly colored pale rectangle across the lower temporal region. There is often an orange to yellow canthal-supraocular-temporal line which intensifies the dark brown mask above, as the mask is delimited by the orange temporal rectangle below. The transverse nuchal and scapular bars are obscure or absent in adults, their places being marked by a series of dark brown dots on the dorsal crest scales. Specimens from Haiti tend to have a series of three nuchal and scapular bars still visible in full adults, but this is not exclusively diagnostic of the Haitian popula-

tions. The hindlimbs are dark green, flecked with yellow-green and the forelimbs are tan. The ventral coloration varies from green, especially the underside of the hindlimbs which is often blue-green, to a paler yellow-green. The throat is greenish, often with a yellow suffusion, and usually dusky without any clearly defined bars. There may also be some scattered dusky smudges, which are most prominent along the sides of the throat. The mental scale may be all or partly dark brown or black, or it may not be darkly pigmented at all. The sides of the tail are brick and the upper side of the tail is brown, rather weakly chevronate in full adults.

Females are tan to dark brown above with the dorsolateral lines buffy to cream and yellow and with four dark brown to black chevrons anterior to the hindlimbs. The lateral lines are white or yellow and very bold in most specimens, and the sides are tan to dark brown, usually showing darker brown longitudinal dashes within the fields. The venter is very pale greenish-white or opalescent and the throats are white to gray with heavy discrete black spots with some tendency to form transverse dark bars anteriorly behind the chin. The venter is marked with pale to dark gray dots or longitudinal dashes, usually most prominent laterally.

Juvenile males are indistinguishable from young females; at least in Dominican specimens the adult male dusky or faintly smudged throat appears in males with snout-vent lengths of only 45 mm.

L. p. scalaris is closest in characteristics to *L. p. actites* and *L. p. tarachodes*. From the races *personatus*, *trujilloensis* and *mentalis*, *scalaris* differs in having a green venter (rather than yellow in *mentalis*), and in lacking the extensive throat and head black pigmentation of *personatus* and *trujilloensis*. The mask is much more prominent in *mentalis* than it is in *scalaris*. From both *actites* and *tarachodes*, *scalaris* may be differentiated in lacking any clearly defined throat bars (although the throats of some *actites* resemble closely the throats of some *scalaris*), and in being larger than *tarachodes* and smaller than *actites*. The dorsal and ventral coloration of all three races is quite similar.

Scalewise, *scalaris* with a modal head scale formula of 3-4-5 differs from *tarachodes* and *actites*, both of which have formulae of 3-4-4, and resembles *trujilloensis* and *mentalis*, both of which have formulae of 3-4-5. The race *personatus* is distinct with a formula of 3-5-4. *Tarachodes* also differs from *scalaris* in having the semicircles more often incomplete than complete.

The distribution of *L. p. scalaris* encompasses in part the dry and hot north-central regions of Hispaniola, in the Valle de Cibao. In this region, specimens were taken in well shaded cactus woods, in *Opuntia* thickets, along the open hot shore of a mangrove lagoon, along the open borders of a sisal field, in xeric *Acacia* woods, and in shady *Euphorbia* woods near the coast. The subspecies is not restricted to such bleak habitats, however, and reaches an elevation of 800 meters. In more mesic situations, *scalaris* was encountered along a rocky roadcut in pine woods (Santiago de la Cruz), in a *cafetal* on the southern slopes of the Cordillera Septentrional (La Cruz de Guayacanes), along a rocky stream bordered by deciduous woods (Martín García), and in a roadside ditch adjacent to a grassy field (Loma de Cabrera). Mertens (*op. cit.*:51) collected the type series of *pulcherrimus* in open pine woods. From the above, it can be seen that in the República Dominicana, *scalaris* occupies a variety of habitats and occurs at moderate elevations. The specimens from Bánica may well have come from still higher, but rather less mesic, situations.

The Haitian range of *scalaris* seems to be the northern coast from Cap-Haïtien eastwards, and inland to St. Michel de l'Atalaye and Cerca-la-Source. Too few specimens are available from these more interior localities (three from Cerca-la-Source, one from St. Michel) to say with complete assurance that this region is inhabited by *scalaris*. What specimens are available (including three adult males) do indicate that at least the lizards in this region are related closely to (if not identical with) *scalaris*. The single specimen from Isla Monte Chico in the Siete Hermanos group is presently not distinguishable from *scalaris*. It is interesting that Richard Thomas visited the islets of Ratas, Torurú, and Muertos without finding *L. personatus* on any of them.

L. p. scalaris is separated from *actites* by the Cordillera Septentrional, and intergrades with *tarachodes* to the east of Santiago (see discussion under *L. p. tarachodes*). The relationships of *scalaris* with the race to the south in the Cordillera Central will be discussed below.

Specimens examined: Haiti, Dépt. du Nord, Cap-Haïtien, 8 (MCZ 46918-19-paratypes, 63251-52, 63253-56); Ti Guïnin, near Cap-Haïtien (not mapped), 74 (MCZ 66710-83); Citadelle Laferrière, 1 (MCZ 66809); Grande Rivière du Nord, 2 (MCZ 63250, 66784-808); Nacocol, 2 (USNM 72636-37); Forr Liberté, 6 (USNM 76764-69); Cerca-la-Source, 3 (USNM 76777-79); Dépt. de l'Artibonite, St. Michel de l'Atalaye, 1 (USNM 76651); República Dominicana, Monte Cristi Province, 4 km E Pepillo Salcedo, 4 (ASFS V1156, V1163-65); 5 km SE Pepillo Salcedo, 3 (ASFS V1454-55, V1461); 1 km SE Pepillo Salcedo, 1 (ASFS V1456); 10 km N Copey, 1 (ASFS V1161); Monte Cristi, 2 (MCZ 43823-24); 3 km NE Monte Cristi, 5 (ASFS V1270-74); 2 km SE Monte Cristi, 29 (ASFS V1182-202, V1260-65, RT 809-10); 4 km E Los Conucos, 1 (ASFS V1348); 3 km E Los Conucos, 7 (ASFS V1515-21); 9 km NW Villa Vásquez, 2 (ASFS V1226-27); 7 km N Guayubín, 2 (ASFS V1492-93); 5 km W Guayubín, 4 (ASFS V1509-10, ASFS V1607-08); Isla Monte Chico, Siete Hermanos, 1 (USNM 76714); Dajabón Province, 1 km S Loma de Cabrera, 900 feet (295 meters), 1 (ASFS V1468); 3 km E Santiago de la Cruz, 750 feet (246 meters), 3 (ASFS V1242-44); San Rafael Province, Bánica, 2 (MCZ 58066-67); 3 km E Bánica, 1 (MCZ 58065); Valverde Province, 7 km NW La Cruz de Guayacanes, 1 (ASFS V1236); 2 km N Esperanza, 9 (ASFS V1746-54); Santiago Rodríguez Province, 19 km SE Martín García, 600 feet (197 meters), 8 (ASFS V1245-52); 2 km S Monción, 450 meters, 1 (UIMNH 44699, SMF 25748-56, 25782-84—paratypes of *pulcherrimus*); 3 km S Los Quemados, 1 (ASFS V1767); Santiago Province, Santiago, 11 (MCZ 58039-43, 58045-50); 7 km W Santiago, 1 (ASFS V2928); Licey al Medio, 2 (MCZ 58321-22).

Leiocephalus personatus budeni,
new subspecies

Holotype: MCZ 81089, an adult male, from 12 km NE Jarabacoa, 2000 feet (656 meters), La Vega Province, República Dominicana, one of a series collected 27 November 1964 by Donald W. Buden and native collector. Original number V4223.

Paratypes: ASFS V4224-35, same data as holotype; CM 40566-69, same locality as holotype, 30 November 1964, native collector; USNM 156738-40, same locality as holotype, 30 November 1964, D. W. Buden, R. Thomas; UIMNH 61620-23, same locality as holotype, 2 December 1964, native collector; KU 93316-21, same locality as holotype, 3 November 1963, R. Thomas.

Associated specimens: República Dominicana, La Vega Province, La Vega, 1 (AMNH 40973); between Jarabacoa and La Vega (not mapped), 1 (SMF 25684).

Diagnosis: A subspecies of *L. personatus* characterized in males by a combination of grayish-brown dorsal zone with prominent buffy dorsolateral stripes and one transverse nuchal and one transverse scapular bar, sides darker gray-brown with no green or brick scales, lateral stripes faintly pinkish, venter white with a faint greenish tinge, throat greenish with prominent dark brownish-gray smudges and usually a transverse bar at the level of the second chin shield (Fig. 5e); size small (males to 66 mm, females to 52 mm in snout-vent length), low number of loreals (4.0), median head shields modally 4, frontoparietals modally 4, and supraorbital semicircles usually complete (59.4 percent).

Distribution: Known only from intermediate elevations on the north slopes of the Cordillera Central and presumably from La Vega, all in La Vega Province, República Dominicana (Fig. 3).

Description of holotype: An adult male with the following measurements and counts: snout-vent length 66 mm, tail 108 mm; dorsal crest scales occiput-vent 45, dorsal crest scales occiput-axilla 16, dorsal crest scales on trunk 29, one half midbody scales 21, subdigital fourth toe tricarinate scales 21 22, loreals 4, temporals 10, enlarged auriculars 3 4; 3 prefrontal scales, row complete; 5 median head shields; 3 frontoparietal scales, row incomplete; 6/6

supraocular scales, supraorbital semicircles incomplete; parietal scales in contact.

Dorsal ground color dark grayish-brown, dorsolateral stripes buffy and conspicuous; a single nuchal and a scapular transverse dark bar; sides darker grayish-brown, lateral stripe pinkish. Mask present, somewhat hollowed centrally, and bounded below by a loreal buffy rectangle, a pair of buffy subocular blotches and a buffy lower temporal stripe, but not bordered with pale above. Top of head brown with some darker brown suffusion. Upper surface of both fore- and hindlimbs brown. Throat and venter white with a greenish tinge; throat with rather conspicuous blackish-brown smudges as far as the chest, and a barely discernible transverse black bar at the level of the second chin shield. Tail reddish-brown above, distinctly chevronate for its entire length, and bright orange below.

Variation: The series of 23 *L. p. budeni* has the following scale counts: dorsal crest scales occiput-vent 45-59 (mean 49.9), dorsal scales occiput-axilla 16-23 (mean 18.9), dorsal crest scales on trunk 26-35 (mean 30.8), one half midbody scales 20-25 (mean 22.0), subdigital fourth toe tricarinate scales 18-24 (mean 20.7), loreals 3-5 (mean 4.0), temporals 8-12 (mean 10.5), supraoculars 6/6 (25 specimens), 5/5 (1), 5/4 (1), 6/5 (3), 6/7 (1), semicircles more often complete than incomplete (59.4 percent), and parietals always in contact (100 percent). The prefrontal row always consists of 3 scales, the median head shields vary between 4 and 7 (mode 4), and the frontoparietal row has 2 to 5 scales (mode 4); the prefrontal row is always complete (30 specimens) and the frontoparietal row is more often complete than not (22 of 31 specimens). There is only one more specimen with 4 median head shields than with 5. The largest male measures 66 mm and the largest female 52 mm in snout-vent length; both are topotypes.

The series of male paratypes resembles the holotype in coloration and pattern, except that in subadult males the dorsal pattern is even more contrasting, the buffy lines being especially conspicuous. The tails may be more pink than orange in some males and the throat may have a distinctly

greener tinge than the venter. There is never any green on the back or sides, and the sides likewise lack any red or brick pigments.

The females are gray-brown dorsally with prominent cream to buffy dorsolateral stripes and a series of four to seven transverse black bars before the hindlimbs, the lesser number resulting from the suppression of the alternating bands in larger specimens. In one female (ASFS V4229) the bars are reduced to a series of black points bordering the upper margins of the dorsolateral lines. The sides are dark brown (almost black) and the lateral stripes between the limbs are cream to yellowish. The venters are white in young females and with a greenish tinge in adults. The underside of the tail varies from yellow-orange to bright orange or pink. The throat is extremely mottled with black, and the venter is also heavily marked with black to dark gray dots and dashes.

Juvenile males resemble the adult females in coloration and pattern, but at times their throats (KU 93320) are even more densely spotted with black, almost forming a pale whitish reticulum in contrast to the thickly set spots.

Comparisons: *L. p. budeni* is distinctly different from its neighbor to the north, *L. p. scalaris*. These two races differ in depth of dorsal pigmentation, the one being very dark and the other considerably lighter. *Budeni* lacks the green hindlimbs and green venter of *scalaris*, and lacks both green and red in the lateral fields and on the dorsum. From all other subspecies, *budeni* differs in the very pale whitish-green venter, from *personatus* and *trujiilloensis* in extensive throat and head dark coloration, from *mentalis* in lacking a conspicuous dark brown mask and in being very much darker dorsally and not having a yellow venter, and from *tarachodes* in lacking transverse throat bands. *L. p. budeni* is the smallest of the races of *L. personatus*. In having 4 frontoparietals modally, *budeni* differs from *trujiilloensis*, *mentalis* and *scalaris*, all of which usually have 5. The extremely heavy ventral dotting of juvenile males and females helps in distinguishing these specimens from all other subspecies.

Although the median dorsal crest scales

of *L. p. budeni* are slightly attenuate and imbricate, in the available specimens of this race the scales are less attenuate than in all other subspecies. Perhaps none of the specimens is fully adult. However, in comparably sized males of other subspecies the scales already show the distinctly attenuate conformation. I can only assume that this particular character of *L. personatus* is not so well expressed in *budeni* as it is in other races.

Remarks: The single specimen from La Vega (AMNH 40973) I consider *L. p. budeni*; it is a female with a snout-vent length of 52 mm and thus is equal to the largest female of the subspecies. The very heavy throat spotting agrees well with the definition of *budeni*, and the dark dorsal color and prominent dorsolateral stripes likewise confirm this diagnosis.

Aside from the specimens from La Vega and between that city and Jarabacoa, all other material of *L. p. budeni* was taken about old buildings near the town of Buena Vista at an elevation of 2000 feet (656 meters). The lizards were not uncommon but were observed only on sunny days; since the region is extremely wet and rain is fairly regular as a daily occurrence, the lizards were rather difficult to secure except on particularly favorable and not rainy days. The general floral picture at the type locality is pine woods with ravines heavily wooded with deciduous trees. Mertens (*op. cit.*:49) reported taking a female "*L. p. mentalis*" (SMF 25684) from the pine-woods between Jarabacoa and La Vega.

L. p. budeni lies between the ranges of *L. p. scalaris* to the north and the very distinctive subspecies in the interior uplands of the Cordillera Central to the south. I imagine that *budeni* will be found to occur along the eastern flank of the Cordillera Central and also along the northern flank where the range does not abut directly upon the Valle de Cibao; in the latter situation, *L. p. scalaris* is the intermediate elevation race.

Leiocephalus personatus agraulus,
new subspecies

Holotype: MCZ 81090, an adult male, from 1 mi. WSW Constanza, 4000 feet (1311 meters), La Vega Province, República Dominicana, one of a series collected 4

July 1963 by native collector. Original number X8658.

Paratypes: AMNH 94245-52, MCZ 81091-95, same data as holotype; CM 40570-75, UF 21328-34, same locality as type, 2 July 1963, native collector; ASFS V8612-19, V8640-47, USNM 156741-46, UIMNH 61624-32, KU 93322-29, RT 681-82, same locality as holotype, 3 July 1963, native collector; MCZ 79261-62, Constanza, La Vega Province, República Dominicana, 31 December 1963, J. D. Lazell, Jr.; MCZ 57983, Tiroo, La Vega Province, República Dominicana, 23 July 1958, C. E. Ray and A. S. Rand.

Associated specimens: República Dominicana, San Juan Province, Río Arriba del Norte, 1950 feet (639 meters), 5 (ASFS V516-20); 7 km N Carpintero, 1 (MCZ 58068).

Diagnosis: A subspecies of *L. personatus* characterized in males by a combination of a tan to brown middorsal zone with dirty tan dorsolateral lines, a dark blackish-brown head with white supraorbital stripes, sides pea-green flecked with orange, venter and upper surfaces of hindlimbs bright pea-green, and throat immaculate but blackish and with some bright orange on the chin; size moderate (males to 74 mm, females to 60 mm snout-vent length), moderate number of loreals (4.5), median head shields modally 6, and supraorbital semicircles more often complete (88.7 percent).

Distribution: The interior uplands of the Cordillera Central in the Valle de Constanza and the Valle de Tiroo, and the southern slope of the Cordillera Central in the region north of San Juan, República Dominicana (Fig. 3).

Description of holotype: An adult male with the following measurements and counts: snout-vent length 70 mm, tail 98 mm; dorsal crest scales occiput-vent 50; dorsal crest scales occiput-axilla 17, dorsal crest scales on trunk 23, one half midbody scales 23, subdigital fourth toe tricarinate scales 21 21, loreals 5, temporals 11, enlarged auriculars 3 4; 3 prefrontal scales, row complete; 5 median head shields; 5 frontoparietal scales, row complete; 6 7 supraocular scales; supraorbital semicircles complete; parietal scales in contact.

Dorsal ground color tan, clearest medially

and much suffused with black laterally; dorsolateral lines dirty tan, beginning as white supraocular lines on the head and extending onto the base of the tail; sides bright pea-green, much flecked with orange; lateral line dirty tan and conspicuous. Dorsum with indications of about eight or nine transverse dark bars before the hindlimbs, of which the nuchal and scapular bars are the most obvious. Venter and throat bright pea-green as are also the upper surfaces of the hindlimbs; forelimbs tan above. Throat pea-green, much suffused with blackish anteriorly and chin bright orange. Tail brown above with prominent black to dark brown chevrons.

Variation: The series of 75 *L. p. agraulus* has the following scale counts: dorsal crest scales occiput-vent 41-55 (mean 46.7), dorsal crest scales occiput-axilla 13-21 (mean 15.7), dorsal crest scales on trunk 26-37 (mean 31.7), one half midbody scales 19-24 (mean 22.5), subdigital fourth toe tricarinate scales 18-25 (mean 21.7), loreals 2-8 (mean 4.5), supraoculars 6/6 (47 specimens), 5/5 (2), 5/6 (3), 6/7 (7), 7/7 (3), 6/8 (1), 11/9 (1), 9/9 (1), 6/9 (1), 11/10 (1), semicircles more often complete (88.7 percent), and parietals more often in contact (66.7 percent). The prefrontal row consists of 2 to 5 scales (mode 3), the median head shields vary between 3 and 9 (mode 6), and the frontoparietal row has 3 to 10 scales (mode 5); the prefrontal row is almost always complete (70 to 71 specimens) and the frontoparietal row is more often complete than not (57 of 66 specimens). The largest male has a snout-vent length of 74 mm and the largest female measures 60 mm; both are topoparatypes.

The males from Constanza are remarkably constant in coloration and pattern. The dorsal transverse bar remnants noted in the holotype are not a regular feature of adult males of that size, and usually all but one nuchal and one scapular bar disappear in full adults; even these two bars may be absent, either with or without their old position shown by slightly darker crest scales in this anterior region. The white supraorbital line and the green venter, orange chin and dusky suffused throat are all regular features in subadult and adult males.

The single male from Río Arriba del Norte basically agrees with the Constanza males but is somewhat lighter with a tan middorsal zone, the lateral portions of which are dotted with maroon. The sides are green, flecked with maroon, and are especially bright green above the hindlimbs. The hindlimbs are green, distinctly flecked with black and pale green. The mask, which is not especially prominent in Constanza males due to their dark coloration, is black and prominent in the Río Arriba specimen, and is set off by a longitudinal gray subocular stripe; this feature may be present but much less obvious in Constanza males. The venter is green, washed centrally with yellow-orange, and the green throat is overlaid with orange. Although in some details of coloration this male does not agree completely with the specimens from the type locality, it certainly is related to the material from the more interior highlands and I group it with them *pro tem*.

Females from Constanza are reddish-brown dorsally with the dorsolateral lines indistinct and primarily delimited by black pigment—the black bases of the four to seven dorsal crossbars and the black dashes in the lateral fields. The ventral ground color is opalescent greenish, the chin and throat whitish-green. The throat is heavily marked with black spots or smudges, and the venter with black dashes laterally; centrally the venter is almost patternless. There is a distinct tendency for the anterior throat spots to fuse behind the chin to give one or two ill-defined crossbars.

Only one subadult and one juvenile male (MCZ 79261-62) show any indication of the female throat pattern; the smaller of these (36 mm snout-vent) is like the females both above and below, whereas the larger individual (51 mm snout-vent) shows the loss of the throat spots. Other males of comparable size already have lost all traces of the female throat pattern.

The female (56 mm) from Río Arriba del Norte is brown with a darker dorsal pattern, buffy dorsolateral lines, sides yellowish-tan with black dashes and the ventral ground color is yellowish, heavily spotted on the throat (and venter, especially laterally) with black.

Two features of the scalation of *agraulus*

are of interest. This is the only subspecies of *L. personatus* which lacks parietal contact in so many specimens (23 of 69); the highest incidence of this character other than in *agraulus* occurs in *scalaris* (6 of 207). Of all specimens of *L. personatus* examined, only 55 lack parietal contact, and of these 35, 23 are *agraulus*. Secondly, the wide variation of number of supraoculars is striking. In *agraulus* there are ten categories of supraocular combinations, ranging from 5/5 to 11/10. No other subspecies is comparable, the closest being *personatus* with seven categories. No other subspecies has any supraocular counts so high as *agraulus* except *mentalis* with one individual having a count of 11/10, the next highest in *mentalis* being a more orthodox 7/8.

Comparisons: *L. p. agraulus*, by virtue of its dark dorsal coloration, green and orange sides, white supraorbital line, immaculate but dusky green throat and bright orange chin, is easily separable from all other subspecies. Two more different subspecies than the "adjacent" *agraulus* and *budeni* are difficult to imagine; the vivid green sides and venter, and orange chin of *agraulus* stand in direct contrast to the less colorful and more sombre tones of *budeni*. *L. p. agraulus* is the only subspecies which has a head scale formula of 3-6-5, since only *agraulus* has six median head shields as the modal condition. The diversity of number of supraoculars has already been commented upon, as has also the relatively high number of specimens with parietals not in contact.

Remarks: The distribution of *L. p. agraulus* is the interior highlands of the Cordillera Central and apparently the southern slopes of this massif as well. Three races of *L. personatus* are associated with the periphery of the Cordillera Central: *scalaris* in the northwest, *budeni* in the northeast and *agraulus* in the south. Of these three subspecies, *agraulus* is the only one restricted to the Cordillera itself. Although the closest localities for *budeni* and *agraulus* are separated by only about 30 kilometers airline and although we collected extensively within this intermediate area, no *Leiocephalus* were encountered. In fact, none of the specimens of *agraulus* from near Constanza was secured by us. Natives told us that the lizards had been collected

under rocks in a large open meadow, studded with a few pines, and partly under cultivation, in the Valle de Constanza. Since the weather at Constanza, even during the summer, is often very cool and usually rainy, to encounter these lizards abroad probably requires a warm and dry day—something which was seldom available during the two weeks we spent in the Constanza region. The small series from Rio Arriba del Norte was secured by Richard Thomas by turning rocks in a pasture; the day was overcast and wet.

There are five other specimens from the central República Dominicana which require comment. These are all from *San Juan Province*, and from the following localities: 17 km E Vallejuelo, 1500 feet (492 meters), 1 (ASFS V298); 15 km E Vallejuelo, 1600 feet (525 meters), 1 (ASFS V299); 10 km E Vallejuelo, 3 (ASFS V300-01, V391). This lot of lizards comes from the Sierra de Neiba, which is separated from the Cordillera Central in this region by the Valle de San Juan, a high but dry valley which appears not to be inhabited by *L. personatus*. Thus the Sierra de Neiba populations are not in genetic continuity (at least directly) with *agraulus* on the southern slopes of the Central. The series consists of one adult (65 mm) and one tiny juvenile male, and three females. The adult male resembles *agraulus* in general, but is much paler (dorsal zone tan), has yellowish dorso-lateral lines, has an orange chin and entirely green venter, with some rust on the sides which are *not* green. The hindlimbs are pea-green like those of *agraulus*. The throat is clear green and lacks the very conspicuous dusky wash of *agraulus*. When sufficient material from the Sierra de Neiba is available, I imagine that it will be found to differ from *agraulus* in several characters, although obviously derived from, or allied to, the more northern subspecies.

The Sierra de Neiba lizards lie approximately between the subspecies *personatus* in Haiti and *trujilloensis* in the south-central República Dominicana. However, they show no affinities with either of these two races but do break the extensive gap between the southern Haitian and Dominican segments of the species.

Specimens from St. Marc, Haiti

There are two other specimens of *L. personatus* which have not been mentioned. These are both from St. Marc, Dépt. de l'Artibonite, Haiti; one (AMNH 77569) is a young male with a snout-vent length of 48 mm and the other (MCZ 65455) is a female with a snout-vent length of 42 mm. Both were collected in 1928 and now are much faded. Both have a pale tan dorsal zone without any markings, a darker brown lateral band, prominent lateral stripes (but lack dorsolateral stripes). Both have the throats heavily blotched with black, and the female has some diffuse dark gray markings on the sides of the venter. In having a small preauricular and distinctly overlapping crest scales (although they are not especially attenuate nor would I expect them to be in so small a male) they are surely related to *L. personatus*. The geographically closest subspecies of *L. personatus* is *scalaris* to the northeast; the latter occurs at St. Michel de l'Atalaye, about 52 kilometers airline. The two localities are separated by the important Rivière de l'Artibonite and the Montagnes Noires (Monts Cahos), and St. Michel additionally lies on the relatively high Plateau Central at an elevation of 420 meters, whereas St. Marc is on the coast. It seems unlikely that the St. Marc specimens are *scalaris* (and they do not agree with that subspecies in pattern), and I merely assign them to the species *L. personatus* with the above comments.

Leiocephalus lunatus Cochran, 1934

Leiocephalus personatus lunatus Cochran, 1934, Occ. Papers Boston Soc. Nat. Hist., 8:153 (type locality—Santo Domingo, Distrito Nacional, República Dominicana).

Definition: A species of *Leiocephalus* characterized by a combination of 1) small size (males to 67 mm, females to 60 mm snout-vent length), 2) sexually dichromatic, males with black nuchal and shoulder patches usually at least indicated, and with a pair of enlarged postanal scales in males, 3) absence of a lateral fold, 4) dorsal scales imbricate, weakly denticulate, and keeled, ventral scales imbricate, smooth, and denticulate, 5) median dorsal crest scales enlarged, greatly attenuate and strongly over-

lapping (Fig. 2b and c), slightly lower than median dorsal caudal scales, 50 to 68 in occiput to vent distance, 6) one half midbody scales 19 to 27, 7) supraoculars usually 6-8, 8) loreals 2-8, 9) temporals 7-14, 10) supraorbital semicircles usually complete, 11) parietals always in contact, 12) median head scales varying between 3 and 10 (modally 4), 13) preauricular scale small (Fig. 2a), 14) throat in males with bold and discrete black spots on a white to pale gray ground, in females with faint gray dots, 15) ventral color pale yellowish to tan or lavender, 16) ventral pattern absent in both sexes, 17) mask absent, and 18) black neck and shoulder patches present.

Leiocephalus lunatus lunatus Cochran, 1934

Type locality: Santo Domingo, Distrito Nacional, República Dominicana.

Holotype: Field Museum of Natural History (= Chicago Natural History Museum) 166, an adult male with a snout-vent length of 64 mm (*vide* Cochran, 1941:233).

Diagnosis: A subspecies of *L. lunatus* characterized in males by a combination of tan to brown dorsal zone, often dotted with yellow, dorsolateral lines creamy and prominent, usually at least one nuchal and one scapular bar, lateral nuchal and scapular patches large, extensive and black (Fig. 7a), throat white to gray with large more or less uniformly sized black spots extending onto chest (Fig. 8a), ventral ground color variable from white and creamy to tan, extremely pale translucent green, or pale lavender on the sides of belly; size large (males to 67 mm, females to 55 mm snout-vent length), high number of loreals (4.7), median head shields modally 4.

Distribution: Southeastern shore of the República Dominicana from just west of Santo Domingo east across the Río Ozama to east of Boca Chica (Fig. 6).

Variation and discussion: The series of 28 *L. l. lunatus* has the following scale counts: dorsal crest scales occiput-vent 52-67 (mean 61.3), dorsal crest scale occiput-axilla 19-27 (mean 22.0), dorsal crest scales on trunk 33-45 (mean 39.0), one half midbody scales 21-27 (mean 24.2), subdigital fourth toe tricarinate scales 21-27 (mean 23.2), loreals 3-7 (mean 4.7), tem-

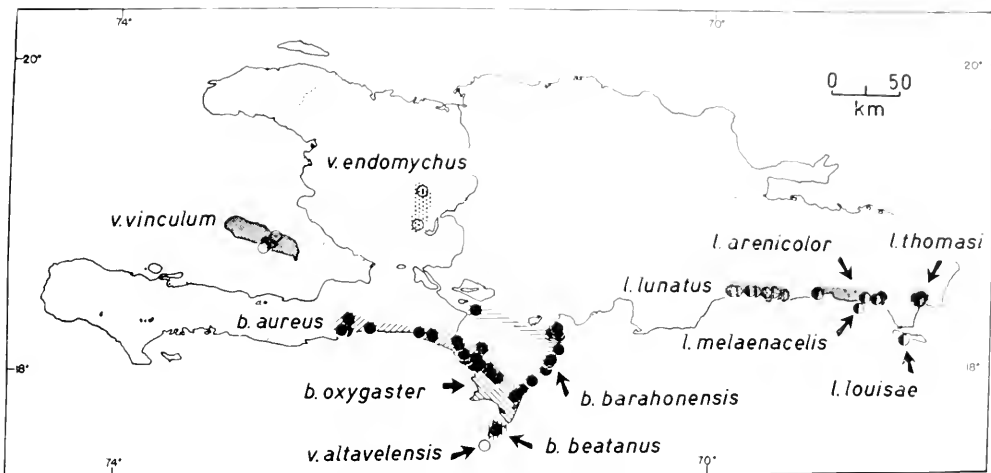


Figure 6. Hispaniola, showing the known distributions of three species of *Leiocephalus*, as follows: *L. lunatus* (semi-solid symbols); *lunatus*, fine vertical lines; *arenicolor*, fine diagonal lines, upper right to lower left; *thomasi*, fine diagonal lines, upper left to lower right; *L. barahonensis* (solid symbols); *barahonensis*, widely spaced horizontal lines; *oxygaster*, widely spaced diagonal lines, upper left to lower right; *aureus*, widely spaced diagonal lines, upper right to lower left; *beatanus*, widely spaced vertical lines. *L. vinculum* (hollow symbols): *vinculum*, light stippling; *endomychus*, dark stippling. Overlap of symbols in the region of Pedernales, República Dominicana, indicates area of intergradation between *oxygaster* and *aureus*.

porals 9-13 (mean 10.5), supraoculars 6-6 (19 specimens), 6-7 (4), 7-7 (3), semi-circles usually complete (78.6 percent), and parietals always in contact (100 percent). The prefrontal row consists of 2 or 3 scales (mode 3), the median head shields vary between 4 and 7 (mode 4), and the frontoparietal row has 3 to 5 scales (mode 5); the prefrontal row is always complete (27 specimens) and the frontoparietal row is more often complete (19 of 25 specimens). The largest male measures 67 mm in snout-vent length, the largest females 55 mm; all are from 8.6 miles east of Santo Domingo.

When Mertens (1939:46-47) described *L. p. trujilloensis*, he pointed out that, at least insofar as his specimens indicated, the "subspecies" *trujilloensis* and *lunatus* (both described from the city of Santo Domingo) were separated by the Río Ozama. This wide river courses through the capital city, and although there are various names for districts of the city both on the east and west banks, with propriety all can be called Santo Domingo. With the recent collection of *L. lunatus* on the west side of the river (and thus within the supposed range

of *trujilloensis*) and of a *trujilloensis* relative far to the east of the river within *lunatus* country, it is obvious that not only does the river not separate the two "subspecies" *trujilloensis* and *lunatus* but also that there are two distinct species involved, both of which occur on both sides of the river.

The series of specimens for which the data are presented above all originated on the east side of the river, and thus within orthodox *lunatus* territory. Males of this series are tan to brown with creamy and prominent dorsolateral lines. The head is brown and is not usually suffused with darker brown except rarely on the supraoculars. A nuchal and a scapular transverse bar are fairly common and some (not the largest) specimens have heavy dorsal yellow flecking. The sides are brightly colored; they vary from orange to brownish with green scales, and yellow and brick scales may also be admixed. The green scales often form vertical lateral bars which become yellow bars on the lower sides and lateral portions of the abdomen. The lateral line between the limbs is indistinct to absent. On the sides of the neck and shoulders above the forelimb insertion is a large jet black

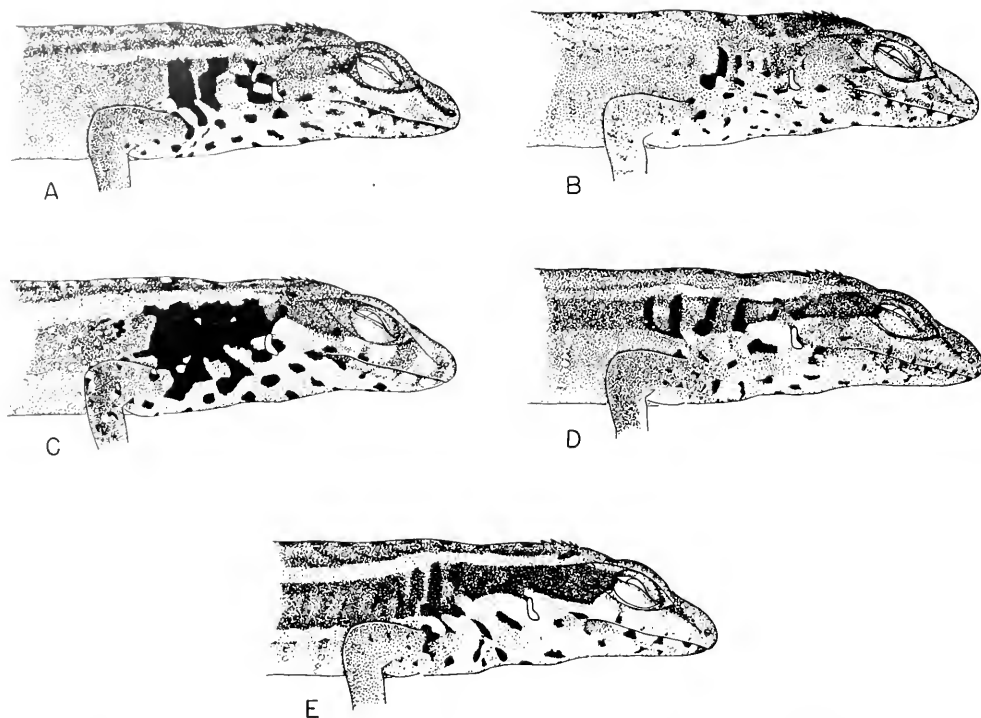


Figure 7. Lateral view of head and neck of five subspecies of *L. lunatus*, as follows: a) *L. l. lunatus*, ASFS V641, 0.9 km E Boca Chica, Distrito Nacional, República Dominicana; b) *L. l. arenicolor*, ASFS X8194, 0.5 mi. S San Pedro de Macoris, San Pedro de Macoris Province, República Dominicana; c) *L. l. melaenacelis*, MCZ 81096, holotype, western end, Isla Catalina, La Romana Province, República Dominicana; d) *L. l. thomasi*, MCZ 81097, holotype, 0.5 mi. NW Boca de Yuma, La Romana Province, República Dominicana; e) *L. l. louisae*, ASFS V3005, environs of Mano Juan, Isla Saona, República Dominicana.

patch, usually bi- or tripartite, but often complete and extensive. If any portion of the blotch is missing, it is the most anterior (nuchal) third. The blotch is never absent completely, and may be especially well delineated. The venter is regularly pale, varying from very pale green to pale tan, pale yellow, or even pale lavender, especially on the sides. The throat is white to pale gray, and is rather evenly covered by large black spots which usually extend onto the chest. These spots are bold, discrete, sharp-edged and all of about the same general diameter, so that there is an impression of rather uniform throat and chest spotting. These spots are comparable to, but certainly very distinct from, the dusky smudges which occur in the males of several races of *L. personatus*. The upper side of the hindlimbs may be pea-green, but usually they are tan. The tail is brownish-orange above,

vaguely chevronate proximately and more boldly marked distally; the underside of the tail is orange.

Females resemble males dorsally, with a sandy to brown dorsal zone bounded by buffy dorsolateral lines. The sides are tan, lack longitudinal dark dashes which occur in female *L. personatus*, and at times have some scattered creamy scales as well. There are about seven vague dorsal chevrons before the hindlimbs. The tails are tan to brown above and are chevronate. The venter is immaculate white to grayish. The throat is pale grayish with slightly darker gray dots.

The smallest males (snout-vent lengths of 47 mm) are already patterned like adult males with heavy black throat and chest spotting.

The three specimens from west of the Río Ozama (ASFS V2471-73) are two males (snout-vent lengths 65 and 61 mm)

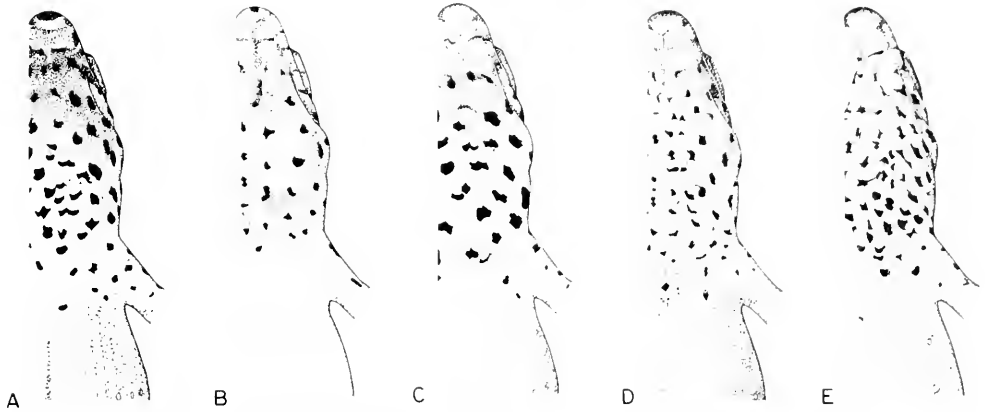


Figure 8. Ventral view of throats of males of five subspecies of *L. lunatus*; same specimens as Figure 7.

and a female (53 mm). They conform in size and scalation with the material from east of the river. The males do differ slightly, however, in having the throat dots much smaller and more widely separated than *lunatus* from the east side. If more material from west of the river becomes available, the differences in throat markings, if constant, should easily differentiate the two populations. This will also require examination of the type specimen which I have not studied. From Cochran's drawing (1941:Pl. 6A), at least the illustrated specimen agrees much better with specimens from east of the river.

As has been previously noted, *L. l. lunatus* occurs in part sympatrically with *L. p. trujilloensis*. The two can be readily distinguished by the nuchal-scapular blotch and heavy throat spotting in the former, in contrast to the black face, green venter and smudged throat of the latter. Females of the two species are equally distinct, the heavily dotted throat and venter of female *trujilloensis* contrast with the unspotted venter and very lightly spotted throat of *lunatus*. Since I have not taken both species at the same locality, I do not know if they occur syntopically.

L. l. lunatus is not especially abundant. The largest series was taken from a semi-arid cultivated area at the foot of the limestone bluffs which parallel the coast east of the Río Ozama. Here the lizards were taken on and among large concrete slabs and trash. Elsewhere they were collected

in coastal situations, such as *Cocos* groves, but seldom were encountered commonly.

Specimens examined: República Dominicana, Distrito Nacional, 8.6 km W Santo Domingo, 1 (ASFS V2471); 5.9 km W Santo Domingo, 2 (ASFS V2473-74); Tres Ojos (not mapped), 1 (SMF 25552); 6 km E Santo Domingo, 2 (ASFS, V2481, V2484); 8.6 mi. (13.8 km) E Santo Domingo, 12 (ASFS X7822-31, RT 615-16); 16.7 mi. (26.9 km) E Santo Domingo, 1 (ASFS X7766); La Caleta (not mapped), 8 (SMF 25561, 25590-96); Boca Chica, eastern edge, 4 (ASFS V680-83); 0.9 km E Boca Chica, 10 (ASFS V639-48); 7 mi. (11.3 km) E Boca Chica, 1 (ASFS X7764).

Leiocephalus lunatus arenicolor
Mertens, 1939

Leiocephalus personatus arenicolor Mertens, 1939, Abh. Senckenberg. Naturf. Ges., 449:48.

Type locality: Sandy seashore at San Pedro de Macorís, San Pedro de Macorís Province, República Dominicana.

Holotype: SMF 25715, a male with a snout-vent length of 53 mm (*vide* Mertens, *loc. cit.*).

Diagnosis: A subspecies of *L. lunatus* characterized in males by a combination of sandy to tan dorsal zone, often with a bronzy metallic sheen or flecked with creamy, dorsolateral lines faint (= unicolor with back) to white, grayish-sandy or buffy, at times one nuchal and one scapular transverse dark bar, but these are usually absent

reduced to a series of dark dots on the dorsal crest scales, lateral nuchal and scapular patches always restricted and at times completely absent (Fig. 7b), throat white to gray with relatively few black dots of unequal sizes (which also may be absent completely) rarely extending onto chest (Fig. 8b), ventral ground color white to pale greenish, pale yellow-green, pale buffy or creamy, with sides of belly lavender-gray; size large (males to 65 mm, females to 53 mm snout-vent length), high number of loreals (4.5), median head shields modally 4.

Distribution: Southeastern coast of the República Dominicana from San Pedro de Macorís east to Boca Chavón (Fig. 6).

Variation and discussion: The series of 62 *L. l. arenicolor* has the following scale counts: dorsal crest scales occiput-vent 53-66 (mean 58.1), dorsal crest scales occiput-axilla 16-26 (mean 21.3), dorsal crest scales on trunk 33-46 (mean 36.7), one half midbody scales 20-26 (mean 23.0), subdigital fourth toe tricarinate scales 20-27 (mean 22.4), loreals 3-8 (mean 4.5), temporals 7-14 (mean 10.5), supraoculars 6-6 (32 specimens), 4-5 (2), 5-5 (5), 5-6 (5), 6-7 (2), 7-7 (3), 6-9 (1), semicircles usually complete (75.0 percent), and parietals always in contact (100 percent). The prefrontal row consists of 2 to 5 scales (mode 3), the median head shields vary between 3 and 10 (mean 4), and the frontoparietal row has 1 to 6 scales (mode 4 or 5 with equal frequencies); the prefrontal row is almost always complete (61 of 63 specimens) and the frontoparietal row is more often complete (40 of 59 specimens). The largest males measure 65 mm in snout-vent length, the largest female 53 mm; the female is from San Pedro de Macorís and the males are from this locality and La Romana.

A series of 39 topotypes showed the following coloration and pattern. In males, the dorsum is tan to slightly darker with a bronzy metallic sheen. The dorsolateral lines are indistinguishable from the ground color to buffy. The head is light brown with some darker suffusion on the supraocular scales. The nuchal and scapular transverse brown bars are indicated by a median series of dark dots on the crest scales.

The sides are slightly darker than the dorsum, and occasionally have some green or bronzy scales admixed. The lateral line between the limbs is always very obscure or absent. The sides of the neck and shoulder above the forelimb insertion have a much reduced black tripartite patch, which is often restricted to a few black fragments on the neck or may be absent entirely (ASFS X8195). The venter is white, pale greenish, or buffy. The throats are white to pale gray, and the black throat dots are small, rather irregularly scattered, of varying sizes, and may be completely absent except along the margin of the lower jaw. The upper side of the hindlimbs is dull green. The tail is brown dorsally with the chevrons poorly defined or absent and pale orange to pink below.

Females are like the males dorsally, but the dorsolateral lines are even less prominent. Females lack dorsal chevrons or transverse bars and instead have at least the neck and scapular region, and at times the entire back, with dark dots on the crest scales. The throats are pale gray dotted with vague slightly darker gray dots. The ventral ground color is pinkish to whitish and immaculate, and the underside of the tails is pale orange.

I include seven specimens (five males, two females) from La Romana and a series from Boca Chavón, both localities to the east of San Pedro de Macorís, with *arenicolor*. The La Romana series, which I did not see in life, resembles the topotypes fairly closely in pattern, although three of the males have the black neck and shoulder patch somewhat better developed than topotypes, and the throats of all males have the black dots somewhat more widely scattered than most San Pedro males. The two La Romana females have completely immaculate throats. The series of twenty-one specimens from Boca Chavón includes males with dorsal cream dotting, and the black neck and shoulder spot is restricted to absent. The sides are flecked with turquoise. The venter is pale yellow-green to creamy with lavender sides. The main difference between this lot and the topotypes is the presence of nuchal and scapular transverse bars, which persist into even the largest male. Since these specimens are inter-

mediate geographically between *arenicolor* and the race next to the east, it is not surprising that they resemble the latter in some characters, such as the persistent transverse bars. One of the series (one of two males from the east side of the Río Chavón) is very like the more eastern race in all dorsal features, but is closer to *arenicolor* in throat spotting. Everything considered, I place the Boca Chavón material with *arenicolor*, although acknowledging its intermediate characteristics.

L. l. arenicolor occurs with *L. personatus* in part of its range (San Pedro de Macorís, Río Cumayasa). If the two occur syntopically, there should be no difficulty in separating them, since the *L. personatus* males from this region lack any prominent throat markings and the females have the throats and venters heavily dotted with dark gray to black. The subspecies *lunatus* and *arenicolor* are easily differentiated on the basis of the paler dorsal coloration, less prominent dorsolateral lines, and less spotted throat in the latter. The equal incidence of 4 and 5 frontoparietals (21 specimens in each category) in *arenicolor* differs from the mode of 5 in *lunatus*. Both subspecies are equally large.

The range of *lunatus* is separated from that of *arenicolor* by about 28 kilometers airline. There is one major barrier in this region—the Río Macorís which lies just to the west of San Pedro de Macorís; this river possibly separates the two subspecies. The topotypes were collected about the lighthouse just south of San Pedro de Macorís on sandy soil in and about a garbage dump, which they occupied with *Ameiva chrysolasma*, although the latter were much less abundant. The specimens from the mouth of the Río Chavón were collected in shady sea-grape stands along the beach, and here *L. l. arenicolor* was associated with *Ameiva taeniura*. The lizard from northeast of Boca Chavón was taken in wet rocky woods on a limestone ridge behind the settlement.

Specimens examined: República Dominicana, San Pedro de Macorís Province, 0.5 mi. (0.8 km) S San Pedro de Macorís, 4♂ (ASFS X8192-230, RT 647-50); La Romana Province, La Romana, 7 (MCZ 57135-37, 75079-82); mouth of Río Chavón, west

side, 19 (ASFS V1042-60), Boca Chavón, 1 (ASFS V1073); 1 mi. (1.6 km) NE Boca Chavón, 1 (ASFS V1074).

Leiocephalus lunatus melaenacelis,
new subspecies

Holotype: MCZ 81096, an adult male, from the western end, Isla Catalina, La Romana Province, República Dominicana, one of a series taken 20 August 1963 by David C. Leber, Ronald F. Klinikowski, Albert Schwartz, and Richard Thomas. Original number V571.

Paratypes: ASFS V572-75, V578-81, AMNH 94253-56, UIMNH 61633-36, RT 786-87, same data as holotype.

Diagnosis: A subspecies of *L. lunatus* characterized in males by a combination of tan to grayish-tan dorsal zone with very prominent gray to buffy dorsolateral lines, prominent black nuchal and scapular transverse bars in adults, large jet black nuchal and shoulder patch (Fig. 7c), upper surface of hindlimbs tan, spotted with dark brown and cream, throat white to pale gray with relatively few but large black spots which extend onto the chest (Fig. 8c), venter pale yellow with lavender sides; tail bright orange above; size moderate (males to 61 mm, females to 60 mm snout-vent length), high number of loreals (4.4), median head shields variable, with 5 and 6 having the same frequency.

Distribution: Isla Catalina, off the coast near La Romana, República Dominicana (Fig. 6).

Description of holotype: An adult male with the following measurements and counts: snout-vent length 58 mm, tail 76 mm; dorsal crest scales occiput-vent 56, dorsal crest scales occiput-axilla 20, dorsal crest scales on trunk 36, one half midbody scales 25, subdigital fourth toe tricarinate scales 24, loreals 5, temporals 2, enlarged auriculars 4+4; 3 prefrontal scales, row complete; 4 median head shields; 3 frontoparietal scales, row complete; supraocular scales 7-6; supraorbital semicircles 2, parietal scales 2.

Dorsal ground color tan, medially with a pale creamy zone which is crossed by a series of pale tan "chevrons"; dorsal crest scales alternately cream and tan, depending upon the ground color on either side of

the crest; a black nuchal and a black scapular transverse bar, the latter the wider and more conspicuous; dorsolateral lines very bold and grayish and extending onto the base of the tail. Sides of neck and shoulder region above forelimb with a large and more or less solid jet black patch which extends anteriorly to (but not including) the temporal region. Upper surface of hindlimbs tan with cream and brown scales; forelimbs tan above with cream spots over entire member and black spots mostly on the brachium. Lateral line between limbs buffy and very distinct; sides very pale orange with pale greenish or tan scales admixed. Venter very pale yellow, lavender on sides, with contrasting rows of cream to greenish scales descending onto abdomen from sides. Throat pale gray with large black spots, all of about uniform size and uniform distribution, extending onto chest. Tail bright orange above, bright orange with some cream scales below.

Variation: The series of 17 *L. l. melaenacelis* has the following scale counts: dorsal crest scales occiput-vent 54-68 (mean 59.8), dorsal crest scales occiput-axilla 19-25 (mean 22.3), dorsal crest scales on trunk 32-44 (mean 36.8), one half mid-body scales 21-27 (mean 24.3), subdigital fourth toe tricarinate scales 23-27 (mean 24.7), loreals 3-6 (mean 4.4), temporals 10-13 (mean 10.9), supraoculars 6/6 (6 specimens), 6/7 (4), 7/7 (3), semicircles more often complete (75.0 percent), and parietals always in contact (100 percent). The prefrontal row consists of 2 to 4 scales (mode 3), the median head shields vary between 4 and 7 (mode 5 and 6), and the frontoparietal row has 2 to 5 scales (mode 5). The prefrontal row is always complete (16 specimens) and the frontoparietal row is more often complete (10 of 14 specimens). The largest male has a snout-vent length of 61 mm, the largest female 60 mm.

Males resemble the description of the holotype in coloration and pattern with the following exceptions. Subadult and young males have the back more completely chevronate than the type, and the two bold black transverse bars are a late ontogenetic feature. No other male has so much black dotting on the forelimbs as the type. The black lateral nuchal and shoulder patch is always

bold and conspicuous but may be somewhat less in extent than in the type. The tan hindlimbs with dark and light spots are a common feature of all the males.

The females are like males dorsally except that, because of a dark brown ground color, the buffy to yellowish dorsolateral lines are extremely bold. In contrast to females of other races, the backs of female *melaenacelis* are more or less chevronate for their entire lengths with about nine dark brown incomplete chevrons bordered posteriorly by pale tan before the hindlimbs. The sides are dark brown with no dark longitudinal dashes. The tail is orange-brown above and bright orange below. The venter is whitish to gray and the throat has a few very faint gray dots.

Young males resemble the females except that the throat spots are slightly darker and more prominent.

In scalation, the variation in mode of median head shields (5 or 6, five individuals in each category; four lizards have 4 median head shields) is unusual.

Comparisons: *L. l. melaenacelis* differs from *L. l. arenicolor* on the adjacent mainland in having large and equally sized throat spots and a large nuchal-shoulder patch, in having a boldly lineate dorsum and tan (versus green) hindlimbs, and an orange tail. Female *melaenacelis* are chevronate, whereas *arenicolor* females are not. The Catalina subspecies most closely resembles *lunatus* to the west, but the two can be differentiated by the much lighter dorsum and more contrasting pattern of male *melaenacelis*, the orange tails in both sexes of the insular subspecies, the green hindlimbs of male *lunatus*, and the chevronate pattern of female *melaenacelis*. Both *lunatus* and *arenicolor* reach a larger size than *melaenacelis*, and both have the median head shields modally 4, in contrast to 5 or 6 in the insular subspecies.

Remarks: The series of *L. l. melaenacelis* was taken in the late afternoon (after about 1400 hours), especially along the sandy beach under low coconut palms; a few specimens were seen and collected in rather mesic hammock woods, and others were taken in a grassy savanna where they sought refuge under blocks of limestone. When running, the bright orange underside of the

tail is very conspicuous, and even at rest the orange upper surface makes the lizards stand out in contrast to the pale sandy substrata. The lizards became active only in the mid-afternoon; on the day of our visit to Isla Catalina the weather was extremely hot and dry, and the more barren areas inhabited by *L. l. melaenacelis* were undoubtedly too hot at midday for these lizards. *L. l. melaenacelis* was collected with both *Ameiva lineolata* and *Ameiva chrysolaelma*.

Leiocephalus lunatus thomasi,
new subspecies

Holotype: MCZ 81097, an adult male, from 0.5 mi. (0.8 km) NW Boca de Yuma, La Romana Province, República Dominicana, one of a series collected 30 August 1963 by Albert Schwartz. Original number V856.

Paratypes: ASFS V857-60, RT 797, same data as type; ASFS V816-24, 0.3 mi. (0.5 km) NW Boca de Yuma, La Romana Province, República Dominicana, 29 August 1962, A. Schwartz, R. Thomas; MCZ 75083-123 + one unnumbered specimen (FN 5374), Boca de Yuma, La Romana Province, República Dominicana, 28 March 1963, C. E. Ray and R. Allen.

Diagnosis: A subspecies of *L. lunatus* characterized in males by a combination of grayish-tan dorsal zone, often chevronate and with a nuchal and a scapular black transverse bar, buffy dorsolateral lines bold and contrasting, a bold and extensive black nuchal-shoulder patch which often, because of the dark reddish-brown sides, is indistinct (Fig. 7d), upper surface of hindlimbs tan with scattered dark brown and pale tan scales, throat greenish-white to pale yellowish with bold black dots which are scattered, usually few in number, and of varying sizes on any throat (Fig. 8d), venter pale greenish, tail brownish-orange above; size large (males to 66 mm, females to 55 mm snout-vent length), low number of loreals (3.8), median head shields modally 4.

Distribution: Known only from the vicinity of Boca de Yuma in extreme eastern República Dominicana (Fig. 6).

Description of holotype: An adult male with the following measurements and

counts: snout-vent length 58 mm, tail 97 mm; dorsal crest scales indeterminate; one half midbody scales 22, subdigital fourth toe tricarinate scales 23 23, loreals 3, temporals 11, enlarged auriculars 2 5; 3 prefrontal scales, row complete; 4 median head shields; 5 frontoparietal scales, row complete; supraocular scales 6 6; supraorbital semicircles complete, parietal scales in contact.

Dorsal ground color grayish-tan, crest scales alternately black and golden, chevrons barely indicated, nuchal and scapular transverse bars slightly darker than chevron remnants; dorsolateral lines buffy and fairly prominent, extending onto the base of the tail. Sides of neck and shoulder region with a series of four black spots, the most posterior behind the forelimb insertion, and the one above the limb the largest. Upper surface of hindlimbs tan with scattered darker brown and turquoise scales; forelimbs tan speckled with buffy above. Lateral line between limbs obsolescent; sides dark reddish-brown with scattered turquoise flecks. Venter very pale greenish. Throat greenish-white with black dots of varying size but in general small and rather widely and variably separated from one another, and extending onto chest. Tail orange brown above, weakly chevronate proximally, and pale orange below.

Variation: The series of 52 *L. l. thomasi* has the following scale counts: dorsal crest scales occiput-vent 50-66 (mean 58.0), dorsal crest scales occiput-axilla 16-25 (mean 19.7), dorsal crest scales on trunk 32-44 (mean 37.8), one half midbody scales 19-24 (mean 22.1), subdigital fourth toe tricarinate scales 20-26 (mean 22.8), loreals 2-6 (mean 3.8), temporals 9-12 (mean 10.3), supraoculars 6 6 (33 specimens), 5 5 (1), 5 6 (4), 6 7 (5), 7 7 (2), 7 5 (1), semicircles more often complete (66.0 percent), and parietals always in contact (100 percent). The prefrontal row consists of 2 to 5 scales (mode 3), the median head shields vary between 2 and 7 (mode 4), and the frontoparietal row has 2 to 6 scales (mode 5). The prefrontal row is almost always complete (49 of 50 specimens) and the frontoparietal row is more often complete (29 of 47 specimens). The largest male has a snout-

snout length of 66 mm, the largest female 55 mm.

L. l. thomasi is the most variable of the subspecies of *L. limatus* as far as throat pattern is concerned. Dorsally, most males agree with the description of the holotype in coloration and pattern although fairly regularly the dorsa are weakly to moderately prominently chevronate. The nuchal and scapular transverse bars are usually much darker than in the type. Due to the dark sides, the black nuchal-shoulder patch is often not so obvious (MCZ 75115) as it is in the type, but it is always large and extensive, and may be solid or fragmented. The throat color varies between greenish-white and pale yellowish. The throat spots always vary in size on each throat, and are usually well separated. In some specimens (MCZ 75093, 75098 for instance) there is a tendency for the black spots on the central portion of the throat to form a pair of paramedian longitudinal lines, although the dots maintain their individuality and do not fuse—they are merely aligned into longitudinal rows. The black dots regularly extend onto the chest and onto the sides of the neck.

The females are dark reddish-brown dorsally with about nine complete or incomplete dark brown chevrons before the hindlimbs. The dorsolateral lines are creamy to buffy and distinct against the darker dorsum and the dark brown to black sides. The lateral line is cream to tan and is irregular or almost scalloped into a series of pale ovals extending between the limbs. The ventral ground color is white and there are some very pale gray dots on the throats; the abdomen as usual is immaculate. The tails are orange-brown above, weakly chevronate distally, and pale orange ventrally. The hindlimbs are brown, spotted with cream above. Juvenile males are patterned like females, even having the lateral lines scalloped; the throat dots are slightly darker, however.

Comparisons: From its adjacent neighbor, *L. l. arenicolor*, *thomasi* differs in having a much darker dorsum with prominent longitudinal lines, weakly chevronate males, brown versus green hindlimbs, and much larger black nuchal-shoulder patches and more heavily spotted throat. Females of

arenicolor are not chevronate as are female *thomasi*, and lack the scalloped lateral line. From *limatus*, *thomasi* differs in dark and lined dorsum, less heavily spotted throat (although the spots are comparable in these two races), and in having chevronate females. *L. l. thomasi* most closely resembles *melaenacelis*. The more strongly chevronate dorsum and dark reddish-brown lateral fields distinguish male *thomasi*. The entire chromatic picture of *thomasi* is brighter than *melaenacelis*, especially the pigments on the sides. Both races lack green hindlimbs in males. Females of the two can be distinguished by the darker coloration and the scalloped and irregular lateral lines of *thomasi*.

Remarks: The region between Boca de Yuma in the east and Boca Chavón in the west is presently inaccessible by road. I have already commented on the resemblance of one of two males from Boca Chavón (east side of the river) to *thomasi*, which has been interpreted to indicate that even this far west the genetic influence of *thomasi* is expressed in *arenicolor* populations.

At Boca de Yuma, specimens were collected on the mesic forested limestone ridge behind the settlement. Here the lizards were fairly abundant on and about rocks. The orange undersides of the tails made the lizards rather obvious against the more sombre leaf litter of the forest floor. In this area, *L. l. thomasi* was encountered with the shade-dwelling *Ameiva taeniura*.

Only 22 kilometers to the northeast of Boca de Yuma is Juanillo, the easternmost locality for *L. p. mentalis*. Presumably somewhere in this intermediate region the two species come in contact. Where they do, they should be easy to differentiate since *mentalis* has a solid yellow and immaculate throat and a prominent face mask.

Leiocephalus limatus louisae Cochran, 1934

Leiocephalus personatus louisae Cochran
1934, Occ. Papers Boston Soc. Nat. Hist.,
8:177.

Type locality: Isla Saona, República Dominicana.

Holotype: MCZ 37551, an adult male with a snout-vent length of 56 mm.

Diagnosis: A subspecies of *L. limatus* characterized in males by a combination of

dark gray dorsal zone with chevrons usually indicated, dorsolateral lines white to creamy and bold, lateral nuchal and scapular patches variable, but usually restricted and often indistinguishable anteriorly from the dark gray to black lateral fields (Fig. 7e), throat white to faintly greenish with either very tiny and discrete, or large and discrete, dots extending onto the chest (Fig. 8e), ventral ground color pale yellow-green, hindlimbs tan, usually not spotted with dark or pale; size small (males to 57 mm, females to 50 mm snout-vent length), low number of loreals (3.9), median head shields modally 4.

Distribution: Isla Saona, República Dominicana (Fig. 6).

Variation and discussion: The series of 18 *L. l. louisae* has the following scale counts: dorsal crest scales occiput-vent 50-62 (mean 57.1), dorsal crest scales occiput-axilla 16-25 (mean 20.1), dorsal crest scales on trunk 32-46 (mean 37.0), one half midbody scales 21-26 (mean 22.3), subdigital fourth toe tricarinate scales 20-26 (mean 22.6), loreals 2-5 (mean 3.9), supraoculars 6 6 (12 specimens), 4 5 (1), 5 5 (1), 6 7 (1), 7 7 (1), semi-circles usually complete (70.6 percent), and parietals always in contact (100 percent). The prefrontal row consists of 2 to 4 scales (mode 3), the median head shields vary between 4 and 7 (mode 4), and the frontoparietal row has 2 to 5 scales (mode 5); the prefrontal row is always complete (17 specimens), and the frontoparietal row is more often complete (12 of 16 specimens). The largest male measures 57 mm and the largest female 50 mm in snout-vent length.

The dorsal zone in males is charcoal gray with chevron remnants usually fairly prominent and with nuchal and scapular dark brown transverse bars. The dorsolateral lines are cream to white and thus stand out very boldly against the darker dorsal ground. The sides are dark gray to black, especially anteriorly, and thus the nuchal-shoulder black patch may be somewhat obscured. The patch itself is variable in extent, and may be entire or reduced to a sequential series of two or three discrete spots. In the known specimens it is never absent. The lateral line between the limbs

is obsolete, and scalloped anteriorly. The tails are straw colored dorsally and mottled rusty to nearly uniform orange ventrally. The throats and chests are white to faintly greenish with dark brown to black spots. The spots themselves are extremely variable in size, the type (and especially the paratype, MCZ 37552) being at the lower extreme in throat spotting with very tiny and widely scattered dots. In some males the dots are quite large (ASFS V3006) and in others (ASFS V3005) somewhat smaller but still much larger than in the type. The anterior dots show a tendency in some lizards to form a pair of transverse bands at the level of the first and fourth chin shields. The throat dots regularly extend onto the chest. The venter is pale yellow-green with a series of greenish-yellow scales forming ventrolateral lines extending toward the midline from the sides.

The females are like the males dorsally, but have the chevrons more prominent and have the lateral line obvious and scalloped as well. The sides are very dark brown without longitudinal dark dashes. The venter is white, and the throats are faintly grayish with slightly darker indications of gray spotting. One female (ASFS V3014) lacks throat dots completely. The tails are brownish and distinctly chevronate above, and orange below.

The single juvenile male resembles the females in both coloration and pattern but has darker gray throat spots.

L. l. louisae is obviously most closely related to *L. l. thomasi* which presumably occupies the adjacent mainland. The Saona subspecies is distinctly smaller (57 versus 66 mm in males), and lacks the reddish-brown sides (having instead dark gray to black sides). Females of the two races are very similar but again the lateral coloration will separate them. The throat patterns of both *thomasi* and *louisae* are quite variable, but my impression is that the throat of *louisae* is in general less heavily marked than that of *thomasi*.

Since *louisae* is the smallest subspecies of *L. lunatus*, it is distinct from the balance of the races, being approached most closely by *melaenacelis*. From *arvicolor* and *lunatus*, *louisae* differs in having a less densely marked throat than the latter and a more

heavily marked throat than the former. The chevronate pattern of female *louisae* is not matched by females of these two western subspecies. The nuchal-shoulder patch in *louisae* is much more extensive than that of *arenicolor*. The differences in hindlimb coloration will separate *louisae* from both *lunatus* and *arenicolor*. *Louisae* differs from *melaenacelis* in having more (but smaller) throat dots in males and in much darker dorsal coloration; females of the two subspecies can be distinguished since *melaenacelis* lacks a scalloped lateral line.

Remarks: *L. l. louisae* is moderately abundant on Isla Saona where it occupies semiarid scrub grading into mangrove flats, and adjacent to shady woods. It occurs with *Ameiva taeniura* in the region about Mano Juan on the south coast.

Specimens examined: República Dominicana, Isla Saona, no other locality, 4 (MCZ 37551—type; MCZ 37552-54—paratypes); environs of Mano Juan, 14 (ASFS V3004-17).

Leiocephalus barahonensis Schmidt, 1921

Leiocephalus barahonensis Schmidt, 1921, Bull. Amer. Mus. Nat. Hist., 44(2):15 (type locality—Barahona, Barahona Province, República Dominicana).

Definition: A species of *Leiocephalus* characterized by a combination of 1) moderate size (males to 80 mm, females to 64 mm snout-vent length), 2) sexual dichromatism not pronounced dorsally but throat pattern somewhat variable between sexes, and males with two pairs of enlarged post-anal scales, 3) absence of a lateral fold, 4) dorsal scales imbricate, strongly denticulate or tricuspid, and keeled, ventral scales imbricate, smooth, and denticulate, 5) median dorsal crest scales slightly enlarged, not attenuate, slightly imbricate (Fig. 9b and c), slightly lower than median dorsal caudal scales, 42 to 57 in occiput to vent distance, 6) one half midbody scales 16 to 24, 7) supraoculars usually 6/6, 8) loreals 2-8, 9) temporals 3-7, 10) supraorbital semicircles usually incomplete, 11) parietals always in contact (one exception of 346 specimens examined), 12) median head scales varying between 2 and 6, 13) preauricular scale extremely enlarged (Fig. 9a), 14) throat in both sexes with a gray to black reticulum, black transverse bars, or

dark smudges, 15) ventral color bright orange or orange-yellow, 16) ventral pattern absent in both sexes, 17) mask absent, and 18) black neck and shoulder patches absent.

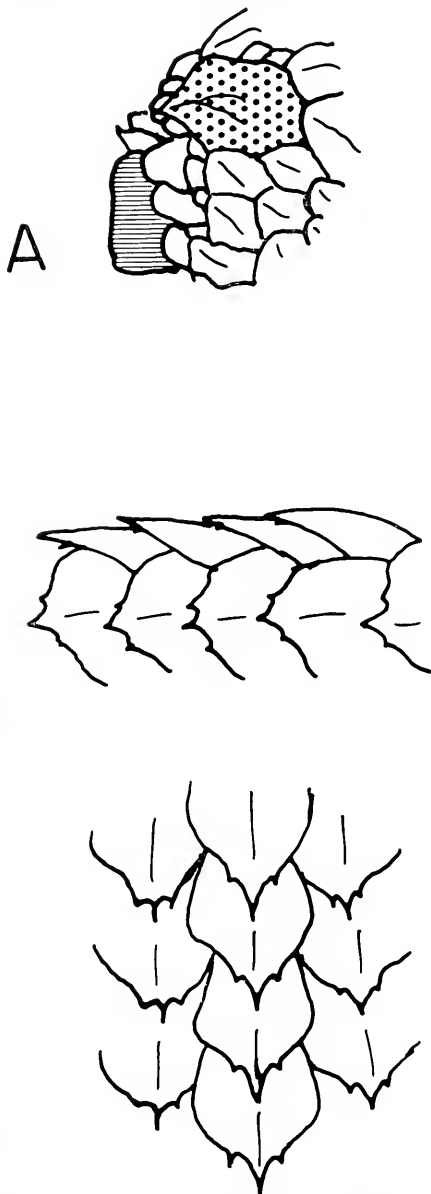


Figure 9. Scale features of *L. barahonensis*, showing a) auricular opening (horizontal lines) and enlarged preauricular scale (stippled); b) lateral view of median dorsal crest scales; and c) dorsal view of median dorsal crest scales. *L. vinculum* agrees with *L. barahonensis* in (b) and (c) but resembles Fig. 2(a) in preauricular scale size.

Leiocephalus barabonensis barabonensis
Schmidt, 1921

Type locality: Barahona, Barahona Province, República Dominicana.

Holotype: AMNH 2736, an adult male with a snout-vent length of 70 mm (George W. Foley, pers. com.).

Diagnosis: A subspecies of *L. barabonensis* characterized in males by a combination of a broad dorsal zone varying from golden-yellow to slightly reddish or brown, and without an included pair of paramedian dorsal stripes, dorsolateral light stripes indistinct, throat dark (gray, dirty orange, gray with bronzy sheen) with a heavy black pattern of lines and smudges, indistinct on the dark ground color (Fig. 11a), ventral ground color yellow-orange to bright orange, frontoparietals modally 5.

Distribution: Independencia and Barahona provinces in the República Dominicana, from near El Naranjo on the west to Paraíso on the south, both to the north and east of the Sierra de Baoruco (Fig. 6).

Variation and discussion: The series of 18 *L. b. barabonensis* has the following scale counts: dorsal crest scales occiput-vent 48-54 (mean 51.1), dorsal crest scales occiput-axilla 15-20 (mean 17.6), dorsal crest scales on trunk 30-36 (mean 33.4), one half midbody scales 18-21 (mean 19.8), subdigital fourth toe tricarinate scales 20-26 (mean 22.5), loreals 2-6 (mean 4.1), temporals 7-10 (mean 8.2), supraoculars 6-6 (10 specimens), 5/5 (2), 5/6 (3), 6/7 (2), 7/7 (2), semicircles always incomplete (100 percent) and parietals always in contact (100 percent). The prefrontal row consists of 2 or 3 scales (mode 3), the median head shields vary between 3 and 6 (mode 4), and the frontoparietal row has 4 to 7 scales (mode 5); the prefrontal row is always complete (18 specimens) and the frontoparietal row is usually complete (14 of 18 specimens). The largest male measures 74 mm in snout-vent length, the largest female 60 mm; both are topotypes.

L. b. barabonensis is poorly represented in collections in contrast to the larger series of the three other subspecies of *L. barabonensis*. The coloration (but not especially the pattern) seems to be quite variable. Males are golden-yellow to slight-

ly reddish (Barahona) or brown (southwest of Barahona) dorsally and lack any clear-cut paramedian dark lines, although these may be slightly indicated. The dorsolateral stripes are inconspicuous and fuse almost imperceptibly with the dorsal zone, thereby giving the dorsal zone somewhat paler (but concolor) edges. The head is tan and distinct from the dorsal zone in color. The sides are dark brown with or without a few green or turquoise scales. The lateral stripe between the limbs is dull and inconspicuous. The venter is bright orange to yellow-orange, always very vivid, and these colors continue onto the underside of the tail and hindlimbs. The throats vary from gray to dirty orange (= orange greatly suffused with gray) or gray with a bronzy sheen, and the throat pattern consists of a more or less random series of black lines or smudges on a darker background, extending onto the chest. The entire throat pattern is much clouded by the dark ground color and is not boldly distinct. Often there are a few yellow scales scattered on the throat. The chin is either white (and thus in strong contrast to the balance of the throat) or pale gray, the latter color if the balance of the throat is darker gray. The hindlimbs are brown above, with some darker brown marblings; the forelimbs are tannish-brown.

Females are tan to grayish-tan dorsally, either with or without some darker smudges (= chevron remnants) in the dorsal zone, and without conspicuous dorsolateral stripes. The sides are gray or dark brown with a pale blue-green suffusion and without longitudinal dark dashes; the lateral line is gray. The throats are white with a random gray to black pattern of transverse lines and smudges. The venter is opalescent. The underside of the tail is white to pale tan.

A juvenile male with a snout-vent length of 27 mm has the throat bright orange and the underside of the tail orange also. The pattern of this young individual is comparable to that of young females. No females of comparable size had an orange throat.

L. b. barabonensis occupies the foothills and associated lowland areas on the north and east sides of the Sierra de Baoruco, from El Naranjo in the west to Paraíso in

the south. It does not invade the arid Valle de Neiba and prefers somewhat more mesic situations, such as forest. Specimens have also been collected along the coast in palm groves, although in the city of Barahona, *L. b. barabonensis* is greatly outnumbered by *L. schreibersi*. Mertens (*op. cit.*:44-45) reported *L. b. barabonensis* (as *L. p. barabonensis*) from Barahona (where he collected four females), Fondo Negro on the north side of the Rio Yaque del Sur, and also considered a half-grown female from Azua as this subspecies. The latter two records are based upon specimens which Mertens himself doubted were *barabonensis*, since both have completely unmarked throats—a condition not known in the species *L. barabonensis*. Although I have not examined these lizards, I too doubt very strongly that they are *L. b. barabonensis* and there is no reason to extend the range of the subspecies into the Fondo Negro region. The habitat noted for the Fondo Negro individual (*Kakteen-Buschwald*) likewise is not typical for *L. b. barabonensis*. The four females taken by Mertens south of Barahona on the road to Paraíso were collected in dry forest in a stone pile. Altitudinally, *L. b. barabonensis* occurs from sea level to 1000 feet (328 meters) near El Naranjo.

As noted above, *L. b. barabonensis* is sympatric (but usually not syntopic) with *L. schreibersi*. The two are easily distinguishable on the basis of the lateral fold in *schreibersi* and the much more vivid colors of *barabonensis*; *schreibersi* has a pale sandy-tan to pale gray overall coloration and lacks an orange or yellow-orange venter.

There is a single specimen (USNM 75906) from "Bayeux, near Port-au-Prince" which is *L. barabonensis*. Bayeux is presently not locatable. The lizard is an adult male with a snout-vent length of 79 mm, has incomplete semicircles and also, remarkably, lacks frontoparietal scales completely. The throat pattern consists of a few dark smudges on a lighter ground. This pattern does not resemble that of *L. b. barabonensis* and is even somewhat extreme for the south coastal *L. b. aureus*, which has a lightly patterned throat. Since *L. b. barabonensis* occurs so close to the Dominico-Haiti border at El Naranjo, it is to be expected in Haiti along the northern flank of the Morne des

Enfants Perdus. However, I doubt that the Bayeux specimen is a Haitian *L. b. barabonensis*. The specimen was collected by J. S. C. Boswell, who also collected a specimen of *L. b. aureus* from the "Artibonite Valley", far to the north of, and separated by the Massif de la Selle and the Cul de Sac Plain from the known distribution of that subspecies. Boswell also collected the holotype of *aureus*. It is thus certain that Boswell collected within the range of *aureus*. I suspect that USNM 75906 is in actuality a specimen of *L. b. aureus* from within the recognized distribution of that subspecies.

Specimens examined: Republica Dominicana, Independencia Province, 1 km W El Naranjo, 1000 feet (328 meters), 3 (ASFS X9940-42); *Barahona Province*, Barahona, 4 (ASFS X9709-12); Barahona Aviation Field, Barahona, 1 (MCZ 43810); 4 km NW, 1 km SW Barahona, 2 (ASFS V202, RT 769); 4 km NW, 2 km SW Barahona, 500 feet (164 meters), 3 (ASFS V205-07); 2 km SE Barahona, 2 (ASFS X9518-19); 3.3 mi. (5.3 km) NE La Ciénaga, 1 (ASFS X9383); 9 mi. (14.5 km) SW La Ciénaga, 1 (ASFS X9449); Paraíso, 2 (ASFS V298-99); 6 km SW Paraíso, 1 (ASFS V297).

Leiocephalus barabonensis oxygaster,
new subspecies

Holotype: MCZ 81098, an adult male, from 13.1 mi. (21.1 km) SW Enriqueillo, Pedernales Province, República Dominicana, one of a series collected 22 July 1963 by Albert Schwartz and Richard Thomas. Original number X9417.

Paratypes: ASFS X9418-26, RT 710-11, same data as holotype; USNM 156747-49, same locality as holotype, 30 July 1963, D. C. Leber, A. Schwartz, R. Thomas; ASFS V4419, same locality as holotype, 10 December 1964, R. Thomas; CM 40576, 1.3 mi. (2.1 km) NW Oviedo, Pedernales Province, República Dominicana, 30 July 1963, R. Thomas; KU 93330-32, 5 mi. (8.1 km) NE Oviedo, Pedernales Province, República Dominicana, 30 July 1963, D. C. Leber, A. Schwartz; AMNH 94257-59, 5 mi. (8.1 km) NE Oviedo, Pedernales Province, República Dominicana, 7 August 1963, D. C. Leber, R. Thomas; UF 21335-37, 3 km SW

Enriquillo, Barahona Province, República Dominicana, 7 August 1963, D. C. Leber, R. Thomas; MCZ 58031-33, Oviedo, Pedernales Province, República Dominicana, 20 August 1958, C. E. Ray and A. S. Rand.

Associated specimens: República Dominicana, Pedernales Province, 30 km NW Oviedo, 4 (MCZ 58027-30); 20 km NW Oviedo, 1 (ASFS X9889); 22 km SE Pedernales, 2 (ASFS X9887-88); 16 km SE Pedernales, 1 (MCZ 58037); 15 km SE Pedernales, 1 (ASFS X9885).

Diagnosis: A subspecies of *L. barahonensis* characterized in males by a combination of brown broad dorsal zone which is usually dark (some shade of brown) but varying toward brownish-orange or vivid orange-red, usually without an included pair of paramedian dark stripes, dorsolateral stripes moderately distinct, throat pale cream to dark gray with a pattern of either about three or four black crossbars or a bold black reticulum (Fig. 10a and 11b), ventral ground color golden yellow-orange to bright orange; frontoparietals modally 4.

Distribution: The Península de Barahona, from south of Enriquillo in the east to about 22 kilometers southeast of Pedernales in the west; intergradation between *oxygaster* and *aureus* occurs in a narrow zone 12 to 16 kilometers southeast of Pedernales (Fig. 6).

Description of the holotype: An adult male with the following measurements and counts: snout-vent length 72 mm, tail 76 mm, practically all regenerated; dorsal crest scales occiput-vent 42, dorsal crest scales occiput-axilla 13, dorsal crest scales on trunk 29, one half midbody scales 19, subdigital fourth toe tricarinate scales indeterminate; loreals 5, temporals 9, enlarged auriculars 2/4; 3 prefrontal scales, row complete; 4 median head shields; 4 frontoparietal scales, row complete; supraocular scales 6/6; supra-orbital semicircles incomplete, parietal scales in contact.

Dorsal ground color brown with buffy dorsolateral stripes moderately distinct; dorsal zone suffused with darker above dorsolateral stripes but there are no clearly defined paramedian lines; neck with some scattered dark brown flecks, top of head brown. Sides dull orange with scattered blue-green scales; lateral lines absent. Throat pale yellow, suffused with some gray before

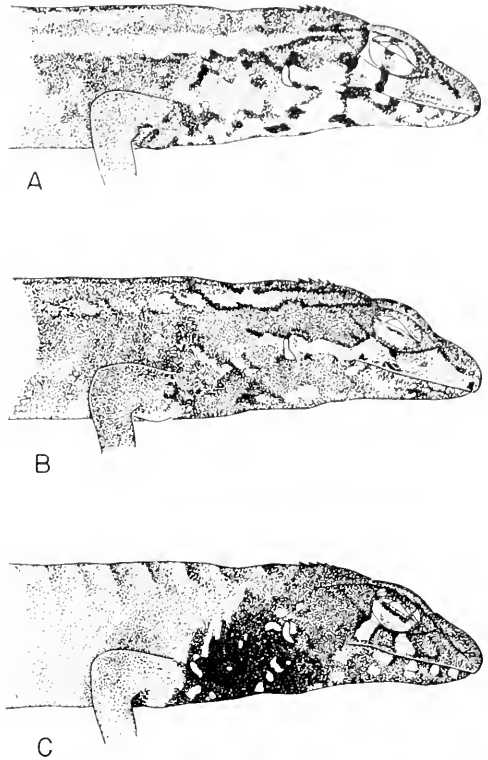


Figure 10. Lateral view of head and neck of one subspecies of *L. barahonensis* and two subspecies of *L. vinculum*, as follows: a) *L. b. oxygaster*, MCZ 81098, holotype, 13.1 mi. SW Enriquillo, Pedernales Province, República Dominicana; b) *L. v. vinculum*, ASFS X2491, 1.5 mi. S Etroits, Ile de la Gonave, Haiti; c) *L. v. endomychus*, MCZ 81099, holotype, 3.4 mi. NE Barrage de Péligre, Dépt. de l'Ouest, Haiti.

chest, chin white; throat pattern four complete transverse black bars (the last two continuous dorsally with black subocular and postocular stripes on the face and temporal region) followed by a series of about six ill-defined and incomplete transverse bars, two of which are on the chest; these latter bars are composed of series of black (anteriorly) to gray (posteriorly) smudges. Ventral color bright golden yellow-orange, continuous onto underside of tail and hindlimbs. Upper side of hindlimbs brown with scattered darker brown flecks; forelimbs tan above. Tail tan and without chevrons above.

Variation: The series of 35 *L. b. oxygaster* has the following scale counts: dorsal crest

scales occiput-vent 42-52 (mean 47.3), dorsal crest scales occiput-axilla 12-20 (mean 15.6), dorsal crest scales on trunk 29-37 (mean 31.9), one half midbody scales 17-21 (mean 19.0), subdigital fourth toe tricarinate scales 20-26 (mean 22.9), loreals 2-6 (mean 3.9), temporals 7-10 (mean 8.6), supraoculars 6-6 (23 specimens), 5-5 (1), 5-6 (3), 6-7 (5), 7-7 (3), semicircles more often incomplete (75.0 percent), and parietals always in contact (100 percent). The prefrontal row consists of 2 to 5 scales (mode 3), the median head shields vary between 3 and 5 (mode 4), and the frontoparietal row has 3 to 5 scales (mode 4). The prefrontal row is almost always complete (36 of 37 specimens) and the frontoparietal row is more often complete (26 of 37 specimens). The largest male has a snout-vent length of 80 mm, the largest female 60 mm; the male is from 30 km NW Oviedo and the female is from Oviedo.

The males agree in details of coloration and pattern with the description of the holotype. A male from 22 km SE Pedernales (and thus approaching the area of intergradation between *oxygaster* and *aureus*) is dull golden-orange above, with the sides and hindlimbs rust, and with a

vivid bright orange-red venter—a brilliantly colored lizard. No other more eastern specimens of *oxygaster* are so brightly colored above. This individual, however, has the throat pattern of *oxygaster*. In eastern males, the chin varies from white to pale whitish-green, and the throat from pale gray to yellow, overlaid with the black throat pattern. The pattern itself is variable but usually consists of about four transverse black bars followed by an area of black to gray smudges, at times (as in the type) oriented into a series of additional (but less complete and well defined) black bars. This basic pattern may be much distorted and obscured by the dark ground color in some specimens, or the two more posterior transverse bars may be fragmented. In general there is usually some indication of transverse markings. The dorsa are usually dark (most often some shade of brown) and there may be faint indications of dark paramedian stripes, but these are never bold. The neck often has a few scattered dark flecks as in the type. The blue-green lateral scales extend onto the venter as rows of isolated blue-green scales, and stand out in strong contrast to the ventral color.

The females are brown above like the males, and often have a series of about ten

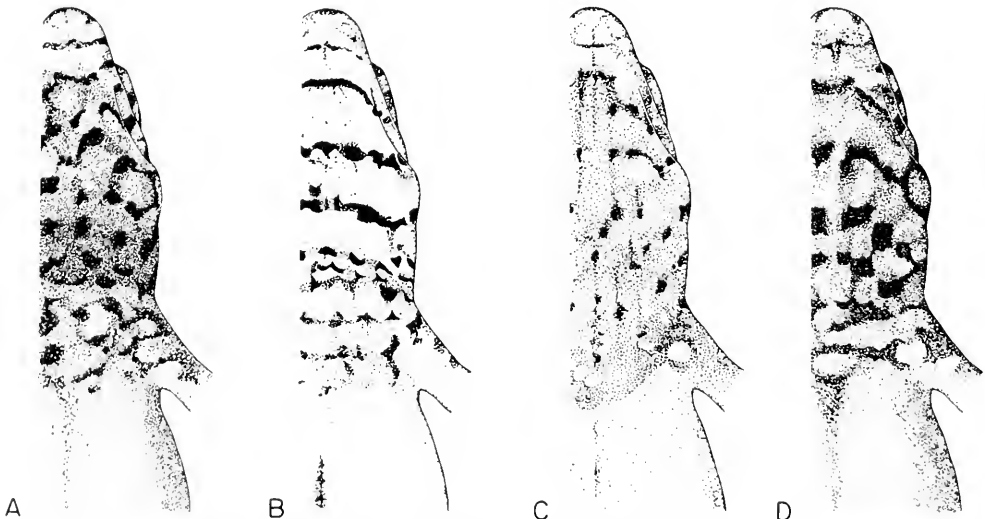


Figure 11. Ventral view of throat of males of four subspecies of *L. barahonensis*, as follows: a) *L. b. barahonensis*, ASFS X9708, Barahona, Barahona Province, República Dominicana; b) *L. b. oxygaster*, MCZ 81098, holotype, 13.1 mi. SW Enriquillo, Pedernales Province, República Dominicana; c) *L. b. aureus*, ASFS X9756, 1 km E Pedernales, Pedernales Province, República Dominicana; d) *L. b. beatanus*, ASFS V2732, Isla Beata, República Dominicana.

paramedian dark brown chevron remnants above the buffy dorsolateral lines. The throats are pale cream and the venter dull yellowish-gray. The throat pattern is much as described for the males, with a series of four transverse bars followed by some dark gray smudges; however, as in the males, the throat pattern is variable and may even be reticular. There is always, however, some indication of the transverse bars. The sides are dark brown and have no longitudinal dark dashes. The undersides of the hindlimbs are pale yellow-orange. The tail is a dull orange brown above and is usually chevronate. The hindlimbs are brown with both darker and lighter flecking, and the forelimbs are brown above.

Comparisons: The races *barabonensis* and *oxygaster* can be differentiated by the throat pattern, which in the nominate subspecies is not transversely oriented and lacks bars. The modal frontoparietal condition of 4 scales in *oxygaster* differs from the 5-scale mode in *barabonensis*. In coloration above the males of the two races are comparable, but *oxygaster* in general is darker than *barabonensis*; the dorsolateral lines are more prominent in *oxygaster* than in the more northern race.

Remarks: The distribution of *L. b. oxygaster* includes the major portion of the Península de Barahona, to the southeast and south of the Sierra de Baoruco. At the type locality, the lizards were abundant in shady hammock woods and in dried mangrove flats adjacent to the Laguna de Oviedo, preferring the latter habitat to the former. On the north, *oxygaster* (3 km SW Enriquillo) approaches *barabonensis* (6 km SW Paraíso) in Barahona Province; the distance separating the two races at this point is about 12 kilometers airline. As has been pointed out by myself and others, the eastern coast of the Península de Barahona lacks any coastal plain in many areas, the mountains descending into the ocean. The region between Enriquillo in the south and La Ciénaga on the north (and thus including Paraíso) is characterized by this abrupt coast. In fact, Paraíso lies in a valley which has associated with it a small bit of coastal plain and beach. Undoubtedly this abrupt coastline has caused the differentiation of *L. barabonensis* into two races in this area, as it has in other reptiles.

L. b. oxygaster grades rather rapidly into *aureus*, the subspecies to the west. This area of intergradation, which lies about 12 and 16 kilometers southeast of the town of Pedernales, lies in the arid region of the Península de Barahona and is not correlated with any obvious topographic features. At least to the east (within the range of *oxygaster*) some specimens are closer to *aureus* than to the expected subspecies (see comments above on the specimen from 22 km SE Pedernales). The two races may be divided fairly well at the line mentioned.

As far as known, *L. b. oxygaster* has a completely lowland range. No specimens have been taken on the mountain slopes. Both *barabonensis* to the north and *aureus* to the west occur at higher elevations, and it is likely that *oxygaster* does so as well. No other species of *Leiocephalus* is sympatric with *L. b. oxygaster*.

Leiocephalus barabonensis aureus Cochran,
1934

Leiocephalus personatus aureus Cochran
1934, Occ. Papers Boston Soc. Nat. Hist.,
8:175.

Type locality: Jacmel, Dépt. de l'Ouest, Haiti.

Holotype: USNM 75909, an adult male, with a snout-vent length of 68 mm (*vide* Cochran, 1941:224).

Diagnosis: A subspecies of *L. barabonensis* characterized in males by a combination of broad dorsal zone gray to golden with moderately prominent gray to cream dorsolateral stripes, usually without a pair of included paramedian dorsal dark stripes, throat white to gray with a pattern of scattered gray to black spots, seldom aligned into transverse rows (Fig. 11c), ventral ground color dirty yellowish to bright orange; frontoparietals modally 5.

Distribution: From Jacmel and Méyer along the southeastern coast of Haiti east to the vicinity of Pedernales, República Dominicana (Fig. 6).

Variation and discussion: The series of 127 *L. b. aureus* has the following scale counts: dorsal crest scales occiput-vent 44-57 (mean 50.8), dorsal crest scales occiput-axilla 13-22 (mean 17.0), dorsal crest scales on trunk 28-39 (mean 33.9), one half midbody scales 17-23 (mean

19.8), subdigital fourth toe tricarinate scales 19-29 (mean 23.7), loreals 2-8 (mean 4.0), temporals 7-10 (mean 8.8), supraoculars 6-6 (100 specimens), 5-5 (3), 5-6 (8), 6-7 (15), 7-7 (7), 7-8 (1), 8-8 (1), semicircles usually incomplete (84.1 percent) and parietals always in contact (one exception of 142 specimens examined). The prefrontal row consists of 2 to 6 scales (mode 3), the median head shields vary between 3 and 7 (mode 4), and the frontoparietal row has 2 to 6 scales (mode 5); the prefrontal row is almost always complete (143 of 145 specimens) and the frontoparietal row is almost always complete (109 of 138 specimens). The largest male measures 79 mm in snout-vent length, the largest female 62 mm; the male is from Saltrou and the female from Gormand.

Brightly colored males of *L. p. aureus* attest to the complete appropriateness of the name. Although the dorsal ground color is quite variable, ranging from gray with paler gray to cream dorsolateral stripes to golden (Pl. 9K7, Maerz and Paul, 1950) with or without paler dorsolateral lines, the latter condition provides an extremely showy lizard. The sides and hindlimbs are brick-red to orange-red, spotted with cream in some males, and in others are tan to vivid orange-brown with scattered green to turquoise scales. The heads are tan to vivid orange-brown, often speckled with a few dark brown flecks. The lateral stripe is gray to reddish-brown and often inconspicuous against the coloration of the sides. The upper surface of the hindlimbs varies between brick-red and orange-red to rusty orange and has a few inconspicuous brownish flecks. The venter is dirty yellowish to orange (Pl. 9L10) and the green and turquoise scales from the sides extend ventrad as lines of individual scales onto the bright belly. The throat is white to gray, and the chin white. The throat pattern consists of black to gray smudges, either reticular or individual, but seldom arranged in any transverse linear pattern (if so, there are never four transverse bars) and in general not especially distinct against the grayish background. Often the throat pattern is much reduced and is limited to scattered dusky smudges, comparable to the throat pattern of some of the subspecies of *L. personatus*

from the northern República Dominicana. The upperside of the tail is unicolor with that of the back, and thus may be gray to golden. Usually the tail is prominently chevronate only distally. The underside of the tail is light gray to orange.

Females are much less showy, with the dorsum sandy to dirty brownish-gray, and lacking completely the orange and reds of the males. The dorsolateral lines are buffy and conspicuous and the dorsal zone often has paramedian zones of chevron remnants. The tail is prominently chevronate above and orange below. The throat is white to pale gray with a slightly darker gray pattern which in its variation is precisely comparable to that of the males, although there may be as many as three weakly expressed gray bands behind the chin. The ventral color is very pale yellow to very pale greenish. The hindlimbs may have a slightly rusty tinge, but are usually brown with faint darker flecking.

Of the two specimens which I consider intergrades between *aureus* and *oxygaster*, one is a male (ASFS V2534) and the other a female (ASFS X9886). The male has a gray and vermiculate throat pattern, and a rusty-brown dorsal zone. The female has a black vermiculate throat pattern with a "grayish-tan dorsum and a pale gray head. The two specimens are intermediate in intensity and configuration of throat pattern between *aureus* and *oxygaster*. Attention has already been called to the occurrence of golden specimens within the western position of the range of *oxygaster*, so that the zone of intergradation may be somewhat broader than these few specimens indicate. One of these two intergrades (ASFS V2534) has the unique count in *L. barabonensis* of 24 midbody scales.

The distribution of *L. b. aureus* extends from Jacmel in the west along the southeastern coast of Haiti to the town of Pedernales and its environs on the Dominican-Haitian border. In both countries, *aureus* extends into the southern portion of the Massif de la Selle and the Sierra de Baoruco, being known in the former from Marbial at an elevation of about 200 meters and in the latter from above Las Mercedes at an elevation of 1900 feet (623 meters).

There is a specimen (USNM 75916) of

aureus from the "Artibonite Valley": this specimen was collected by J. S. C. Boswell, and once again the locality is surely incorrect. *L. barabonensis* is not known to occur north of the Cul de Sac Plain (although a related species does occur there); since Boswell collected the holotype of *L. b. aureus* and since this specimen is clearly that race rather than any other, I assume that the specimen was mislabeled in the past and probably originated near Jacmel or at least on the south coast.

At one locality (Marbial) *L. b. aureus* occurs with *L. melanochlorus*. The two are readily differentiable on the basis of the lateral fold and dorsal pattern of dark mottling in the former. Neither appears to be common at Marbial, and I suspect that the Marbial vicinity is at the upper altitudinal or ecological limits of the lowland *aureus* and at the lower limits of the (eastern) upland *melanochlorus*.

At least in the República Dominicana (and judging also from the quantity of Haitian specimens) *L. b. aureus* is quite common. It occurs primarily in wooded situations, such as shady *Acacia* stands and about the edges of cultivated and cleared areas, and shuns the more open hot and arid regions. Its occurrence in the foothills in more mesic surroundings indicates the predilection of *L. barabonensis* for less rigorous environments.

Specimens examined: Haiti, Dept. de l'Ouest, Jacmel, 4 (MCZ 37535-38); Méyer, 4 (MCZ 65156-57, CM 37827-28); Marbial, 21 km NE Jacmel, 2 (MCZ 65155, CM 37826); one half way between Cayes Jacmel and Marigot, 1 (MCZ 57134); between Cayes Jacmel and Marigot (not mapped), 5 (AMNH 49756-60); Saltrou, 24 (MCZ 57145-46, AMNH 50011-32); Lan Banane, nr. Saltrou, 10 (MCZ 68597-601, CM 38527-31); Trou Roche, nr. Saltrou, 15 (MCZ 68587-96, CM 38522-26); Tête à l'Eau, nr. Saltrou, 17 (MCZ 68602-11, CM 38532-38); Gormand, nr. Saltrou (not mapped), 2 (MCZ 68612-13); Tean, nr. Saltrou (not mapped), 10 (MCZ 69393-402); "Artibonite Valley", 1 (USNM 75916); República Dominicana, Pedernales Province, Pedernales, 16 (ASFS V2552-63, V2664-66, V2805); 5 km N Pedernales, 2 (ASFS V2542-43); 1 km E Pedernales,

8 (ASFS X9754-60); 3 km E Pedernales, 10 (ASFS X9870-78, X9890); 4 km E Pedernales, 4 (ASFS V2508, MCZ 58034-36); 5 km E Pedernales, 3 (ASFS V2530-32); 5 km SE Pedernales, 4 (ASFS X9761-64); 6 km SE Pedernales, 6 (ASFS X9879-83, RT 750); 10 km SE Pedernales, 1 (ASFS V2533); 7 km S Las Mercedes, 1 (ASFS V2654); 4 km NE Las Mercedes, 1900 feet (623 meters), 1 (ASFS V2653). Intergrades between *L. b. aureus* and *L. b. oxygaster*: República Dominicana, Pedernales Province, 12 km SE Pedernales, 1 (ASFS V2534); 16 km SE Pedernales, 1 (ASFS X9886).

Leiocephalus barabonensis beatanus
Noble, 1923

Leiocephalus beatanus Noble, 1923, Amer. Mus. Novitates, 64:5.

Type locality: Isla Beata, República Dominicana.

Holotype: AMNH 24330, an adult male, with a snout-vent length of 76 mm (*vide* Noble, *loc. cit.*).

Diagnosis: A subspecies of *L. barabonensis* characterized in males by a combination of a broad ashy-gray dorsal zone with a pair of paramedian and a median dark stripes, dorsolateral pale lines distinct and outlined medially by the paramedian dark stripes, throat light to dark gray with a pattern of five or six bold transverse bars (often incomplete medially) followed by a few black flecks on the chest (Fig. 11d), ventral ground color orange (sometimes greenish- or grayish-orange); frontoparietals usually 5.

Distribution: Isla Beata, República Dominicana (Fig. 6).

Variation and discussion: The series of 42 *L. b. beatanus* has the following scale counts: dorsal crest scales occiput-vent 43-54 (mean 48.8), dorsal crest scales occiput-axilla 13-20 (mean 16.9), dorsal crest scales on trunk 25-36 (mean 31.9), one half midbody scales 17-22 (mean 19.7), loreals 3-6 (mean 4.2), temporals 7-10 (mean 8.7), supraoculars 6-6 (39 specimens), 5-5 (1), 5¹/₆ (1), 6¹/₇ (2), 7-7 (8), semicircles usually incomplete (84.3 percent), and parietals always in contact (100 percent). The prefrontal row consists of 2 to 4 scales (mode 3), the

median head scales vary between 3 and 6 (mode 4), and the frontoparietal row has 2 to 7 scales (mode 5); the prefrontal row is always complete (53 specimens) and the frontoparietal row is more often complete (32 of 43 specimens). The largest male measures 80 mm snout-vent length, the largest female 64 mm.

Males are ashy-gray above with a pair of darker paramedian stripes and a dark middorsal stripe, as well as with a pair of pale dorsolateral stripes—the net effect being that of a dorsally striped or lined lizard. The sides below the dorsolateral lines are dark (charcoal to reddish) with scattered blue flecks, the blue flecking extending ventrad as isolated scales onto the belly. The lateral line is buff to reddish and the lower sides are greenish-gray to faintly reddish with a heavier concentration of blue scales. The venter and underside of hindlimbs and tail are usually orange, although occasional lizards have these areas greenish-orange or grayish-orange. The throats and chests are some shade of gray, usually rather dark, and the throat pattern consists of five or six bold black transverse bars, often incomplete medially, followed by a few scattered black or dark gray smudges on the chest. Occasional specimens have the bars somewhat fragmented, but nonetheless discernible. The heads are gray to brown, usually with some random darker brown markings. The hindlimbs are immaculate tannish-orange above, and the forelimbs are dull grayish-tan with some darker gray mottling.

The females are colored like the males dorsally but the longitudinal stripes are even more bold. The ground color of the throat is pale gray and the throat pattern is comparable to that of the males, although there is a distinct tendency toward fragmentation of the bars and subsequent formation of a reticulum, especially posteriorly. The venter is usually greenish to grayish-white and lacks the brighter shades of orange.

Juvenile males are patterned like the females and are boldly lineate above.

The dorsal striped pattern of *beatanus* will distinguish the insular subspecies from all other races; occasional males from the mainland are striped dorsally, but never so boldly as *beatanus*. The throat pattern of

beatanus differs widely from that of *barabonensis* and *aureus* and most closely resembles that of *oxygaster*. In the latter the throat pattern consists of three or four transverse bars followed by a rather large area of dark smudges and may even be reticular, whereas in *beatanus* there are five or six bold bars with less posterior area devoted to smudges. The striped dorsal pattern (which occurs occasionally in *oxygaster*) will also separate *beatanus*. In having a mode of 4 frontoparietals *oxygaster* differs from *beatanus* with a mode of 5; in *beatanus* there are 17 specimens with 5 frontoparietals (the modal class) and 16 with 4 frontoparietals, so that the modality of 5 is almost equalled by a modality of 4.

Judging from the number of specimens available, *L. b. beatanus* is quite common in Isla Beata. *L. b. beatanus* occurs in open areas on the limestone platform on Beata, both on exposed limestone and in stands of a small arborescent cactus. Its closest affinities are obviously with *oxygaster* of the adjacent mainland, these two subspecies being the only two with distinct throat barring. The prominently striped dorsum and different coloration details of *beatanus* are characteristic of the insular subspecies.

Specimens examined: República Dominicana, Isla Beata, 57 (ASFS V2723-42, MCZ 17737—paratype, 33382, 28726-40 + two untagged, 37539-50 + three untagged; RT 933).

Leiocephalus vinculum Cochran, 1928

Leiocephalus vinculum Cochran, 1928, Proc. Biol. Soc. Washington, 41:54 (type locality—Pointe à Raquettes, Ile de la Gonâve, Haiti).

Definition: A species of *Leiocephalus* characterized by a combination of 1) moderate size (males to 77 mm, females to 73 mm snout-vent length), 2) sexual dichromatism not pronounced dorsally but throat pattern dichromatic in one subspecies, and males with a pair of enlarged postanal scales, 3) absence of a lateral fold, 4) dorsal scales imbricate, denticulate, and keeled, ventral scales imbricate, smooth, and weakly to strongly denticulate, 5) median dorsal crest scales slightly enlarged, not attenuate, slightly imbricate (Fig 9b and c), lower than median dorsal caudal scales, 51 to 65

in occiput to vent distance, 6) one half midbody scales 18 to 28, 7) supraoculars usually 6-8, 8) loreals 3-7, 9) temporals 8-13, 10) supraorbital semicircles most often complete, 11) parietals always in contact, 12) median head scales varying between 3 and 7, 13) preauricular scale small (Fig. 2a), 14) throat in one or both sexes black, or with a pair of paramedian dark longitudinal lines, 15) ventral color yellow, 16) ventral pattern absent in both sexes, 17) mask absent, and 18) black neck and shoulder patches absent.

Leiocephalus vinculum vinculum

Cochran, 1928

Type locality: Pointe à Raquettes, Ile de la Gonâve, Haiti.

Holotype: MCZ 25435, an adult female, with a snout-vent length of 66 mm.

Diagnosis: A subspecies of *L. vinculum* characterized in males by a tan to metallic tan dorsum with prominent dorsolateral buffy stripes, the dorsal zone with a vague pair of paramedian dark stripes which enclose about twelve chevron arm remnants on each side, throat clouded yellowish-gray with a dark gray to black pattern consisting of a pair of paramedian dark lines preceded by one or two dark transverse bars and bordered laterally by parallel lines or line remnants (Figs. 10b, 12a), ventral ground color pale yellow; size large (males to 77 mm, females to 73 mm snout-vent length), frontoparietals modally 5.

Distribution: Ile de la Gonâve, Haiti (Fig. 6).

Variation and discussion: The series of 45 *L. v. vinculum* has the following scale counts: dorsal crest scales occiput-vent 51-60 (mean 55.8), dorsal crest scales occiput-axilla 15-24 (mean 18.6), dorsal crest scales on trunk 32-41 (mean 37.0), one half midbody scales 18-24 (mean 20.5), subdigital fourth toe tricarinate scales 21-26 (mean 23.3), loreals 3-7 (mean 4.8), temporals 8-12 (mean 9.8), supraoculars 6/6 (49 specimens), 5/6 (1), 6/7 (1), semicircles usually complete (68.6 percent) and parietals always in contact (100 percent). The prefrontal row consists of 2 to 5 scales (mode 3), the median head shields vary between 3 and 7 scales (mode 4) and the frontoparietal row has 2

to 5 scales (mode 5); the prefrontal row is always complete (53 specimens), and the frontoparietal row is usually complete (40 of 52 specimens). Although presence of 3 prefrontals is distinctly modal (33 lizards), the high incidence of 2 prefrontals (19 lizards) is noteworthy. The largest male measures 77 mm snout-vent length, the largest female 73 mm (and is the largest female of any member of the *L. personatus* complex); the male is from Etoits, and the female from Ti Palmiste.

The males have a tan to metallic tan broad dorsal zone bounded by a pair of prominent buffy dorsolateral stripes. The dorsal zone also includes a pair of darker paramedian stripes with a series of about twelve darker areas which, upon comparison with the females, are shown to be the remnants of the arms of the chevrons. The head is tan with occasional dark suffusions and dark dots. The neck may have as many as three complete chevrons but these are not black or outstanding as are the nuchal and scapular bars of some races of *L. personatus*. The sides are darker brown than the back with scattered clear yellow (not green, blue, turquoise, brick, or orange) scales. The throat is pale yellow, much clouded with gray, and the venter is also pale yellow. The throat pattern consists of gray to black markings, including a pair of paramedian longitudinal lines which do not extend onto the chest, preceded by one or two fainter dark transverse bars and bordered laterally either by two more longitudinal lines or remnants thereof. The chest is usually gray with some darker gray spots and yellow scales admixed. The yellow scales on the sides of the body extend onto the venter in irregular rows but remain distinct despite the pale yellow ventral ground color. The underside of the hindlimbs is heavily mottled with clear yellow scales. The tail is tan above and weakly chevronate, and is pale clear orange below. There is a deep orange suffusion on the sides of males in the region of the groin. The hindlimbs are brownish dorsally with some yellow flecks; the forelimbs are tan above with vague darker mottling.

Females are colored above like the males, but lack the metallic sheen. The dorsolateral stripes are moderately prominent and

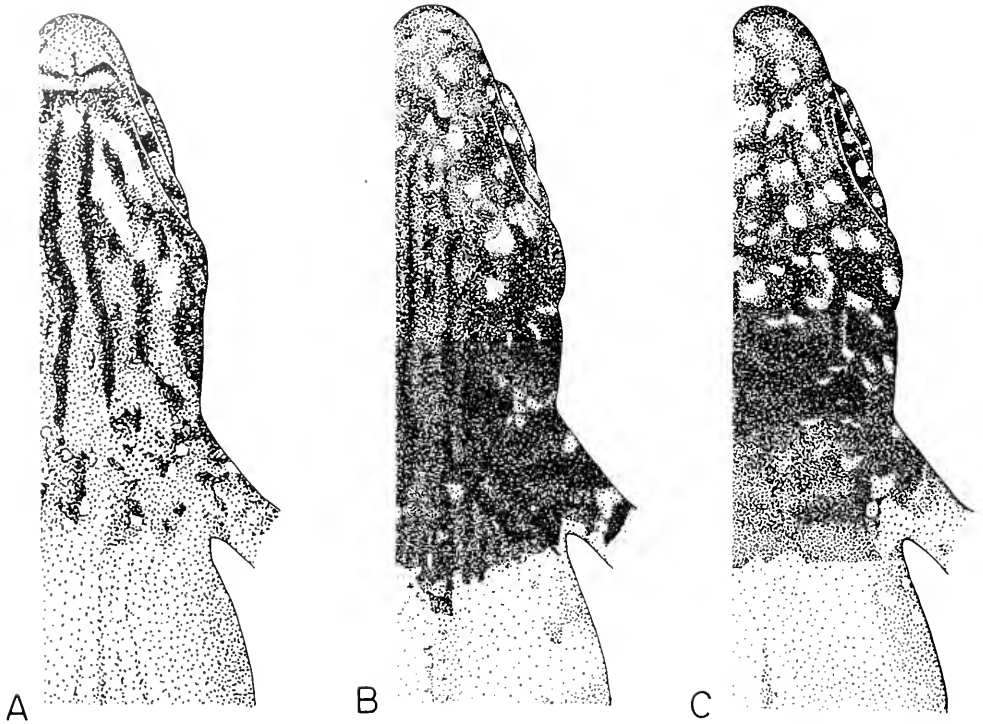


Figure 12. Ventral view of throat of males of three subspecies of *L. vinculum*, as follows: a) *L. v. vinculum*, ASFS X2491, 1.5 mi. S Etroits, Ile de la Gonâve, Haiti; b) *L. v. endomychus*, MCZ 81099, holotype, 3.4 mi. NE Barrage de Péligre, Dépt. de l'Ouest, Haiti; c) *L. v. altavelesis*, MCZ 79374, Isla Alto Velo, República Dominicana.

the dorsal zone includes two paramedian dark stripes which contain about twelve chevron tips. The median dorsal zone has the remainder of the chevrons strongly to weakly indicated, so that the net effect is one of a herringboned or transversely banded lizard. The throat is pale gray and the pattern is comparable to that of the males; the paramedian throat lines may be preceded by two or three dark transverse bars and bordered laterally by about three diagonal lines (pointed anteromedially) or their remnants. The throat pattern is most distinct in young females, and these smaller specimens (and an occasional subadult) have some gray flecking extending onto the anterior and lateral portions of the abdomen. The lateral line between the limbs, which is absent in adults of both sexes, is only very weakly indicated in young females. The sides of young females may have some indications of lateral longitudinal dark dashes, but this is not the rule.

The single juvenile male with a snout-vent length of 42 mm is colored and patterned like the young females, and has some gray chest and lateral abdominal streaking.

L. v. vinculum is the only species of the genus known from Ile de la Gonâve. It is widespread on the island, occurring from Pointe Ouest (Cochran, 1941:238) in the north to the southern portion of the island at Pointe à Raquettes. Near Etroits, the lizards were abundant on the rocky hillside at the foot of the hills which form the central Gonâve uplands. The flora here was xeric scrub with some large shade trees. The lizards were sunning on rocks in the early afternoon (1300 hours) and had not been seen between 1100 hours and that time.

Specimens examined: Haiti, Ile de la Gonâve, 1.5 mi. (2.4 km) S Etroits, 15 (ASFS X2491-505); Pointe à Raquettes, 2 (MCZ 25435 — holotype, MCZ 25437 — paratype); Ti Palmiste, 6 km from Pointe à

Raquettes, 31 (MCZ 80769-99); Nan Café, 5 (MCZ 61059-63).

Lerocephalus vinculum **endomychus**,
new subspecies

Holotype: MCZ 81099, an adult male, from 3.4 mi. (5.5 km) NE Barrage de Péligre, 1100 feet (361 meters), Dépt. de l'Ouest, Haiti, one of two taken 11 July 1962 by David C. Leber and Albert Schwartz. Original number X2215.

Paratype: ASFS X2216, same data as holotype.

Associated specimen: Haiti, Dépt. de l'Artibonite, Hinche, 1 (MCZ 25431).

Diagnosis: A subspecies of *L. vinculum* characterized in males by a combination of a pale greenish-tan dorsal zone without dorsolateral stripes, the dorsal zone crossed by a series of about twelve grayish herringbones, throat and chest solid black with scattered green scales on chin and throat, the black pigment extending dorsally onto the sides of the neck and onto the anterior surface of the forelimbs (Figs. 10c and 12b), ventral ground color yellow; size moderate (male 69 mm, female 59 mm snout-vent length), frontoparietals 4.

Distribution: Known only from the type locality in central Haiti and very questionably from Hinche to the north of the type locality (Fig. 6).

Description of holotype: An adult male with the following measurements and counts: snout-vent length 69 mm, tail 79 mm, distal two-thirds regenerated; dorsal crest scales occiput-vent 57, dorsal crest scales occiput-axilla 19, dorsal crest scales on trunk 38, one half midbody scales 21, subdigital fourth toe tricarinate scales 21 -, loreals 4, temporals 10, enlarged auriculars $4\frac{1}{3}$; 3 prefrontal scales, row complete; 4 median head shields; 4 frontoparietal scales, row complete; supraoculars $6\frac{1}{6}$; supra-orbital semicircles complete, parietal scales in contact.

Dorsal ground color greenish-tan with no indication of dorsolateral stripes or lines; a series of about twelve grayish herringbones separated by pale greenish scales, the entire back having a distinctly transversely banded or herringbone pattern. Sides grayish-tan with scattered green scales,

lateral line between limbs absent. Head tan above. Throat and chest black (slightly less intense on anterior two-thirds of throat) with scattered green scales on throat; black throat pigment extending dorsally onto the sides of the neck and onto the anterior aspect of the brachia. Hindlimbs greenish above, marbled with gray; forelimbs gray marbled with darker gray above. Tail (unregenerated portion) grayish with vague darker gray chevrons. Venter yellow with irregular lines of green scales extending ventromedially from sides. Underside of tail yellow.

Variation: The paratype is an adult female with a snout-vent length of 59 mm, dorsal crest scales occiput-vent 65, dorsal crest scales occiput-axilla 19, dorsal crest scales on trunk 46, one half midbody scales 23, subdigital fourth toe tricarinate scales 20 20, loreals 5, temporals 13, supraoculars 6 6, semicircles complete, parietals in contact; 2 prefrontals, row complete; 4 median head shields; 4 frontoparietals, row complete.

The female is dull brown above with about fourteen dull brownish transverse bars or herringbones. In details of pattern the female resembles the male, lacking a lateral line and with very pale greenish scales extending from the sides onto the venter. The throat is very dark but allows the appearance of a pair of longitudinal paramedian lines bordered by a dark gray reticular area on each side. The venter and the underside of the tail are yellowish-green. The tail is brown with distinct chevrons above. Both fore- and hindlimbs are brown, marbled with paler brown or tan.

Comparisons: Male *L. v. endomychus* can be easily differentiated from male *L. v. vinculum* by the black throat with scattered green scales of the former versus a patterned throat in the latter. The tan dorsa of *vinculum* with their prominent dorsolateral stripes contrast with the transversely barred and greenish dorsum without longitudinal stripes in *endomychus*. Females are similar, but the throat of the single female *endomychus* is much darker than that of any of the many female *vinculum*, and the pattern is reminiscent but less prominent. Apparently, *endomychus* has a higher number of dorsal scales in occiput to vent and a

greater number of temporals; these differences need confirmation by additional specimens. The modal number of 5 median head shields in *vinculum* contrasts with the mode of 4 in *endomychus*.

Remarks: The type and topoparatype of *L. v. endomychus* were collected on the hillside above the lake formed by the Barrage de Péligre. The male was taken on the rocky wall of a roadcut, and the female was secured in a shady cavity in the same roadcut about 3.5 meters above the road. The general area was mesic but sunny and exposed. No other lizards were observed.

The associated specimen (MCZ 25431) is from Hinche, which lies about 28 kilometers directly north of the type locality. I associate this lizard with *endomychus* only extremely tentatively. It is an adult male with a snout-vent length of 73 mm and is thus larger than the type. The specimen is presently discolored and shows only the very vaguest dorsal pattern, which includes prominent dorsolateral stripes. The throat, although dark, is not black and has a pattern of a pair of paramedian dark lines bordered by areas of dark smudges and longitudinal dashes. The specimen is clearly *L. vinculum*, but it does not agree in pattern with the very distinctive specimens from Péligre. It has 56 dorsals in occiput-vent distance (thus just one scale below the lowest count of *endomychus* and not significant), but has extremely high fourth toe counts of 28 and 27—much higher than the counts of 20 and 21 in the two *endomychus*. Hinche lies on the Plateau Central, and the type locality of *endomychus* is on the southern slopes of the Montagnes Noires; conceivably there is another subspecies of *L. vinculum* on the Plateau.

Although no other species of *Leiocephalus* is known from the region of the type locality, it is noteworthy that *L. personatus scalaris* occurs nearby both in Haiti (at Cerca-la-Source, 40 kilometers northeast) and in the República Dominicana (Bánica, 40 kilometers east-northeast). These localities are even closer to Hinche. If the two species occur together in this region, they can easily be distinguished by the attenuate crest scales and practically unpatterned throat of *scalaris* in contrast to the non-

attenuate scales and dark or lined throats of *L. vinculum*.

Leiocephalus vinculum altavelensis Noble and Hassler, 1933

Leiocephalus altavelensis Noble and Hassler, 1933, Amer. Mus. Novitates, 652:14.

Type locality: Isla Alto Velo, República Dominicana.

Holotype: AMNH 51055, an adult male, with a snout-vent length of 60 mm (*vide* Noble and Hassler, *op. cit.*:15).

Diagnosis: A subspecies of *L. vinculum* characterized in males by a combination of a yellowish-brown dorsal zone not outlined by dorsolateral stripes and usually with a series of about twelve transverse bands giving a faintly crossbarred or herringbone effect, throat and chest dark blue-gray spotted with white (Fig. 12c), ventral ground color yellowish; size moderate (males to 71 mm, females to 63 mm snout-vent length), frontoparietals modally 5.

Distribution: Isla Alto Velo, República Dominicana (Fig. 6).

Variation and discussion: The series of 21 *L. v. altavelensis* has the following scale counts: dorsal crest scales occiput-vent 54-61 (mean 57.2), dorsal crest scales occiput-axilla 15-23 (mean 19.6), dorsal crest scales on trunk 31-43 (mean 37.7), one half midbody scales 23-28 (mean 25.5), subdigital fourth toe tricarinate scales 24-29 (mean 26.3), loreals 3-5 (mean 3.7), temporals 9-13 (mean 10.8), supraoculars 6/6 (15 specimens), 6/7 (5), 7/7 (3), 7/8 (1), 6/8 (1), 9/10 (1), semicircles equally divided between incomplete and complete, and parietals always in contact (100 percent). The prefrontal row always consists of 3 scales (26 specimens), the median head shields are 3 to 5 (mode 4), and the frontoparietal row has 3 to 6 scales (mode 5); both the prefrontal and frontoparietal rows are always complete. The largest male has a snout-vent length of 71 mm, the largest female 63 mm.

L. v. altavelensis is one of the two members of the *personatus* complex which I have not seen in life, and this is especially unfortunate, since *altavelensis* is certainly the most puzzling lizard of the group. Fortunately, Noble and Hassler (*op. cit.*:16)

have given some information on the coloration of this form in life, and I have drawn on their notes. The dorsum is yellowish-brown, without dorsolateral longitudinal pale lines, and with a golden-bronze sheen. The dorsal pattern is variable, since these authors stated that the males lacked any dorsal pattern except for one lizard that, prior to shedding, showed faint cross-lines which became indistinct after shedding. Of the six males before me, only one (AMNH 51054, the largest male known) lacks dorsal crossbars, and this lizard is presently badly worn. A slightly smaller male (AMNH 51060, snout-vent length 66 mm) clearly shows the bars or at least their remnants. It is possible that large males lose these crossbars, but even this is not certain since so few male *altavelensis* are known. The legs are darker than the back and have light spots, but no barring. The tail is light yellowish-brown above with faint chevrons. The sides are greenish with scattered metallic green scales. The throat is dark bronzy brownish-black with small white spots which are at times confluent. The venter is yellowish with sometimes a slightly green tint.

Noble and Hassler noted that there was no sexual dichromatism, and there appears to be none in pattern (and probably also in coloration) in the specimens before me. The females are all distinctly crossbarred dorsally, and all have the throat pattern like that of the males. The dorsally spotted head of both sexes is a very distinctive feature of *altavelensis*.

L. v. altavelensis is said to be common on Alto Velo, "living among rocks, leaves and grass along the coast and ranging to the top of the higher ridge in the center of the island" (Noble and Hassler, *loc. cit.*).

I have debated the affiliation of *altavelensis* since I first examined the specimens. Its closest geographic relative (on Isla Beata, which lies to the northeast of Alto Velo and is separated by a channel 12 kilometers in width) is *L. b. beatanus*. These two forms are extremely different in pattern and size, with *altavelensis* smaller, transversely barred dorsally, and with virtually black throats, and *beatanus* large and stocky, longitudinally lined dorsally, and with transversely barred throats.

The most trenchant scale difference between *L. barabonensis* and *L. vinculum* is the presence in the former of the enlarged preauricular scale. In this character, *altavelensis* clearly is like *vinculum*. *L. barabonensis* is more strongly dimorphic (males to 80 mm, females to 64 mm) than is *vinculum* (males to 77 mm, females to 75 mm). *Altavelensis* is intermediate between these two extremes, but the difference (males to 71 mm, females to 63 mm) is more like that of *vinculum* than *barabonensis*. The dorsal pattern of *altavelensis* is transversely oriented, which is the case also in *vinculum*, but not in *barabonensis*, where the pattern is longitudinally oriented. The yellow venter of *altavelensis* is like that of *vinculum* and different from the very vivid colors (yellow-orange and orange) of *barabonensis*.

In most scale counts (but especially in the three dorsal counts, midbody scales, and number of temporals), *altavelensis* agrees with *vinculum* and *endomychus*. The most obvious exceptions to this are counts of fourth toe scales (which are higher in *altavelensis* than both *barabonensis* and *vinculum*) and loreals (which are less in *altavelensis* than in *vinculum* or *endomychus*, and in fact lower also than any subspecies of *barabonensis*). In extremes of the three dorsal scale counts and temporals, *altavelensis* is like *vinculum*, and only in fourth toe scales are the extremes of *altavelensis* like those of *barabonensis*.

The dark throats of both sexes of *altavelensis* with their scattered white scales are very reminiscent of the dark throat with scattered green scales of *endomychus*. In the latter subspecies, females still show the longitudinal orientation of the throat lines, a feature of *L. v. vinculum*. At least young female *altavelensis* have the throats dark as do adults of both sexes, and there is no evidence from this source as to the basic throat pattern of *altavelensis*. Finally the condition of the supraorbital semicircles might be a useful clue, but the precise division of the available specimens into half with complete semicircles and half with them incomplete precludes any useful information from this character.

There are three interpretations of *altavelensis*: 1) *altavelensis* is an extremely

aberrant subspecies of *L. barabonensis*, both scutellologically and chromatically different from its parent stock; 2) *altavelensis* is a separate species (in which event, the sole character which might distinguish it from both *L. barabonensis* and *L. vinculum* is the black throat in both sexes; 3) *altavelensis*, despite its peculiar geographic position, is a subspecies of *L. vinculum*. Another alternative is that *L. barabonensis* and *L. vinculum* are conspecific, and that *altavelensis* in some ways bridges the gap between these two forms. I reject this latter interpretation as unsatisfactory. If *altavelensis* is not to be regarded as a race of *L. vinculum*, then it must be considered a separate species, and not as a subspecies of *L. barabonensis*. To include it in the latter weakens the diagnosis and concept of *L. barabonensis*, thereby obscuring the distinctive scale and chromatic characters of this southern species.

L. v. altavelensis may be differentiated from *L. v. vinculum* by its yellow-brown dorsal coloration and very dark throat without longitudinal lines. From *L. v. endomychus*, *altavelensis* differs in brown rather than green dorsum and in having black-throated females. Of the two northern races, *altavelensis* seems closer to *endomychus* than *vinculum*.

Specimens examined: República Dominicana, Isla Alto Velo, 26 (AMNH 51051-54, 51056-68, 51070-71—paratypes; MCZ 43950-51—paratypes; MCZ 79373-77).

Leiocephalus eremitus Cope, 1868

Leiocephalus eremitus Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, 20:122.

Mertens (*op. cit.*:10), in discussing the affinities of the Navassan fauna with that of Hispaniola and Cuba, suggested the relationship of *L. eremitus* with *L. personatus*. Such a relationship is not unwarranted, since the Navassan fauna has several elements which are allied to Hispaniolan species. There are but two specimens of *eremitus* known, the holotype (USNM 12016) and a referred juvenile individual (AMNH 16919). The latter in actuality is not conspecific and was presumably collected in Haiti (see Thomas, 1966, and Schwartz, 1966), and represents the western subspecies of *Leiocephalus melanochlorus*. Thus,

comments upon the status of *eremitus* perforce must be based upon only the holotype; the species is presently presumed to be extinct.

The holotype is a large female, with a snout-vent length of 64 mm. The counts are: dorsal crest scales occiput-vent 50, dorsal crest scales occiput-axilla 16, dorsal crest scales on trunk 34, one half midbody scales 21, subdigital fourth toe tricarinate scales 27 28, loreals 6, 7, temporals 13, supraoculars 7 7, semicircles incomplete, parietals in contact; 5 prefrontals, row complete; 7 median head shields; 5 frontoparietals, row incomplete. The dorsum now is gray with about nine transverse bands with paler posterior edges, not uniform in width, narrower toward the midline, and somewhat staggered. The venter is extremely dark brown with many light-tipped scales; the chest and throat are similar to the abdomen and there is no obvious throat pattern.

The most salient structural character of *L. eremitus* is the comb-scales which lie on the outer edges of toes 1 and 2. These scales in *eremitus* are multicarinate, and not unicarinate and cuneiform as they are in all other living West Indian members of the genus.

The peculiar head scalation (with a formula of 5-7-5) and the structure of the comb-scales, as well as the "aberrant" ventral coloration and pattern, all attest to the distinctness of *L. eremitus*. I see no valid reason to associate it with any members of the *personatus* complex (although the dorsal pattern is reminiscent of that of *L. vinculum*), nor for that matter with any other West Indian species. Apparently *L. eremitus* was a very distinctive Navassan endemic which is presently extinct.

The following table summarizes salient features of the four species of the *Leiocephalus personatus* complex described in this paper.

DISCUSSION

In the foregoing account, the species *Leiocephalus personatus* has been shown to be divisible into four species—*personatus*, *lanatus*, *barabonensis*, and *vinculum*. Although each species has in combination both scale and pattern coloration characteristics which distinguish it from each of the others,

Table 1. Chart showing mensural, chromatic and scale characters of the four species of *Leiocephalus* in the *personatus* complex.

	<i>L. barabonensis</i>	<i>L. vinculum</i>	<i>L. personatus</i>	<i>L. lunatus</i>
Maximum size ♂	80	77	86	67
♀	64	73	63	60
Supraorbital semicircles	usually incomplete	usually complete	usually complete	usually complete
Preauricular scale	very large	small	small	small
Dorsal crest scales (♂'s)	not attenuate	not attenuate	attenuate	attenuate
Throat pattern ♂	bold black reticulate or transversely barred	very dark to solid black, usually with longitudinal lines	solid black to pattern except a few diffuse dots	heavy discrete dots
♀	dark gray reticulate or transversely barred	very dark	heavy dots	faint gray dots
Ventral color	orange	yellow	green to yellow	pale yellowish to tan or lavender
Ventral pattern ♂	none	none	none	none
♀	none	none	dots	none
Face mask	absent	absent	present, bold	absent
Neck blotch	absent	absent	absent	present
Dorsal crest scales (occiput-vent)	42 - 57	51 - 65	41 - 64	50 - 68
Dorsal crest scales (occiput-axilla)	12 - 22	15 - 24	13 - 27	16 - 27
Dorsal crest scales (trunk)	25 - 40	32 - 46	22 - 44	32 - 46
One half mid-body scales	16 - 24	18 - 28	18 - 28	19 - 27
Fourth toe scales	19 - 23	20 - 28	18 - 27	20 - 27
Loreals	2 - 8	3 - 7	2 - 10	2 - 8
Temporals	7 - 11	8 - 13	7 - 14	7 - 14

there are two pairs of species involved—*personatus* and *lunatus*, and *barabonensis* and *vinculum*. The character of the dorsal crest scales (attenuate in the first species pair, not attenuate in the second) seems a basic difference. The differences between the species *personatus* and *lunatus* seem to me greater in degree than the differences between *barabonensis* and *vinculum*, although the large versus small preauricular scale in this latter pair is significant. There is no reason to combine *personatus* and *lunatus*, since there is no evidence of intergradation between them, both maintaining their distinctness where they occur

sympatrically. On the other hand, it might be proper to combine *barabonensis* and *vinculum*, especially because of the occurrence of *altavelensis* so far removed from its relatives to the north. However, if *barabonensis* and *vinculum* are combined, we unite two forms which differ strongly in size of the preauricular scale, completeness of the supraorbital semicircles (complete in *vinculum*, incomplete in *barabonensis*), basic dorsal pattern (zonate or lined in *barabonensis*, transversely barred in *vinculum*), and throat pattern (longitudinally lined or solid black in *vinculum*, transversely barred or reticular in *barabonensis*). There

seems no reason at present to weaken the definition of either of these species by including the other.

Of the four species, two are clearly north island (*sensu* Williams, 1961) forms—*personatus* and *lunatus*. The occurrence of *personatus* on the northern coast of the south island suggests that *personatus* has invaded this region from the north and has been prevented further access to the south by the high ranges of the La Hotte and La Selle (although it has apparently been able somewhere to cross to Aquin in the south). There is presently a large gap between the range of the Tiburon subspecies (*personatus*) and that subspecies closest on the south shore of the north island (*trujilloensis*); this gap is partly closed by specimens from the north slope of the Sierra de Neiba, although these Sierra de Neiba populations are not in a direct line, either geographically or as far as relationships are concerned, with either *personatus* or *trujilloensis*, their affinities being with *agraulus* in the Cordillera Central. Much of the area between *personatus* and *trujilloensis* today is inhospitable as far as these lizards are concerned, being the very arid Cul de Sac-Valle de Neiba plain (which in actuality is a fossil strait formerly separating the north and south islands) and the almost equally dry Llanos de Azua. These xeric regions are in general not suitable for *L. personatus* and are today occupied by two other species of *Leiocephalus*, *semilineatus* and *schreibersi*.

Possibly the two specimens of *L. personatus* from St. Marc are pertinent; these specimens (unassignable to subspecies) may represent an *L. personatus* population which once (and perhaps even today) extended along the southern shore of the north island and from which *L. p. personatus* was derived. Collecting in the coastal strip between Port-au-Prince and St. Marc has not revealed *L. personatus*, but this is negative evidence at best. In any event, it seems likely that the range of *L. personatus* on the north island was once more extensive than it is today, and that the species has retracted from some areas where it formerly occurred.

The origin and distribution of *L. lunatus* is difficult to explain. No living population of *L. personatus* approaches *L. lunatus* in details of pattern and coloration. Its

nearest geographical *personatus* races (*trujilloensis*, *mentalis*, *tarachodes*) are all so distinctly different that none can logically be invoked as ancestral to *L. lunatus*. The occurrence of a subspecies of *L. lunatus* on Isla Saona and the occurrence of three mainland subspecies in a relatively restricted area indicate that *L. lunatus* has been in residence here for some time. I consider *L. lunatus* the resident of this southeastern coastal region, and *L. p. trujilloensis* as the invader from the west. Once again, as in *Ameiva lineolata* and two subspecies of *Ameiva chrysolaeama*, *trujilloensis* stops abruptly at about the region of Baní, where the dry Llanos de Azua merge with the more mesic eastern coastal plain. It seems possible that a *trujilloensis*-like lizard formerly inhabited areas farther to the west along the coast of the north island, and has since become increasingly restricted eastward with climatic and vegetational changes in the Llanos de Azua. Perhaps *L. lunatus* was the resident species of these southeastern mesic regions whose distribution has been compressed both by climatic change and invasion by *trujilloensis*, although the latter has apparently not been overly successful.

The northern subspecies of *L. personatus* (*scalaris*, *actites*, *tarachodes*, and, since it intergrades with *tarachodes*, *mentalis*) form a group of races which are obviously related. Of them, *mentalis* is the most distinct. I consider that these subspecies represent one center of differentiation and dispersal, probably from an area in or about the Valle de Cibao. Of all the races of *L. personatus*, only *scalaris* tolerates extremely xeric conditions, although in this dry macrosituation it inhabits more shady microsituations. I consider that *tarachodes* was derived from *scalaris* (and further that *mentalis* is a *tarachodes* derivative) and that *actites* evolved by a northwestward coastal movement from *tarachodes*, rather than across the Cordillera Septentrional from *scalaris*.

It seems logical to consider *budeni* a derivative of *scalaris* (since it is close to *scalaris* geographically) and *agraulus* a derivative of *budeni*. I doubt that this is the true situation, since *budeni* differs radically from both its neighbors in coloration and shows no special relationships to either, although it appears closer to *scalaris*. Both

budeni and *agraulus* have surely had long and independent histories; the latter has presumably evolved in the high Cordillera Central and the former in the pine-clad northeastern slope of this same range.

L. barabonensis is completely restricted to the eastern end of the south island; it occurs on Isla Beata also. There is no evidence that *barabonensis* and *vinculum* are conspecific. I do not know what prevents *barabonensis* from extending west of Jacmel, and perhaps it does. It is not known to occur in the Les Cayes-Cavaillon region which is occupied by *L. melanochlorus*. Along the north slope of the Sierra de Baoruco, *L. barabonensis* occurs very near to the Dominico-Haitian border, and should certainly be looked for along the southern border of the Cul de Sac Plain in Haiti. I have no doubt that *L. barabonensis* occupied at least the eastern portion of the south shore of the inter-island strait. Differentiation of *L. barabonensis* into three subspecies on the Península de Barahona in response to local geographic and edaphic conditions has already been discussed. Why *areus* and *oxygaster* meet and intergrade in the precise area they do is unknown. There is no obvious physiographic reason to single out this region as a dividing line between the two subspecies, but nonetheless it is. *L. b. beatus* is a direct derivative of *L. b. oxygaster* and colonization of Beata from the adjacent mainland can easily account for the similarity of these two races.

Of the four species, only *L. vinculum* presents a real problem of distribution. Occurring on two islands, one to the north of and the other to the south of the south island, and in the interior of Haiti as well, *vinculum* has a most peculiar disjunct distribution. I regard *vinculum* as the earlier and sequential forerunner of *barabonensis*, which was previously more widespread on the south island and which thence migrated to the north island across the inter-island channel. Once on the more northern land mass, *vinculum* occupied the central interior portion of Haiti. Although there is no evidence either pro or con, I suspect that at one time (and probably today) *vinculum* was the dominant *Leiocephalus* of this complex in the poorly known interior of Haiti; it may also have occurred in

favorable localities along the shores of the Golfe de la Gonâve. From this mainland center, *L. vinculum* reached Gonâve and there developed the distinctive *L. v. vinculum*. On the south island, *L. vinculum* had reached Alto Velo, but not Beata; the absence of the species on Beata is fortuitous.

Meanwhile, on the south island, *L. barabonensis* evolved from a *vinculum*-like ancestor; I can suggest no other region for the origin of *barabonensis* than the Península de Barahona. Since today *L. barabonensis* prefers more shady and mesic situations and occurs at least in the forested foothills of both the Massif de la Selle and the Sierra de Baoruco, it is possible that primitively *barabonensis* was an upland (versus *vinculum* as a lowland) species. Whatever the situation, *barabonensis* gradually expanded its range and forced out *L. vinculum* from the Barahona, and invaded Isla Beata. Again fortuitously, *L. barabonensis* has not succeeded in crossing the strait between Beata and Alto Velo, and on this latter islet *L. vinculum* has been able to persist. If the above postulated history of these two species on the south island is reasonable, one might expect that there are residual *L. vinculum* populations on the Península de Barahona—something which has yet to be demonstrated. However, there may well be no colonies of *L. vinculum* in this region due to the success of *L. barabonensis*. On the other hand, the extreme southern portion of the Barahona is still unknown herpetologically, and possibly relict *L. vinculum* may be encountered there.

Hispaniola has the richest *Leiocephalus* fauna of the West Indies. There are now recognized eight living Hispaniolan species (*semilineatus*, *pratensis*, *schreibersi*, and *melanochlorus*, in addition to the four in the *personatus* complex). A key to the eight Hispaniolan species is presented below. There is also an extinct species (*L. apertosalvus* Etheridge) known from the north island. Cuba stands second with diversity of members of the genus, with five species (*carinatus*, *raticeps*, *macropus*, *cubensis*, *stictigaster*). Five species occur in the Bahama Islands (*carinatus*, *loxogrammus*, *greenwayi*, *psammodromus*, *inaguae*) of which two are obviously related to Cuban (*carinatus*, *lox-*

ogrammus) and one (*inaguae*) to Hispaniolan species. (Etheridge, 1964:55, regards *punctatus* in the Bahamas as an additional Bahaman species). There are two recently extinct species, *eremitus* on Navassa and *berminieri* on Martinique, and three fossil species, *cuneus* from Barbuda, *apertosulcus* from Hispaniola, and *jamaicensis* from Jamaica have been described. There are *Leiocephalus* on all of the Cayman Islands (*carinatus*) and the genus is known fossil from Florida (Etheridge, *op. cit.*:57).

From the above summary of the known distribution of the species of *Leiocephalus*, it is clear that Hispaniola has been the primary center of differentiation of *Leiocephalus* in the Antilles. The variety of coloration, pattern, size, structural and scale characteristics of the Hispaniolan forms easily exceeds the lesser diversity of the Cuban species. Between the Cuban and Hispaniolan species, there are no clear-cut indicators of relationships. Each island must have had one or several early independent invasions, with subsequent differentiation *in situ*. The much greater topographic and historical complexity of Hispaniola versus Cuba has contributed to the complexity of the interrelationships of the Hispaniolan species.

The following key will serve to identify Hispaniolan species of *Leiocephalus*. In a third part of my studies on *Leiocephalus* additional races will be described. Until that time a key to the subspecies would be premature.

Key to the Hispaniolan species of *Leiocephalus*

- 1. a) Lateral folds with conspicuously smaller scales present 2
- b) Lateral folds absent 3
- 2. a) Size large ($\delta\delta$ to 130 mm, $\text{♀}\text{♀}$ to 102 mm snout-vent length); dorsal scales 37 to 53 in occiput-vent distance; supraoculars usually 6/6; dorsal pattern not distinctly sexually dichromatic, consisting (by subspecies) of either 9 to 11 dark velvety crossbands or faint, fragmented or obsolete crossbands; throat reticulated or very dark and without pattern in both sexes *L. melanochlorus*

- b) Size moderate ($\delta\delta$ to 107 mm, $\text{♀}\text{♀}$ to 75 mm snout-vent length); dorsal scales 63 to 87 in occiput-vent distance; supraoculars usually 7/7; dorsal pattern distinctly sexually dichromatic, $\delta\delta$ (by subspecies) pale sandy to tan sprinkled with pale dots or with a median dark brown band, $\text{♀}\text{♀}$ with a series of about 8 transverse grayish bars and often with a black to gray axillary spot; throat in males grayish to purplish with scattered clear pale blue to green scales, in females streaked or clouded with darker gray *L. schreibersi*
- 3. a) No regular row of middorsal scales; frontoparietal row almost always complete, preauricular scale not enlarged; dorsal pattern and hindlimbs prominently lined longitudinally; size small ($\delta\delta$ to 64 mm, $\text{♀}\text{♀}$ to 55 mm snout-vent length) *L. pratensis*
- b) A row of median scales present, either conspicuously enlarged or not; size variable 4
- 4. a) Preauricular scale small (= not enlarged in comparison with adjacent temporal scales) 5
- b) Preauricular scale much larger than adjacent temporal scales 7
- 5. a) Dorsal crest scales not attenuate or strongly overlapping; size moderate ($\delta\delta$ to 77 mm, $\text{♀}\text{♀}$ to 73 mm snout-vent length); supraorbital semicircles usually complete; throat pattern very dark in both sexes to solid black in males, usually with remnants of longitudinal lines. *L. vinculum*
- b) Dorsal crest scales attenuate; size moderate 6
- 6. a) Male throat with heavy discrete dots on clear pale ground, female throat with faint gray dots; neck blotch present; face mask absent *L. lunatus*
- b) Male throat solid black to patternless except for a few diffuse dots, female throat heavily patterned with dark gray spots; neck blotch absent; face mask present *L. personatus*

7. a) Size larger ($\delta\delta$ to 80 mm, $\text{♀}\text{♀}$ to 64 mm snout-vent length); dorsal crest scales enlarged but not attenuate or strongly overlapping; throat pattern present, consisting of a reticulum, black transverse bars, or dark smudges (somewhat variable between sexes); venter orange..... *L. barahonensis*
- b) Size smaller ($\delta\delta$ to 53 mm, $\text{♀}\text{♀}$ to 48 mm snout-vent length); dorsal crest scales only very slightly or not enlarged; throat white to pale purplish pink, immaculate or with some faint gray spots (females) or oblique lines (males); venter white to pale yellow..... *L. scmilineatus*

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STUDIES ON THE BIOLOGY OF THE FEEDING REACTION IN *GOBIOSOMA BOSCI*

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STUDIES ON THE BIOLOGY OF THE FEEDING REACTION
IN *GOBIOSOMA BOSCI*H. DICKSON HOESE¹

and

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ABSTRACT

In the naked goby, *Gobiosoma bosci*, an inhabitant of oyster reefs, a feeding reaction was induced with dialyzed oyster extracts. Certain amino acids and amines with similar molecular structure also induced feeding. Basically they have straight chains, 2-5 carbon atoms, and no group interfering with the area of the nitrogen atom. Dialyzed and chromatographed oyster extracts were bitten by gobies in areas corresponding with knowns of alanine, aspartic acid, glutamic acid, glycine, and an unknown. The unknown, which was heat stable, received most of the response with alanine next. Gobies responded to water in which oysters had been held and to water from an oyster reef, but not to sea water. Feeding by *Gobiosoma bosci* is divided into two phases. The first seems to be following a volatile compound, possibly an amine, to the oyster. Feeding itself is induced by a heat-stable unknown, with lesser contribution by certain amino acids.

Hasler (1957) and Teichmann (1962) summarized much of the evidence demonstrating that some species of fishes are at-

tracted to food by chemical perception. However, the compounds perceived by fishes for orientation to food seem to be largely unknown (McBride et al., 1962).

There are two cases where the type of compound is known that produces a specific response in a fish without training: Amines are utilized by lampreys for orientation to prey (Kleerkoper and Mogensen, 1963), and the amino acid serine produces a fear response in salmon (Idler et al., 1956). One recent study (Bardach and Case, 1965) investigated some sensory responses to tissue extracts. A study by Steven (1959) claimed to show feeding responses caused by some compounds.

We have been studying response of the small naked goby, *Gobiosoma bosci* Lacépède to certain smells from the Atlantic oyster, *Crassostrea virginica* (Gmelin). This fish lives in the interstices of oyster reefs. Injured or killed oysters on some reefs always attract this fish (Hoese, 1964). With this in mind we set out to find the compound, or compounds, from oysters that attract fish and cause them to feed.

METHODS

Oyster extracts were prepared from four or five 2-5 inch oysters by pulverizing oysters in a blender, dialyzing the liquid, and

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concentrating the extracts by about a factor of 10 by evaporation. One to 50 ml of extract were chromatographed as paired spots or narrow bands 3-12 inches in length on full or half sheets. The extracts were chromatographed on Whatman grades 3 & 17 paper generally as outlined by Berry et al. (1962). The two main solvents used were *N*-butanol—50% acetic acid (2:1) and water-saturated phenol. The chromatographs were dried 1 or 2 days. The paper was then cut perpendicular to the solvent front dividing the spot chromatograms into 2 sections and the band chromatograms into 2 one inch strips and one longer strip. One strip from each chromatogram was placed in the aquarium with the fishes and the second developed with 0.2% ninhydrin or aniline acid phthalate reagent. The remainder of the strip chromatogram was used for further testing or elution of the bands. In some cases the strips were removed from the aquaria, dried and stained. It was found that the bands had become diffuse, but that the centers of the bands were generally detectable. Duplicate 2-dimensional chromatographs were run, one used for testing, the other stained. The areas selected by the fishes were located by placing rulers beside the strips. Comparison of the intensity of the bands and spots to the intensity of stained known compounds suggested that each band contained between 1 & 20 μ of amino acid.

Oysters were collected from a single intertidal reef off the Port Aransas Causeway. Water was taken from this reef, evaporated or distilled at different pH levels, and chromatographed. Oyster water was prepared by holding four to eight 3-5 inch oysters in 2 liters of sea water for 24 hours or longer, evaporating or distilling and chromatographing. Control water was collected from open bay or local Port Aransas waters and was held for the same period without oysters.

Gobies were seined from an artificial pond at Live Oak Point 3 miles NNE of Fulton, Texas. There are few oysters in the pond, and the gobies feed mainly on polychaetes, so they were not conditioned to oyster meat. The behavior of the pond gobies was not different from that of gobies which had been conditioned to oysters.

Fourteen to 20 *Gobiosoma bosci* that had been held in a 32 liter aquarium were used for tests. The fish were starved at least 7

days to enhance the reaction and were replaced after having been exposed to a maximum of ten compounds. Filter paper soaked with 2cc of usually saturated solutions of compounds was introduced into the aquarium in 5 minute trials. This produced a maximum dilution of 1 part in 161, 250. A positive response was one where each individual bit (or tasted) the paper more than once at each encounter. Control filter paper soaked in sea water rarely produced a bite and never a second one. A total of 62 controls was negative.

Undisturbed gobies in aquaria remained on the bottom. When filter paper or chromatographs were introduced, no increased activity occurred unless they contained extracts or compounds that they recognized. The test was almost always clear-cut and in all cases where an individual bit a particular substance on paper it bit the paper repeatedly. The reaction subsided rapidly so that within 5 minutes control conditions were usually in effect again. A more ideal test could hardly be expected, and perhaps some of the difficulty in previous work has been the use of species which rely less on sense of smell than *Gobiosoma bosci* seemingly does.

THE FEEDING RESPONSE

The feeding response was characterized by rapid movement of a normally quiet, sedentary species and biting of objects in aquaria, including each other. Occasionally an individual would react to the extract with a "jerk" or rapid quiver of the whole body. Sometimes they would bow the head upward and rise up on their pelvics. Then they became excited and proceeded to search the aquarium. Oyster extracts introduced into aquaria in dialyzing membrane made into "bags" always attracted most gobies in an aquarium to the vicinity of the "bag" where the gobies commenced biting the "bag" as if it were food. Moving the "bag" to other areas of the aquarium caused the fish to move with it. Finding the "bag" was accomplished much the same as described for *Microgadus timcod* (Herrick, 1904).

Control "bags" of sea water got no response although some fish occasionally passed very close. To show that no visual cues were involved, extracts and controls were introduced into an aquarium in total darkness. Five minutes later, when the light was turned on, the majority of the gobies

were clustered around the "bag" with the oyster extract and biting was in progress. However, visual cues can be important. Feeding a group of gobies in one aquarium caused those in adjacent aquaria to rush toward the aquarium where feeding was occurring, probably because they saw the excited activity of fish in the adjacent tank. Naked gobies will chase and eat live, moving food, such as *Daphnia* and adult brine shrimp (*Artemia*).

MOLECULAR STRUCTURE OF COMPOUNDS PRODUCING FEEDING RESPONSE

There was considerable molecular similarity between compounds producing a response. Although many of the compounds were probably recognized by the gobies, only those with nitrogen produced a feeding response. Apparently this area of the molecule is most important, because certain groups which could sterically interfere with the amino group inhibit the reaction. For example, methionine produces a response, but S methyl-l-cysteine does not. The latter differs by having one carbon less in the chain and this directs the methyl group towards the amino group. In methionine the terminal methyl group is directed away from the amino group.

The molecules producing feeding are all characterized by being simple, short, and straight-chained with only certain attached groups. Table 1 shows the structural characteristics of molecules causing and not causing feeding. Table 2 lists the positive compounds. The following did not cause feeding: amines—agmatine; acids—acrylic, formic, acetic, propionic, butyric, valeric, succinic, lactic, cyanuric, hydantoin, 2 thio-barbituric; amino acids—arginine HCl, asparagine, p aminobenzoic, 3 aminobutyric, citrulline, cystine, 2, 6 diaminopimelic, glutamine, histidine HCl, isoleucine, lysine, phenylalanine, proline, pyroglutamic, serine, threonine, tyrosine, valine; peptides—glycylglycine, glutathione; sugars—glucose, mannose, arabinose, rhamnose, galactose; miscellaneous—guanidine, creatinine, hydroxylamine, ammonia, urea, butylurea, indole, creatine.

Quantitative data are presented in Table 2 although separate trials are not statistically comparable, because conditions were seldom the same in each set of trials. The data are included in Table 2 to show that more than

TABLE 1
Structural characteristics and examples of molecules investigated

COMPOUNDS PRODUCING FEEDING REACTIONS HAVE
2-5 carbon atoms (glycine, alanine, 5 amino-valeric acid)
amino group on carbon 2 terminal or not (alanine, glutamic acid, 2 aminobutyric acid)
amino group on terminal carbon 3 (β alanine), 4 (4 aminobutyric acid, putrescine), or 5 (5 aminovaleric acid)
1 carboxyl group (glycine, alanine)
2 carboxyl groups (glutamic acid, aspartic acid)
no carboxyl groups (putrescine, trimethylamine)
SH group (cysteine)
methylated nitrogen (trimethylamine)
S-CH ₃ in 4 position (methionine)
COMPOUNDS PRODUCING FEEDING REACTIONS DO NOT HAVE
6+ carbon atoms (lysine, cystine, diaminopimelic acid)
ureido groups (asparagine, citrulline, glutamine)
rings (histidine, phenylalanine, proline, tyrosine)
branched chains (leucine, isoleucine, valine)
hydroxyl groups (serine, threonine, tyrosine)
no amino groups (formic acid, lactic acid, ammonia)
nitrogen on carbon 3 not terminal (3 aminobutyric acid)
S-CH ₃ in 3 position (S methyl-l-cysteine)

one fish was involved and the trials are repeatable. Despite these variables the small molecule of glycine and larger molecules such as 5 aminovaleric acid and methionine appeared less effective than moderate sized ones. Alanine, which is intermediate in size, usually gave the strongest response.

RECOGNITION OF CONSTITUENTS IN OYSTER EXTRACT

Biting of specific areas of paper chromatograph strips occurred repeatedly and most of the bands bitten stained purple with ninhydrin. Four of these bands had Rf values on one-dimensional chromatographs consistent with knowns of alanine, glutamic acid, glycine, and aspartic acid. Much of the biting was centered at an Rf of .60 in phenol and about .35 in butanol-acetic corresponding exactly to our identified spot for alanine. Subsequently fish were exposed to bands of a phenol and butanol-acetic 2-dimensional chromatograph. The bands from the chromatographed extracts selected

by the fishes corresponded to those identified as aspartic acid and alanine, and also to the unknown (Fig. 1).

The 7 most abundant amino acids roughly estimated from chromatographs were (in decreasing order) alanine, glycine, glutamic acid, taurine, arginine, alanine, and aspartic acid. Some of the fish may have bitten β alanine, because it was very close to alanine. They bit only alanine on the 2 dimensional chromatograph.

Most of the biting activity on both 1 and 2 dimensional chromatographs centered at an Rf of about .88-.92 in phenol and .33-.35 in butanol-acetic. Some one-dimensional phenol chromatographed extracts showed a brown proline ninhydrin stain here but some did not. Fish bit the paper there in either case, but the response was much greater when the spot was apparent.

This unknown component was not destroyed by heat or distillation (Table 2). However, boiling oyster extract apparently removed the compound the fish used for orientation and finding the extract then became by chance. Chance also apparently determined finding of the amino acids tested, because the gobies never went directly to the amino acid saturated paper, but began a search pattern.

Basic distillation isolated a compound which did not cause a feeding reaction but attracted about 8 or 9 gobies to the area. This compound had an Rf of about .97 in butanol-acetic. It was absent in acid distillations, and did not stain with ninhydrin.

RESPONSE TO OYSTER WATER

Gobiosoma bosci was able to recognize water that oysters recirculated (oyster water) as well as water from an oyster reef. This species did not recognize local Port Aransas water or open Aransas Bay waters. Table 3 shows the response of 20 gobies to 100 cc of various waters introduced into a 32 liter aquarium. Oyster water was collected from 1 liter of water held with 8 oysters for 9 days. Control water was the same sea water held for 9 days without oysters. Further evidence of their recognition is shown in Table 2. *Gobiosoma bosci* seldom bit filter paper soaked in unconcentrated oyster water, but occasionally they showed a fairly strong feeding response (Table 2).

A single compound (Rf .50 in phenol) found in both oyster water and reef water could be collected from basic but not acid distillation. This substance was brown with-

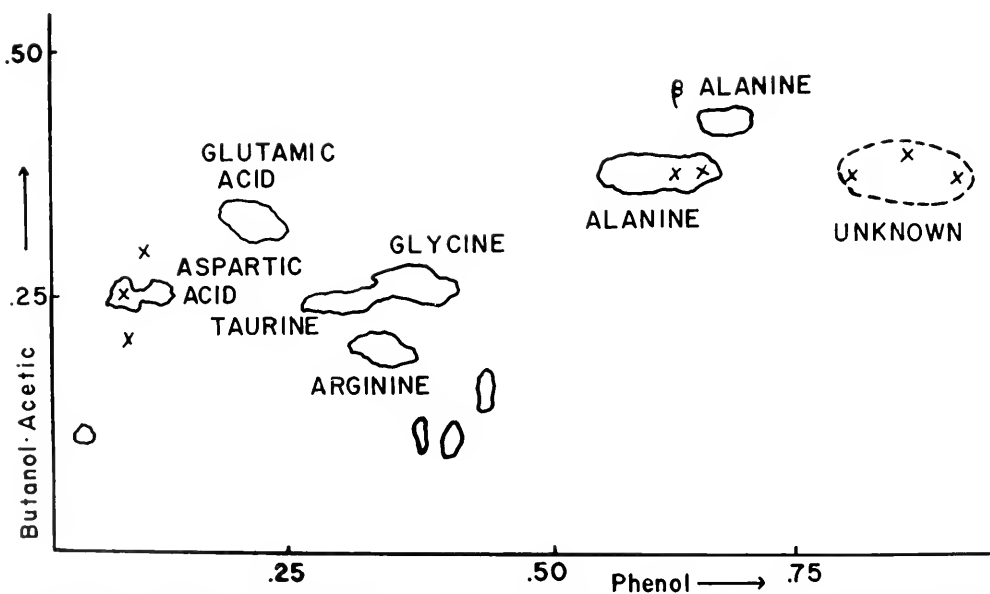


Figure 1. Reproduction of 2-dimensional chromatograph, ninhydrin stained, showing identified amino acids. X marks spots where gobies bit on duplicate chromatograph. Original chromatograph was about 35cm². Unknown area about 2 x 5 cm.

TABLE 2
Number of fish biting filter paper soaked compounds in each time interval

	0-30 sec.	0.5-1 min.	1-2 min.	2-5 min.
Glycine				1
Glycine				1
Glycine			2	1
Glycine				2
DL Aspartic acid	2		5	
"			1	1
"		1	5	
L Glutamic acid	2			
"				2
DL Cysteine			2	
"		1		
DL Alanine	4			
"	4	1		
DL Methionine		2		
"			1	
DL Ornithine		1		
"				1
4 Aminobutyric	1	2	3	2
"	4	1	1	2
Putrescine		1		
"	2			
Trimethylamine		1	2	
"			1	
2 Aminobutyric	2	1		
"			1	1
2, 4 Diaminobutyric			3	2
"		2	1	1
β Alanine		4	1	
"				2
5 Aminovaleric				2
"			1	
Oyster extract		5	4	1
"		6		
Oyster extract		1	1	2
"	4	8	3	1
Boiled oyster extract			8	4
Autoclaved oyster extract	1		3	8
Oyster water (distilled)		1		1
"				2
"		1		
Sea water (62 trials)		All negative		

out staining, but may have been ninhydrin positive. Another compound (Rf .78 in phenol, .48 in butanol-acetic) agreed with our Rf levels of 4 aminobutyric acid except the spot was brown instead of purple. A purple spot (Rf .78 in phenol) was sometimes present in oyster extracts, and once was present in oyster water. The free amino acid content of mollusks is known to vary with environmental factors (Ranke, 1959), which may explain these differences.

DISCUSSION

Simpson et al. (1959) reported alanine, glycine, taurine, glutamic acid, aspartic acid, and arginine, in decreasing abundance, to be the most common free amino acids in

Crassostrea virginica and our chromatographs indicate roughly the same. All of these except taurine and arginine induce feeding in *Gobiosoma bosci*. Alanine, the most abundant in oysters, induces one of the best feeding reactions, and was bitten more often on oyster extract chromatographs than any but the unknown. The effective amino acids were also found to be the 5 most abundant amino acids in Redfish Bay, Texas water (Park, et al., 1963).

It seems that the reaction involving amino acids is related to the area of the nitrogen atom. The remainder of the molecule is probably unimportant as long as it does not interfere with the amine group. Perhaps interference by highly electro-negative

TABLE 3

Response of *G. bosci* to oyster water. Oys = 100cc water held with oysters. Con = 100cc sea water. Asp 1 = 30cc Aspartic acid solution. Asp 2 = 70cc aspartic acid solution. Obs = 5 min observation with no introductions. All trials lasted 5 minutes and were continuous.

	BITES (of any object)	TWITCHES (of any part of body)	RISES (on pelvic fins)
Oys	3	4	8
Con	1	—	—
Obs	1	—	—
Oys	3	4	—
Con	—	—	—
Oys	3	1	—
Obs	—	—	—
Con	—	—	—
Oys	2	2	5
Obs	—	1	1
Asp 1	3	1	2
Asp 2	1	20	1
Con	—	—	—
Oys	7	6	—
Totals	Oys (5 trials) 18	17	13
	Con (4 trials) 1	—	—
	Obs (3 trials) 1	1	1

groups (C=O, OH) or steric interference explains why naked gobies show no recognition to some amino acids. But some molecules with branched chains or more than 5 carbon atoms are ineffective and have none of these characteristics. Perhaps this is explained by a specific compound (our unknown) producing the typical feeding response by fitting completely into a receptor site, with nitrogen producing most of the reaction. Other molecules may fit this space well enough to allow the nitrogen atom to fit in its receptor site, but some with branched chains, or other side groups, or too much length, will not allow the nitrogen molecule to fit completely in its site. Also two separate sites with differing shapes may be involved. The system may be similar to one recently discovered in the house fly (Robbins, et al., 1965) involving several amino acids and the guanosine phosphates. The hypothesis may be further clarified when more compounds and their isomers are tested.

It would seem that food-finding in *Gobiosoma bosci* is divided into two phases. One is following a volatile compound (amine?) to the oyster; the olfactory corridor. The other is inducement of the feeding reaction by amino acids and the heat stable unknown. In some cases this may reach the state of a feeding frenzy. In one

instance we introduced alanine into an aquarium with about 20 *Gobiosoma robustum* and a single pelagic postlarva which was 1/2 the size of the largest goby. The postlarva was attacked several times by gobies swimming to the surface, although this behavior had not been observed for several days previously. Where there was no food present gobies would bite algae, pieces of wood, pieces of paper, and each other when induced to feed. Part of this frenzy seems to develop by vision, although it can also occur to some degree in darkness.

It is important to know how many other animals recognize the same compounds. These compounds occur in many prey animals (Ranke, 1959; Simpson, et al., 1959), and animals as diverse as snails and crabs are attracted by smell to oysters as are gobies. We found that alanine and aspartic acid induced feeding in *Bathygobius soporator* and *Gobiosoma robustum*, and our unknown was bitten avidly by *Fundulus grandis* and *Sphaeroides nebelus*. Studies of this sort may be relatively easy, since both the attractant and the feeding inducer are easily isolated by chromatography.

The function of the compound(s) present in oyster water is less easily explained. Perhaps it may be used in orientation to an oyster reef, and a reef has a characteristic smell differing from a grass flat, just as dif-



Figure 2. One dimensional control chromatograph, phenol developed, in aquarium with 14 gobies.



Figure 3. One dimensional oyster extract chromatograph, phenol developed, in same aquarium with 14 gobies. Fish are congregated at an Rf of about .90.

ferent streams may have recognizable smells to migrating salmon (Fagerlund et al., 1963).

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SYSTEMATICS, FOSSIL HISTORY, AND EVOLUTION
OF THE GENUS *CHRYSEMYS*

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ABSTRACT

An investigation of skull, shell, and foot osteology of *Chrysemys* showed McDowell's (1964) criteria for the subgenera of *Chrysemys* to be invalid when applied to populations in the southern United States, Mexico, and South and Central America. McDowell's synonymy of *Pseudemys* with *Chrysemys* is valid.

The evidence also indicates that the turtles currently included in *Chrysemys scripta* actually represent three distinct species groups: (1) *C. scripta* including *C. s. scripta*, *C. s. elegans*, *C. s. troosti*; (2) *C. gaigeae* including *C. s. gaigeae*, *C. s. taylori*, *C. s. hilltoni*; (3) *C. ornata*, *C. callirostris*, and perhaps *C. dorbigui*.

I. INTRODUCTION

Recently we studied large numbers of fossil and extant specimens of *Chrysemys* (*Pseudemys*). In order to understand the phylogenetic relationships of the fossil forms, it became necessary to clarify the osteological relationships of the extant turtles of the genus *Chrysemys*, particularly those in the eastern United States. Most previous workers have based their taxonomic allocations of these turtles on color and color patterns; osteological comparisons were usually limited to the skull. The degree of conservatism and parallelism exhibited by turtles militates against the use of a single superficial character, such as color, to determine taxonomic relationships. An ideal taxonomy reflects phylogeny and thus depends on fossil evidence. Color, color patterns, and most soft anatomy are not part of the fossil record. Few workers since Hay

(1908) have attempted a comparative osteology of emydine turtles. Because of the lack of such studies, and the fact that large numbers of fossil turtles are now known, our investigation was wholly osteological, dealing with features of the skull, shell, and feet. Most characters used in this study are also present in the known fossil species.

We examined over 20 characters in the following extant and fossil species or races. Fossils are denoted by an asterisk. The number of specimens examined and their geographic origin is shown in parentheses: *Chrysemys concinna suwammienis* (20, Florida), *C. c. concinna* (1, Georgia), *C. c. hieroglyphica* (1, Tennessee), *C. s. scripta* (20, Florida, Georgia, Alabama), *C. s. elegans* (20, Texas; Coahuila, Mexico), *C. s. troosti* (6, Kentucky), *C. s. gaigeae* (12, Chihuahua, Mexico), *C. s. taylori* (2, Coahuila, Mexico), *C. s. callirostris* (13, purchased), *C. s. ornata* (10, Tabasco, Mexico; Vera Cruz, Mexico; Honduras), *C. p. picta* (9, Georgia, Pennsylvania, New York), *C. p. marginata* (12, Tennessee), *C. r. rubriventris* (10, New Jersey, Massachusetts), *C. alabamensis* (1, Alabama), *C. nelsoni* (20, Florida), *C. platymarginata** (20, Florida), *C. inflata** (6, Florida), *C. carri** (20, Florida), *C. williamsi** (20, Florida), *Echmatemys wyomingensis** (1, Wyoming), *C. floridana peninsularis* (20, Florida).

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II. CHARACTER ANALYSIS

Nuchal bone.—The nuchal scute underlap is defined as the length of that part of the nuchal scute lying on the ventral surface of the nuchal bone. In *C. scripta* and *C. nelsoni* the scute sulci are well defined. In *C. floridana* the posterior border is less clear, but the lateral borders are well defined. In *C. concinna* all the ventral sulci are poorly defined and particular care has to be taken not to confuse a more posterior scar marking the skin attachment with that indicating the posterior border of the scute.

These data are compared by dividing the length of the nuchal scute underlay $\times 100$ by the maximum nuchal bone length. The resultant ratios (Fig. 1) show that *C. scripta* has the greatest amount of underlay ($\bar{x}=31.7$) and *C. concinna* the least ($\bar{x}=6.7$). In this regard *C. nelsoni* is closer to *C. scripta* than to either *C. concinna* or *C. floridana*. The Mexican, Central and South American races of *C. scripta* are more similar to *C. floridana* than *C. scripta* (*C. s. gaigeae*, $\bar{x}=11.7$; *C. s. ornata*, $\bar{x}=17.5$).

The nuchal bones of *Chrysemys scripta* and *C. nelsoni* have a rugose dorsal surface compared with the generally smooth surface in *C. concinna*, *C. floridana* and *C. picta*. In *C. concinna* the posterior medial edge of the second marginal scute sulcus occurs on the nuchal bone in 85% of the

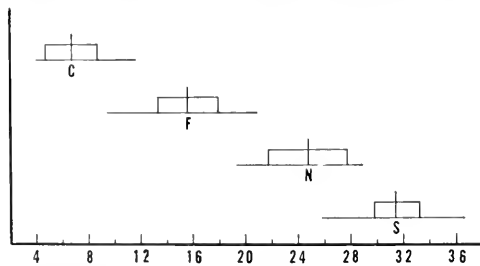


Figure 1. Nuchal scute underlap. C, *Chrysemys concinna*; F, *C. floridana*; N, *C. nelsoni*; S, *C. scripta*. The nuchal scute underlap is the length of that part of the nuchal scute lying on the ventral surface of the nuchal bone $\times 100$ divided by the maximum nuchal bone length. Vertical line — mean; horizontal line — range; white rectangle — one standard deviation.

specimens examined. None of the *C. scripta* have the sulcus of the second marginal scute on the nuchal bone; however, it is present on 36% of the *C. nelsoni* and 21% of the *C. floridana*. The scute areas of the nuchal bone in North American *C. scripta* are strongly sculptured (Table 1), those of *C. floridana*, *C. concinna*, *C. scripta ornata*, *C. s. callirostris*, *C. s. gaigeae* are weakly sculptured.

Gular scute overlap.—The gular scute overlap is defined as the length of that part of the gular scute lying on the dorsal surface of the epiplastral lip at the mid-line. When the measurement $\times 100$ is divided by the nuchal bone length there is no significant difference between *C. scripta* and *C. nelsoni* (Fig. 2). However, there is a

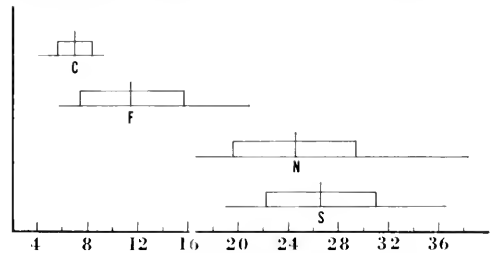


Figure 2. Gular scute overlap. C, *Chrysemys concinna*; F, *C. floridana*; N, *C. nelsoni*; S, *C. scripta*. The gular scute overlap is the length of that part of the gular scute lying on the dorsal surface of the epiplastral lip at the midline $\times 100$ divided by the nuchal bone length. Method of presentation as in Figure 1.

49% difference between the means of *C. nelsoni* and *C. floridana*. *Chrysemys concinna* has the least overlap. The tropical races of *C. scripta* resemble *C. floridana* and *C. concinna* in this respect (i.e., *C. s. gaigeae*, $\bar{x}=9.3$; *C. s. ornata*, $\bar{x}=5.85$).

Plastron.—The xiphiplastral width is defined as the width of the posterior plastral lobe through the center of the xiphi-hyoplastral junction, divided by the length from the posterior end of the plastron to the sulcus marking the posterior border of the abdominal scute.

The xiphiplastron of *C. scripta* and *C. nelsoni* is wider than that of *C. floridana* or *C. concinna* (Fig. 3). Again, *C. scripta* and *C. nelsoni* are more similar to each other than either is to *C. floridana* or *C. concinna*. *C. s. gaigeae* is similar to the latter (Fig. 3).

The plastron of *C. concinna* is generally

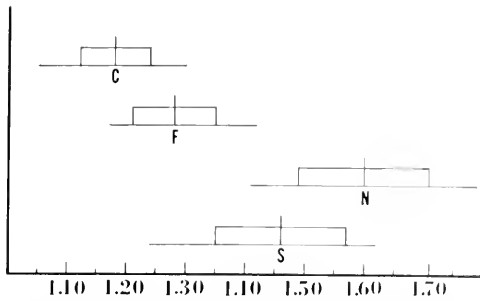


Figure 3. Plastral width/length. C, *Chrysemys concinna*; F, *C. floridana*; N, *C. nelsoni*; S, *C. scripta*. Method of presentation as in Figure 1.

flat and turned upward gently at a point even with the axillae. In *C. scripta*, *C. nelsoni* and *C. floridana* the epiplastron turns abruptly upward and the plastron is convex in the vicinity of the hyo-hyoplastral suture; thus, when placed on a flat surface only a small portion of the plastron touches the surface.

The anterior end of the epiplastron in *C. scripta* and *C. nelsoni* is abruptly truncated and forms a thick epiplastral lip which is overlapped dorsally by the gular scutes. In *C. concinna* and *C. floridana* the anterior end of the epiplastron is rounded and the epiplastral lip is not raised and thick. The Mexican, Central and South American races of *C. scripta* also have poorly developed epiplastral lips.

The posterior end of the xiphiplastron is acutely notched (Table 1) in all the forms examined, except in *C. s. scripta*, *C. s. troosti*, *C. s. elegans*. In these and in some *C. picta*, the notch is shallow. The fossil species *C. carri* and *Echmatemys wyomingensis*; living *C. s. scripta*, *C. s. elegans*, *C. s. troosti*, *C. nelsoni*, *C. rubriventris*, and *C. picta* have a pronounced overlap of the femoral scute onto the dorsal surfaces of the hypo- and xiphiplastra. The femoral scute overlap is restricted in the other species and races.

Pygal projection.—In all of our *C. scripta*, *C. nelsoni* and *C. picta* the posterior tip of the pygal projects ventrally nearly 90 degrees (Table 1). In 43% of the *C. floridana* and 7% of the *C. concinna* the pygal is ventrally directed, but the inclination is slight, not approaching the 90 degree ventral angle of *C. scripta*, *C. nelsoni*, and *C. picta*.

The pygal of *C. scripta* is narrow distally. The width of the distal end divided by the width of the proximal end of the pygal shows that *C. scripta* has the narrowest distal width ($\bar{x}=0.94$). The pygal of *C. floridana* ($\bar{x}=1.44$) is more flared than that of *C. concinna* ($\bar{x}=1.32$). *Chrysemys nelsoni* is intermediate between *C. scripta* and *C. floridana* or *C. concinna* (Fig. 4).

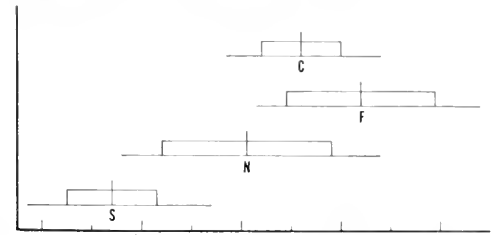


Figure 4. Posterior pygal width/anterior pygal width. C, *Chrysemys concinna*; F, *C. floridana*; N, *C. nelsoni*; S, *C. scripta*. Method of presentation as in Figure 1.

Shell weight.—When comparing *C. nelsoni* to *C. rubriventris* we noted a great difference in bone thickness of the respective shells which was reflected in the shell weights. The weight of the dried shell was plotted against the carapace length (Figs. 5 and 6). The shell of *C. nelsoni* proved much heavier than that of comparable sized *C. rubriventris* (Fig. 5). A similar relationship exists between the shell weights of *C. s. gaigeae*, *C. s. taylori*, and the North American races of *C. scripta*, the latter having a heavier shell (Fig. 6).

Maxilla-quadratojugal junction.—McDowell (1964) stated that members of the *C. floridana* group and *C. nelsoni-rubriventris* group have a strong sutural union between the maxilla and quadratojugal (=McDowell's squamosal) bones; this union being absent in *C. scripta* and *C. picta*. All of the *C. scripta* from North, Central, or South America that we have examined lacked this union; however, 50% of the *C. nelsoni*, 17% of the *C. floridana*, and 30% of the *C. concinna* also lacked this union on one or both sides of the skull.

Width of nares.—The narial opening of *C. picta* and North American *C. scripta* is small compared to the other species of *Chrysemys*. When the narial width x 100 is divided by the skull length (tip of snout to a line even with the posterior tips of the supratemporals) *C. scripta* has an average of

TABLE I
Comparison of Characters in *Chrysemys*

	<i>Chrysemys c. concinna</i>	<i>C. floridana peninsularis</i>	<i>C. ornata</i>	<i>C. gaigeae</i>	<i>C. s. scripta</i>	<i>C. s. elegans</i>	<i>C. s. troostii</i>	<i>C. p. pieta</i>	<i>C. rubriventris</i>	<i>C. nelsoni</i>	** <i>C. platymarginata</i>	** <i>C. carri</i>	** <i>C. williamsi</i>
Long gular scute overlap	—	—	—	—	+	+	+	+	+	+	+	+	—
Wide, thick, rectangular epiplastral lips	—	—	—	—	+	+	+	+	+	+	+	+	—
Humeral-pectoral sulcus behind endoplastron	+	+	+	+	+	+	+	+	+	+	+	+	+
Wide femoral scute overlap	—	—	—	—	+	+	+	+	+	+	+	+	—
Expanded xiphiplastron	—	—	—	—	+	+	+	+	+	+	+	+	—
Acute notch at posterior end of plastron	+	+	+	+	—	—	—	—	+	+	—	+	+
Rugose plastron	—	—	—	—	—	—	—	—	+	+	—	+	—
Long nuchal scute underlap	—	—	—	—	+	+	+	+	+	+	+	+	—
Sculptured scutal areas on nuchal bone	—	—	—	—	+	+	+	—	—	—	+	—	—
Strong peripheral bone notching	+	—	—	+	+	+	+	—	—	—	+	—	—
Acute ventral projection of pygal bone	—	—	—	—	+	+	+	+	+	+	+	+	—
Rugose carapace	—	—	—	—	+	+	+	—	+	+	+	—	—
Wide upper and lower triturating surface	—	—	—	—	—	—	—	—	+	+	—	—	?
Well developed ridge on upper triturating surface	+	+	+	+	+	+	+	—	+	+	?	?	?
Cusps on upper triturating ridge	+	+	—	—	—	—	—	—	+	+	?	?	?
Median symphyseal ridge on lower alveolar surface	+	+	—	—	—	—	—	—	+	+	?	?	?
Flat ventral surface of mandible	+	+	—	—	—	—	—	—	+	+	—	—	—
Notched premaxilla	—	—	+	+	+	+	+	+	+	+	?	+	?
Narrow nasal opening	—	—	+	?	+	+	+	+	—	—	?	?	?
Maxilla and squamosal united in more than 50% of specimens examined	+	+	—	—	—	—	—	—	—	—	?	?	?
Number of phalanges in fifth toe	3	2	3	2	2	2	2	2	2	2	?	?	?

** = fossil forms + character present — character not present

13.3%, *C. nelsoni* 16.6%, *C. floridana* 19.3%, and *C. concinna* 20.6%. Again, *C. nelsoni* effectively bridges the gap between *C. scripta* and the other two species (Fig. 7).

Temporal arch length.—The arch length is defined as the distance from the posterior end of the maxilla to the anterior edge of the distal surface (articulating surface) of

the quadrate x 100 divided by the skull length. The character is highly variable (Fig. 8). *Chrysemys scripta* has an average of 34.0, *C. nelsoni* 13.2, *C. floridana* 28.2, and *C. concinna* 29.6.

Alveolar shelf.—McDowell (1964) separated the subgenus *Pseudemys* into *floridana* and *rubriventris* sections by the features of

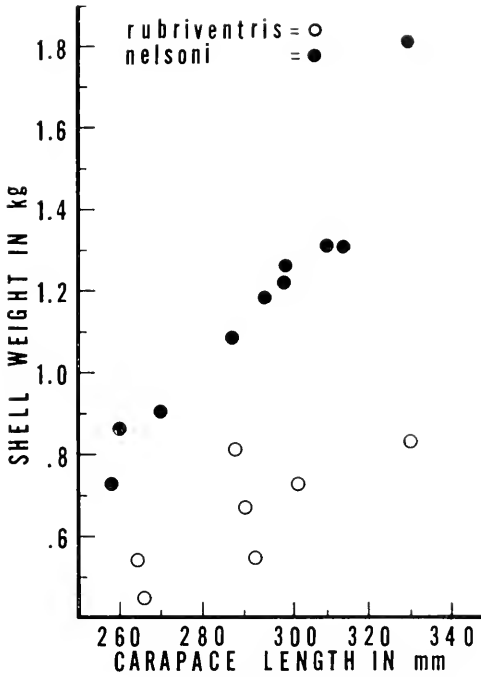


Figure 5. Relative shell weights of *Chrysemys rubriventris* and *C. nelsoni*.

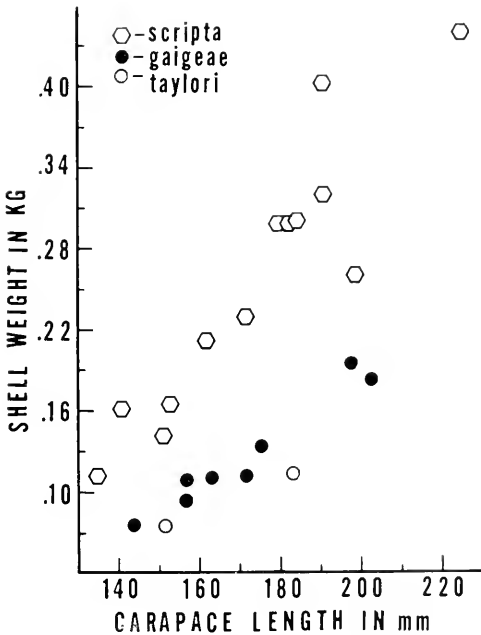


Figure 6. Relative shell weights of *Chrysemys scripta scripta*, *C. s. gaigeae*, and *C. s. taylora*.

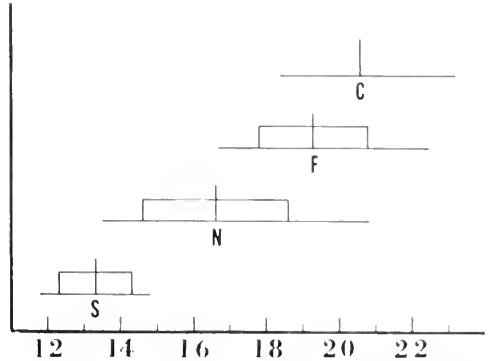


Figure 7. Narial width. C, *Chrysemys concinna*; F, *C. floridana*; N, *C. nelsoni*; S, *C. scripta*. Values determined by narial width X 100 divided by skull length. Method of presentation as in Figure 1.

the vomer and the alveolar surface. In the *rubriventris* section, but not in the *floridana* section, the vomer contributes to the upper triturating surface. Essentially this vomerine contribution results in a wider triturating surface. For purposes of comparison the alveolar width was measured from the anterior tip of the premaxilla to the posterior edge of the anterior median triturating surface x 100 divided by the skull length. *Chrysemys nelsoni* has a triturating shelf about 50% wider than that of the other

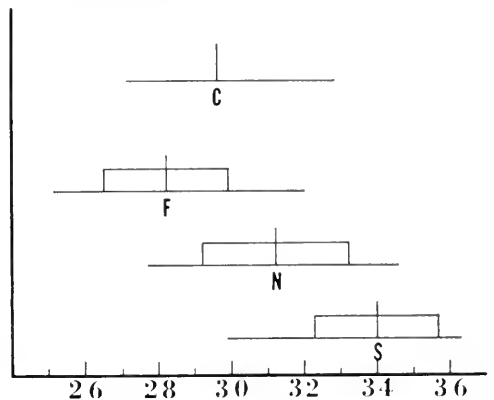


Figure 8. Temporal arch length. C, *Chrysemys concinna*; F, *C. floridana*; N, *C. nelsoni*; S, *C. scripta*. Arch length is the distance from the posterior end of the maxilla to the anterior edge of the distal surface (articulating surface) of the quadrate X 100 divided by the skull length. Method of presentation as in Figure 1. Fewer than 20 specimens of *C. concinna* were measured for this character, thus no standard deviation was calculated.

species. In this respect *C. scripta* is closer to *C. floridana* and *C. concinna* than to *C. nelsoni* (Fig. 9). We found a similarly broad triturating shelf which includes the vomer in *Graptemys*. Thus far no exhaustive work has been done on the food habits of *C. nelsoni* or *C. rubriventris* to determine

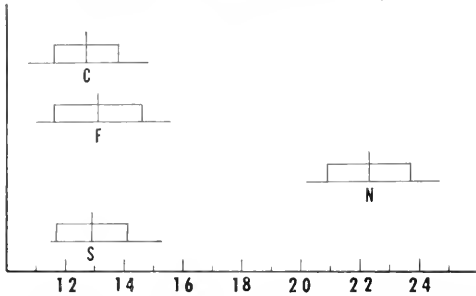


Figure 9. Alveolar width. C, *Chrysemys concinna*; F, *C. floridana*; N, *C. nelsoni*; S, *C. scripta*. Alveolar width is the distance from the anterior tip of the premaxilla to the posterior edge of the anterior median triturating surface X 100 divided by the skull length. Method of presentation as in Figure 1.

whether the broad shelf in these species is used for mollusk crushing as in *Graptemys*.

The upper triturating surface has a well developed longitudinal ridge cusped on its anterior end in *C. floridana*, *C. concinna*, and *C. nelsoni* (Table 1). McDowell uses this as one of the features separating the subgenera *Pseudemys* and *Trachemys*. *Trachemys* usually lacks these cusps. In *C. concinna*, however, the cusp is often reduced, while in *Chrysemys scripta* neither the ridge nor cusps are strongly developed (although by no means entirely absent). In this respect the Neotropical and the North American *C. scripta* are similar to each other.

The lower triturating shelf has a median longitudinal ridge in members of the *nelsoni-rubriventris* section of *Pseudemys* and one lingually positioned in the *floridana* section of *Pseudemys*, and in *Chrysemys*, and *Trachemys*. A ridge from the dorsal anterior tip of the mandibular symphysis back to the median anterior border of triturating shelf occurs in *C. floridana*, *C. concinna*, and *C. nelsoni*. *Chrysemys picta*, and both temperate and Neotropical *C. scripta* lack this ridge. *Chrysemys nelsoni* and *C. rubriventris* also have a much wider, lower alveolar surface than in other species of *Chrysemys*.

Shell depth.—Shell depth is defined as the depth of the shell through the center of the third neural bone x 100 divided by the carapace length. Carapace length is defined as the distance along the mid-line from the anterior end of the nuchal bone to the posteriormost end of the carapace. The data show that the shell of *C. concinna* is flatter than that of the other species (Fig. 10).

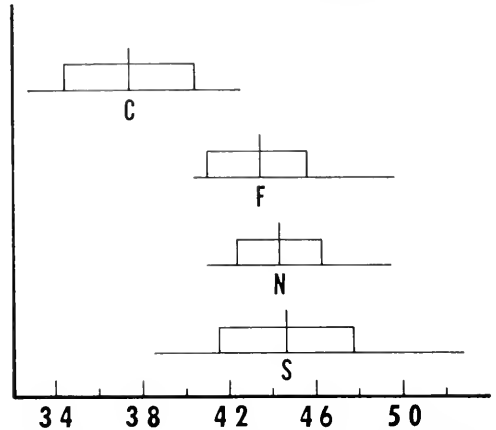


Figure 10. Shell depth. C, *Chrysemys concinna*; F, *C. floridana*; N, *C. nelsoni*; S, *C. scripta*. Shell depth is the depth of the shell through the center of the third neural bone X 100 divided by the carapace length.

Carapace peak.—Viewed laterally the carapace rises to a peak on the mid-line before sloping toward the pygal. In *C. concinna* the peak occurs on either the third neural (56%) or the fourth (44%). The peak shifts posteriorly in *C. floridana*, *C. nelsoni*, and *C. scripta* respectively. In the latter the peak usually is on the fifth neural (60%) (Fig. 11).

Phalanges in the fifth toe.—McDowell's definition of the subgenus *Trachemys* includes the presence of three phalanges on the fifth toe; four in *Pseudemys* (Table 1). We found that the fifth toe of *C. concinna* has three phalanges; *C. floridana*, two; North American *C. scripta*, two or three; *C. picta*, two; *C. s. ornata*, three; *C. terrapin*, two (from Grand Cayman, B.W.I.). The terminal phalanx apparently ossifies late in ontogeny in these turtles. We are investigating the foot architecture of these turtles in more detail.

Posterior pterygoid extension.—The posterior end of the pterygoid extends back to

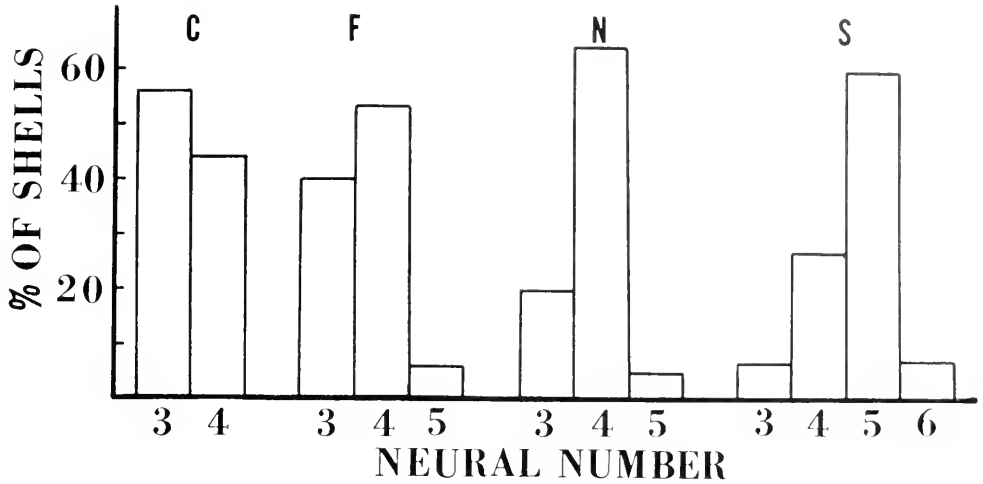


Figure 11. Carapace peak. On the left is the per cent of shells peaking on the neurals indicated at the bottom. C, *Chrysemys concinna*; F, *C. floridana*; N, *C. nelsoni*; S, *C. scripta*.

the level of the exoccipital in some *Trachemys*, but not in *Chrysemys* or *Pseudemys*. In all emydines the posterior pterygoid extension increases in length with age, with its most posterior position occurring in large *C. scripta*.

Constriction of first vertebral scute.—An unconstricted first vertebral scute is a feature used by McDowell to separate the subgenus *Chrysemys* from the subgenus *Trachemys*. In our specimens it is unconstricted in 67% of the *C. picta* and 100% of the adult *C. scripta gaigeae*.

III. DISCUSSION

McDowell (1964), in a review of the aquatic Testudinidae, recognized three subgenera under the genus *Chrysemys*: *Pseudemys*, including the *floridana* and *rubriventris* groups; *Trachemys* (the *scripta* complex), and the monotypic *Chrysemys*. His subgeneric criteria were based on skull osteology and foot architecture. We concur with McDowell that all the species currently listed under *Pseudemys* are best placed in the genus *Chrysemys* on the basis that none of the characters said to separate them (Galbreath, 1948; Hay, 1908) are here considered to be of generic rank. Additionally Zug (1966) showed that the members of *Pseudemys* and *Chrysemys* have a very similar penial morphology.

The close relationship between *C. picta* and *C. scripta* is the best argument for con-

sidering *Pseudemys* synonymous with *Chrysemys*. The primary differences between the two species occur in the shell. The carapace of *C. picta* lacks a dorsal ridge and notched posterior peripheral bones. The pleural bones of old individuals of *C. picta* may have a rugose pattern superficially similar to that of North American *C. scripta*. However, the rugosity of *C. picta* consists of thick, deep, longitudinally curved ridges, much more strongly developed and more numerous on the distal portion of the pleural bones than on the proximal portions. In *C. scripta* the ridges are thinner and comparatively equal in development and abundance over all of the pleural bones, giving a rugose appearance to the entire carapace.

Chrysemys scripta and *C. picta* are similar in the nuchal scute underlap, gular scute overlap, femoral scute overlap, number of phalanges on the fifth toe, and general skull features. Apparently the primitive emydid skull was similar to that of *C. picta* or *C. scripta*, and not *C. nelsoni*, *C. alabamensis*, or *C. rubriventris* as theorized by McDowell. McDowell assumes emydid evolution through forms with wide trituration surfaces such as occur in *C. alabamensis* and *C. nelsoni*. However, we have shown elsewhere (Rose and Weaver, 1966) that *C. nelsoni* arose from a narrow-jawed ancestor. In addition, specimens of the extinct genus *Echmatemys*, here believed ancestral to the remaining North American emydines, have

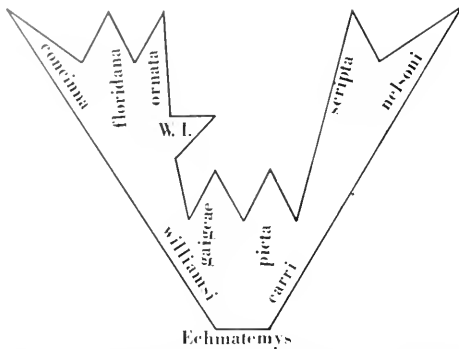


Figure 12. Proposed phylogeny of *Chrysemys*, *Echmatemys*, *Chrysemys williamsi*, and *C. carri* are fossil forms. W.I. indicates the West Indian species of *Chrysemys*.

narrow triturating surfaces. Other skull features we consider primitive include the following: the mandibles lack a median, internal symphyseal ridge, are rounded ventrally; and have a narrow triturating surface with a median longitudinal ridge, but no appreciable development of cusps; the maxillae are provided with a narrow triturating shelf to which the vomer does not contribute; the narrow nasal opening; and a notched premaxilla. Most of these features occur in the North American *C. scripta*. The skull of the closely related *C. nelsoni* is modified from this basic design. That it has been modified from a *picta* or *scripta*-like skull is shown by a fossil jaw found within the shell of a specimen of the Pliocene *C. carri* (Rose and Weaver, 1966). This mandible is practically identical to that of large, Recent *C. scripta scripta*.

We feel that the turtles currently placed in *C. scripta* comprise three species groups: (1) *C. s. scripta*, *C. s. elegans*, *C. s. troostii*, all of North America; (2) *C. s. gaigeae*, *C. s. taylori*, *C. s. biltoni*, found in the Rio Grande valley and northern Mexico; and (3) *C. s. ornata*, *C. s. callirostris* and perhaps *C. dorbignii*, found in southern Mexico and Central and South America (also see Williams, 1956). We believe that species groups 2 and 3 are quite distinct from *C. scripta*. In particular our analysis indicates that groups 2 and 3 are more closely related to *C. floridana* and/or *C. concinna* than to *C. scripta*. *Chrysemys scripta ornata* and *C. s. callirostris* are similar to *C. floridana* and/or *C. concinna* in the extent of the nuchal scute underlap and gular scute over-

lap, the number of phalanges on the fifth toe, the absence of doubly notched posterior peripheral bones, the relatively narrow plastron with a well developed posterior bone, the relatively narrow plastron with a well developed posterior notch, and the shape of the epiplastral lip. Until these populations are studied in greater detail we propose that they be considered distinct at the species level, and be designated as *C. ornata*, *C. callirostris*, and *C. gaigeae*. Tentatively we include *C. s. taylori* and *C. s. biltoni* in *C. gaigeae*.

The Pliocene species *C. williamsi* also has many characters in common with its probably derived species, *C. concinna*, *C. floridana*, *C. ornata*, and *C. callirostris*. It is quite distinct from contemporary species in the same geographic area, *C. carri* and *C. inflata* (Rose and Weaver, 1966; Weaver and Robertson, 1967). *Chrysemys inflata* is unquestionably a member of the evolutionary line leading to North American *C. scripta*, while *C. carri* is similar to both *C. scripta* and *C. nelsoni*, suggesting an even earlier common ancestor for both *scripta* and *nelsoni* (Rose and Weaver, 1966). Thus the genetic separation between the tropical turtles now considered races of *C. scripta* and extant North American *C. scripta* has existed at least since the Pliocene.

The living *Chrysemys scripta* as defined above, shares with the *nelsoni-rubriventris* group a ventrally projecting pygal bone, long nuchal scute underlap, long gular scute overlap, rugose carapace, keel on posterior neural bones, well defined and truncated epiplastral lip, wide posterior plastron, and notched upper jaw. The two groups differ primarily in posterior peripheral notching and the architecture of the triturating surfaces. The taxonomic question thus resolves itself as to what species or races are to be included in the subgeneric framework provided by McDowell. The features used by McDowell to define the subgenera of *Chrysemys* are invalid. Of the four characters he uses to distinguish the subgenera *Pseudemys* and *Trachemys*, two, the dentary shape and anterior triturating cusp, are sufficiently variable to render their validity as subgeneric criteria questionable. The remaining two characters, the number of phalanges on the fifth toe and the nature of the maxilla-quadratojugal junction, are completely invalid as used by McDowell. A

firm union between the maxilla and quadratojugal does not occur consistently in *C. floridana*, in *C. nelsoni*, or *C. concinna* as claimed by McDowell. Similarly we found members of both subgenera *Trachemys* and *Chrysemys* to have both two and three phalanges in the fifth toe and none with four which McDowell stated for the subgenus *Pseudemys*. Furthermore, McDowell's arrangement is contrary to the fossil evidence showing that *C. nelsoni* and *C. rubriventris* are more closely related to *C. scripta* than to *C. floridana* and *C. concinna*. We feel that present knowledge concerning the Mexican, Central and South American, and West Indian forms is insufficient to delimit accurately subgenera of the genus *Chrysemys*.

Though *C. floridana* and *C. concinna* are presently regarded as separate species (Conant, 1958; Carr, 1952) the data upon which this interpretation rests has never been published. These populations, originally listed as races under *C. floridana*, were raised to species rank by John Crenshaw in an unpublished manuscript (Crenshaw, 1955). Our evidence fully supports this division at the species level. However, we find no evidence of hybridization between *C. concinna* and *C. floridana* as reported by Crenshaw (1955, 1965).

The *gaigeae-taylori* populations of the Rio Grande valley area are more difficult to interpret than populations of the *ornata* complex in South and Central America. Some individuals of *C. gaigeae* resemble *C. scripta* (*sensu strictu*) by having doubly notched peripherals and a median carapace keel, although the latter is weakly developed. Generally the carapace is smooth, but when ridges do occur they are on the distal ends of the peripheral bones, as in *C. picta*. *Chrysemys gaigeae* is notable in that the first vertebral scute in all of our specimens is uncontracted, a feature seen elsewhere only in some *C. picta*. The remarkable thinness of the shell of *C. gaigeae* and *C. taylori* also contrasts strongly with the North American *C. scripta* (Fig. 6).

Table 1 summarizes 21 of the characters used in our analysis. Thirteen of these are present in 5 or more of the extant species or races studied. These thirteen are considered to be "primitive," or generalized features of the genus *Chrysemys*. Of these *Echmatemys* has 9; however, the nature of

several characters in this extinct genus remains unknown. The Pliocene *C. carri*, *C. williamsi* and *C. platymarginata* each have 9, 2, and 9 primitive characters respectively. Fossil and Recent *C. picta* and *C. scripta* have 9 and 12, respectively, of these features; fossil and Recent *C. nelsoni*, 11. It is noteworthy that *C. concinna*, *C. floridana*, *C. gaigeae*, and *C. ornata* have only 5 or less of these features, attesting to the modifications from the ancestral condition.

Obviously all of the characters used in this study do not have equal value. In addition, some characters are linked to others. For example, the gular scute overlap seems to be linked with the nuchal scute underlap and perhaps the femoral scute overlap with the xiphiplastral width. Our rationale for including such characters lies in the considerable extent we have relied on fossil evidence in our interpretations. Extinct species are often represented by elements that have poorly diagnostic characters. These characters, however, may be linked to others which are known to be highly diagnostic. We feel, however, that most of the characters listed in Table 1 are significant in determining evolutionary trends and relationships within *Chrysemys*. The most significant features, in our opinion, are those shown in Figures 1-10.

These data indicate that there are two major evolutionary lines in the Recent New World Emydinae. *Chrysemys concinna*, *C. floridana*, *C. ornata*, *C. callirostris*, and possibly *C. gaigeae* form an "advanced" line, while North American *C. scripta*, *C. nelsoni*, and *C. picta* constitute a "primitive" line. The two lines were already distinct by the Pliocene, as witnessed by the presence of *C. williamsi* and *C. carri* in a single deposit in Florida (Rose and Weaver, 1966). The advanced evolutionary line is here referred to as the *floridana* group and the primitive evolutionary line as the *scripta* group.

The large amount of fossil material makes possible a summary of evolutionary trends within *Chrysemys*. A hypothetical phylogeny is shown in Figure 11.

Scutes.—The nuchal scute underlap, gular scute overlap, and femoral scute overlap have become reduced in the *floridana* line. The extant condition was present in the earliest fossil known of that group, *C. williamsi*. The scutal over- and underlaps re-

mained long in members of the *scripta* line (Figs. 1 and 2) as in the fossil *Echmatemys*.

Peripheral bones.—Notching of the posterior peripheral bones (Table 1) appeared in both the *floridana* and *scripta* groups, but was virtually absent in *Echmatemys*. The most pronounced notching occurs in North American *C. scripta*, where peripherals 7-11 on each side are doubly notched. Posterior peripheral bone notching also occurs in the *floridana* group, particularly in *C. concinna*, but the bones are singly notched. The posterior peripherals of the *floridana* group become horizontally flared, and thus provide a streamlined form most highly developed in *C. concinna*. The *scripta* group maintains a primitive unstreamlined shell shape.

Pygal bone.—The sides of the pygal bone are parallel in the Pliocene *C. williamsi* and Recent *C. ornata*, expanded posteriorly in *C. floridana* and *C. concinna*. They are parallel in *C. scripta*, but posteriorly expanded in some *C. nelsoni*, and *C. rubriventris*. In both evolutionary lines median posterior pygal notching became well developed.

Plastron.—Primitively the plastron was expanded laterally both anteriorly and posteriorly, as in *Echmatemys*. Such expansion was maintained in the *scripta* group, but not in the *floridana* group where the plastron became narrow (Fig. 3). In the *scripta* group the plastron tended to become rugose and *C. nelsoni* and *C. rubriventris* developed extreme plastral rugosity (Table 1).

Phalanges.—A reduction from 3 to 2 phalanges on the fifth toe has occurred in both evolutionary lines. Behavioral differences have probably influenced this character.

Carapace Rugosity.—Both evolutionary lines developed a more rugose carapace than their respective fossil ancestors (Table 1). The increase in rugosity became most pronounced in the *scripta* line (Weaver and Robertson, 1967).

Mandible.—The mandible of *Echmatemys* was rounded ventrally and had a narrow triturating surface with a thin longitudinal, lingually positioned ridge. A median, anterior, internal, symphyseal ridge was missing. This type of mandible persisted in extant *C. scripta* and *C. picta*, but was profoundly modified in *C. nelsoni* where the triturating surface became greatly expanded and a median symphyseal ridge developed.

In the *floridana* line *C. ornata* had a lower jaw with a narrow triturating shelf, *C. floridana* and *C. concinna* developed wider triturating surfaces as well as a median symphyseal ridge. Ventrally the mandibles of *C. floridana* and *C. concinna* became somewhat flattened as they did in some large North American *C. scripta*. In both lines this represented a modification of the ancestral condition.

Cranium.—The primitive emyidine cranium was probably similar to that of *C. scripta* and *C. picta*. In these two species the quadratojugal and maxillary bones are separated by the jugal. Both evolutionary lines evolved a firm union between these bones in some of their members.

A notched premaxillary (Table 1) and a relatively narrow nasal opening were primitive features which were maintained in the *scripta* line.

IV. SUMMARY

In order to determine the phylogenetic significance of recently discovered fossil emyidine turtles, over 20 osteological comparisons of 14 extant and fossil species were made. McDowell's subgeneric concept of the genus *Chrysemys* was then compared with the data accumulated. Our results showed that:

(1) McDowell's use of *Chrysemys* to include species currently listed in *Pseudemys* is considered valid.

(2) McDowell's subgeneric classification of *Chrysemys* is shown to be invalid. *Chrysemys scripta* is to be restricted to only the North American races, *C. s. scripta*, *C. s. troosti*, *C. s. elegans*. The Mexican, Central and South America turtles previously considered races of *C. scripta* comprise two distinct species groups. In particular, *C. ornata* and *C. callirostris* (of William's *ornata* subspecies, 1956) are more closely related to *C. floridana* and *C. concinna* than to *C. scripta*. *Chrysemys nelsoni*, *C. rubriventris*, and probably *C. alabamensis* are more closely related to *C. scripta* than to *C. floridana* and *C. concinna*.

(3) Two evolutionary lines occur in *Chrysemys*, an advanced line including *C. concinna*, *C. callirostris*, *C. floridana* and *C. ornata* and a conservative line including *C. scripta*, *C. nelsoni* and *C. picta*. The fossils presently available show that the separation

between these two evolutionary lines has existed since the Pliocene.

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June 12, 1967

A COMPARISON OF TWO MANDIBULAR DIMENSIONS IN *PEROMYSCUS*,
WITH REGARD TO IDENTIFICATION OF PLEISTOCENE
PEROMYSCUS FROM FLORIDA

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ABSTRACT

Recent specimens of *Peromyscus polionotus*, *P. (Ochrotomys) nuttalli*, *P. gossypinus*, *P. floridanus*, *P. leucopus*, and *P. maniculatus* are compared with respect to two mandibular measurements; mandibular-alveolar (M.A.) length and ramus-alveolar (R.A.) length to aid in the identification of Florida Pleistocene *Peromyscus* mandibles. When each measurement is considered separately only *P. polionotus* and *P. floridanus* mandibles can be identified in part of their theoretical range of measurements. When the Florida species are considered with regard to the separate measurements, Student's *t* values are very high ($p < .001$ in all cases). The variance of each measurement is relatively low in all six species. When R.A. length is plotted against M.A. length for each specimen almost all Recent Florida *Peromyscus* mandibles can be identified to species. When *P. leucopus* and *P. floridanus* mandibles are added to this analysis *P. polionotus* and *P. floridanus* mandibles are still almost always identifiable, and *P. gossypinus* mandibles are still identifiable throughout much of their measured size range.

INTRODUCTION

The purpose of this paper is to present data that will aid in identifying Pleistocene species of *Peromyscus* from Florida, utilizing only mandibles, with or without the full complement of teeth. The data are also relevant to the identification of both Pleistocene and Recent *Peromyscus* species throughout the entire southeast and Gulf coastal United States. There is no intent

here to present a complete study of south-eastern *Peromyscus* mandibles, but merely to exhibit data which effectively separate the species. Other mandibular dimensions may prove just as satisfactory for this purpose.

All faunas mentioned in this paper without reference to locality or age are from the Florida Pleistocene.

Bader (1957) listed *Peromyscus* sp. from the Arredondo deposit. Later (1959) he presented comparisons of *P. floridanus*, *P. gossypinus*, and *P. polionotus* based on dental patterns. *P. (Ochrotomys) nuttalli* was mentioned once, as being distinguishable from *P. gossypinus* on qualitative grounds. Ray (1958) identified two left mandibles as *Peromyscus gossypinus* from the Melbourne locale, but listed no measurements other than gross size differences. Ray also stated that *P. gossypinus* could be distinguished from *P. nuttalli* on the basis of the scar configuration of the masseter muscles. Holman (1959) mentioned the presence of *P. gossypinus* in the Williston fauna, based upon measurements of the mandibular tooth row in very small samples of Recent *Peromyscus* from Florida. Gut and Ray (1963) listed all four of the extant Florida species of *Peromyscus* from the Reddick deposit, but no data were mentioned to substantiate the identifications.

MATERIALS AND METHODS

Series of specimens of Recent *Peromyscus* were measured at the U.S. National Museum and the American Museum of Nat-

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tural History. Young individuals, determined by pelage characters, skull suture patterns, and skin measurements were excluded (this usually included only those animals in which the M_2 had not erupted, or was in the process of erupting). Specimens with no tooth wear, but with adult tooth placement were measured. Sexual dimorphism was absent with regard to the two mandibular dimensions. Osgood (1909) showed that sexual dimorphism was negligible in *Peromyscus*.

The mandibular-alveolar length (M.A. length) was measured from the posterior lip of the last alveolus to the anterior lip of the first alveolus. Since the M_1 overhangs the first alveolus, the calipers were slanted either slightly medially or laterally to obtain a true alveolar measurement. The distance from the greatest angle of the posterior border of the ramus to the anterior border of the first alveolus (here termed ramus-alveolar, or R.A. length; see Fig. 1) was measured

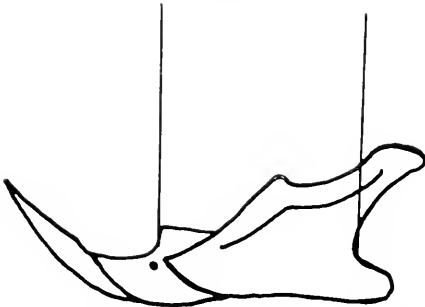


Figure 1. Determination of ramus-alveolar length. The area between the two lines indicates the ramus-alveolar (R.A.) measurement.

with the same modification as the M.A. length.

Measurements were taken with a Helios 7-inch calipers, calibrated to 1/20 mm. Formulae utilized for computations follow

Simpson, Roe, and Lewontin (1960). Normal distribution is assumed in all calculations.

RESULTS AND DISCUSSION

In Figures 2 and 3 we see that only *P. polionotus* and *P. floridanus* mandibles are adequately identifiable when each measurement is analyzed separately (only those specimens in a non-overlap range beyond $\pm 3s$ of the nearest species are considered identifiable).

The low values for the coefficient of variation (Table 1) indicate that the two characters studied are not highly variable within each species ("In mammals the C.V. for linear dimensions is usually between 4 and 10, occasionally between 3 and 4," Mayr, Linsley and Usinger, 1953).

Student's *t* values for the Florida *Peromyscus* species indicate that there is a significant difference between the species for both measurements ($p < .001$ in all cases). When R.A. length is plotted against M.A. length almost all Recent Florida *Peromyscus* mandibles are identifiable to species. (Fig. 4). Mandibles of *P. maniculatus* are not separable from those of *P. leucopus* by this method (Fig. 5), and the plotted distributions of these mandibles overlap much of the plotted distribution of *P. polionotus*, *P. nuttalli* and *P. gossypinus* (cf Figs. 4 and 5).

Peromyscus fossils from Florida consist principally of isolated teeth and mandibles, from which the teeth have usually been lost, making identification of the forms rather difficult. Ray (1958) pointed out that, "Records of the genus in the Pleistocene are highly unsatisfactory and certainly not indicative of true rarity." He included the cotton mouse, *P. gossypinus*, in the Melbourne fauna, and separated it from the other Florida species on the basis of gross size differences of the mandibles. *P. gossypinus* mandibles can probably be differentiated from

TABLE 1

The coefficient of variation (C.V.) and the number (N) of *Peromyscus* specimens studied for both mandibular dimensions.

	N	C.V. R.A. Length	C.V. M.A. Length
<i>P. polionotus</i>	50	3.97	4.18
<i>P. leucopus</i>	26	4.12	4.34
<i>P. maniculatus</i>	27	3.88	3.53
<i>P. gossypinus</i>	49	4.43	3.95
<i>P. nuttalli</i>	41	4.15	3.05
<i>P. floridanus</i>	31	4.42	4.56

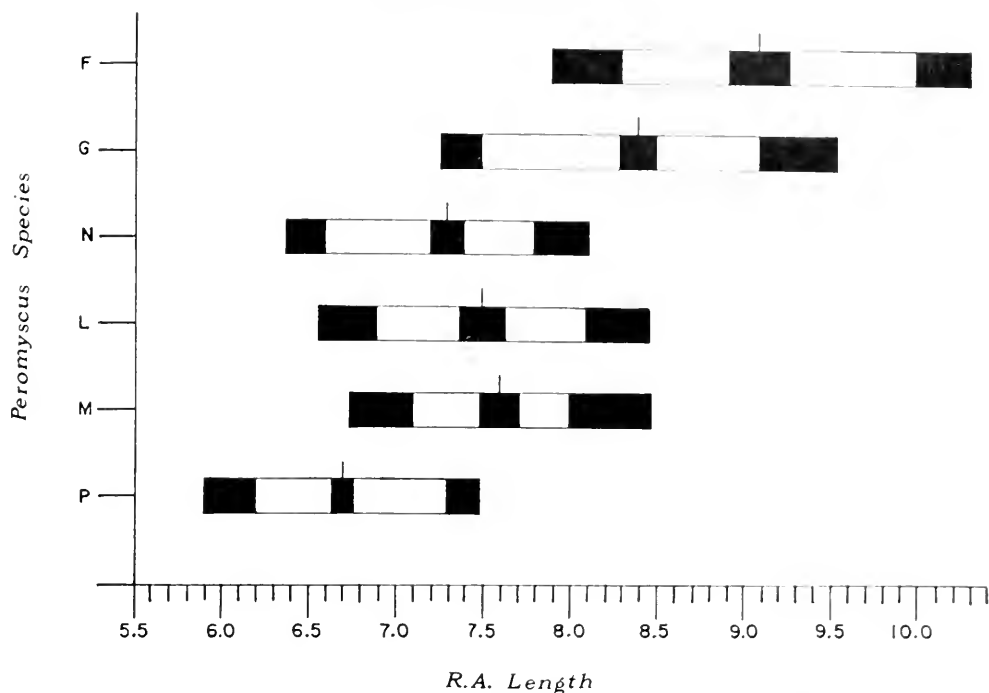


Figure 2. Graphic representation of the relationships of the 6 *Peromyscus* species studied for the R.A. length. The vertical line indicates the mean. The blackened portion of the bar in the immediate area of the mean represents the $\pm 95\%$ confidence limits of the mean. The unshaded area plus the 95% confidence limits of the mean equals the observed range. The blackened end areas of the bar plus the preceding portions comprise $\pm 3s$. The letters along the abscissa indicate the species: F = *P. floridanus*, G = *P. gossypinus*, N = *P. nuttalli*, L = *P. leucopus*, M = *P. maniculatus*, P = *P. polionotus*.

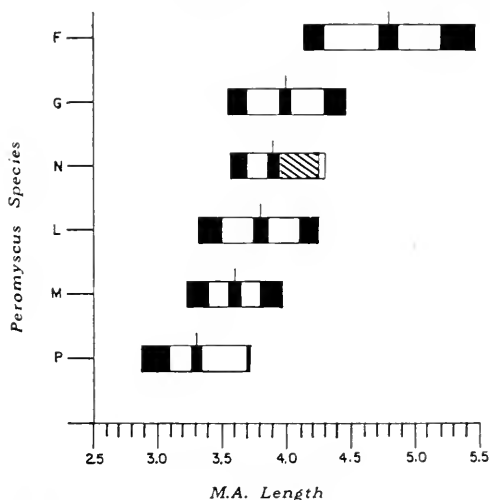


Figure 3. Graphic representation of the relationships of the 6 *Peromyscus* species studied for the M.A. length. Legend as in Fig. 2. The diagonal-lined portion of the bar for *P. nuttalli* (N) indicates the limits of $\pm 3s$. In *P. nuttalli* the observed range exceeds the range inclusive in $\pm 3s$.

those of *P. polionotus* and *P. floridanus* on gross size, but identifications should be supplemented by supporting measurement data. Although Ray (1958) mentioned that *P. nuttalli* mandibles could be separated from those of *P. gossypinus* on the scar configuration of M. Masseter profundus, pars anterior and M. Masseter medialis, pars anterior, I have not found this trait reliable, and Dr. Ray (pers. com.) has recently agreed that it is not a trustworthy character.

Holman (1959) identified *P. gossypinus* from the Williston deposit, and gave the mandibular tooth row measurements of his specimens as 3.8-4.4 mm. As I have not seen these specimens I must assume that they all possessed teeth. Therefore about 0.5 mm must be added to my measurements to convert them to a tooth row measure, since the M_1 slightly overhangs the first alveolus in specimens with teeth. Holman (1959) measured 10 specimens each of Recent *P. polionotus*, *P. gossypinus*, and *P.*

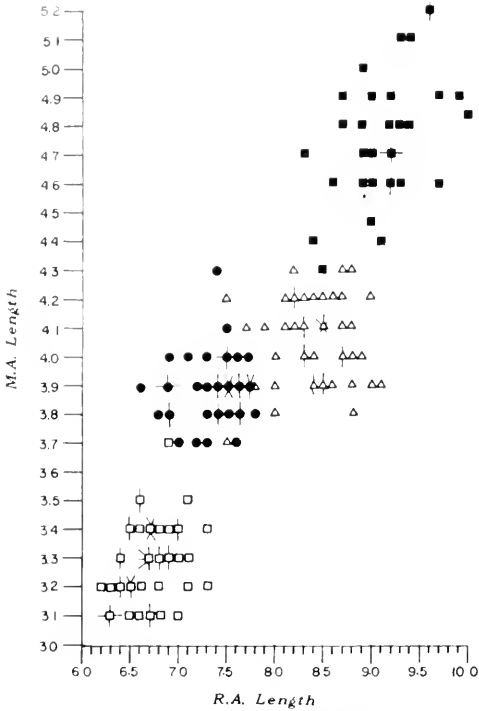


Figure 4. Scatter diagram showing the separation of all Florida *Peromyscus* mandibles when R.A. length (ordinate) is plotted against M.A. length (abscissa) for each individual. Each symbol without lines represents one individual. Where lines are associated with a symbol, they represent the number of individuals at that point. Light squares represent *P. polionotus*. Circles represent *P. nuttalli*. Triangles represent *P. gossypinus*. Dark squares represent *P. floridanus*.

floridanus, and only one specimen of *P. nuttalli* on which he based identification of his fossil forms. The ranges given are as follows: *P. polionotus*: 2.4-3.7 mm, *P. gossypinus*: 3.6-4.3 mm, *P. floridanus*: 4.4-5.0 mm, and *P. nuttalli*: 3.7 mm (cf with Fig. 3).

My measurements show that *P. gossypinus* mandibles cannot be distinguished on the basis of the M.A. length when either *P. leucopus* or *P. maniculatus* is presumed present. Referral of the Williston site to the Illinoian makes a Recent Florida *Peromyscus* aggregation unlikely at that time. As *P. gossypinus* is a derivative of *P. leucopus*, the fact that they hybridize in nature and produce fertile offspring when crossed in the lab (Dice, 1940; McCarley, 1954) indi-

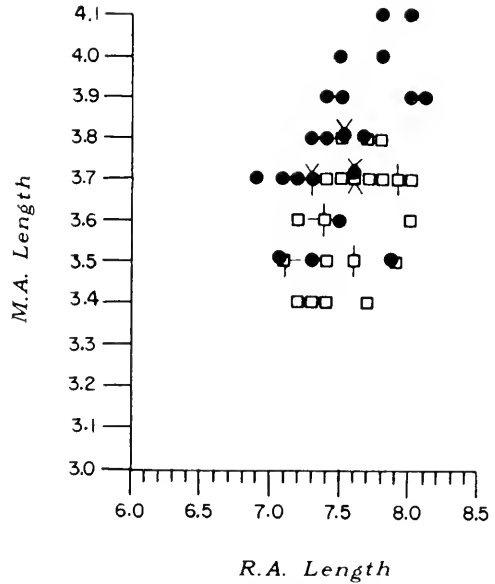


Figure 5. Scatter diagram showing the relationship of *P. leucopus* (circles) to *P. maniculatus* (squares) when R.A. length is plotted against M.A. length. Representation of individual specimens follows Figure 4.

cates that they have not been isolated for very long. Their morphology, with the possible exception of hind-foot length, overlaps greatly (Dice, 1940; McCarley, 1954; and personal observation). Speciation of these forms could then be exclusively a Wisconsin or post-Wisconsin phenomenon. If, however, *P. gossypinus* was distinct from *P. leucopus* by Illinoian time, and the assumption is made that both *P. leucopus* and *P. maniculatus* were absent, a tooth row (or M.A.) measurement will not distinguish *P. gossypinus* from *P. nuttalli*. The tooth row length of 3.7 mm reported for *P. nuttalli* by Holman (1959) is the minimum limit of the M.A. observed range in this study.

Tamsitt (1957) compared mandibles of four *Peromyscus* species: *P. nasutus*, *P. boylii*, *P. pectoralis*, and *P. leucopus* in order to identify a number of *Peromyscus* mandibles from the late Pleistocene Friesenhahn fauna of Texas. He did not statistically compare his fossil or Recent material with *P. maniculatus*, also extant in Texas. He compared the four former species and the fossil forms with regard to seven mandibular dimensions, and his data show that no characters adequately separate any of the

species when each dimension is considered alone (without multivariate analysis). *Peromyscus nasutus* and *P. boylii* are generally smaller for all measurements than are *P. pectoralis* and *P. leucopus*, but measurements within the first and second pairs overlap each other in all cases, and both pairs may overlap for certain characters.

The fossil mandibles referred by Tamsitt (1957) to "*Peromyscus cf. leucopus*" are significantly larger than any *Peromyscus* analyzed in that paper (in four of the seven measurements there is a greater difference in the means between the fossil *P. cf. leucopus* and Recent *P. leucopus* than there is between *P. nasutus* and *P. leucopus*). The ranges of the alveolar length of the Recent *Peromyscus* studied by Tamsitt (1957) conform very closely to the ranges of *P. nuttalli*, *P. leucopus*, *P. gossypinus*, and *P. maniculatus* found in the present study. The range of the fossils however, demonstrates the presence of another *Peromyscus* species. Preliminary analysis of these fossils by myself indicates the presence of more than one *Peromyscus* species. The results will be reported at a later date.

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TURTLE GENERA *CHRYSEMYIS*, *STERNOTHERUS*, AND *TRIONYX*:
A COMPARATIVE STUDY WITH ANALYSIS OF POSSIBLE
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THE CRANIAL ARTERIES AND CRANIAL ARTERIAL FORAMINA OF THE
TURTLE GENERA *CHRYSEMYS*, *STERNOTHERUS*, AND *TRIONYX*:
A COMPARATIVE STUDY WITH ANALYSIS OF POSSIBLE
EVOLUTIONARY IMPLICATIONS

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ABSTRACT

The cranial arterial foramina and bony canals of *Chrysemys*, *Sternotherus*, and *Trionyx* are described and compared, and the cranial arteries that utilize these foramina and canals in the three turtle genera are also described and compared. Cranial arterial variation within a genus is slight; as a result, inferences of the general cranial arterial patterns characteristic of the Testudinidae, Kinosternidae, and Trionychidae are made. Judged by the

cranial arteries the Testudinidae and Kinosternidae have had a long, separate evolution from a common ancestor. Trionychids evolved from an earlier branch of turtles which had evolved parallel to the evolutionary path later taken by the kinosternids. Sixteen new names for anatomical features are introduced in this study.

The Trionychidae, Kinosternidae, and Testudinidae have taken three different lines of evolution in pattern of cranial arteries. As would be expected from the current taxonomy of turtles, members of the super-

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family Testudinoidea have a cranial arterial pattern basically different from that of members of the Trionychoidea (of Romer, 1956). However, this basic difference occurs only in the basisphenoid region of the skull, for most of the other cranial arteries of the soft-shelled turtles are similar to those of the Kinosternidae (of Wermuth and Mertens, 1961). With the exception of the arteries of the basisphenoid region, the trionychids and kinosternids have followed somewhat parallel lines of evolution opposed to the testudinid line.

Relatively little has been published concerning the cranial arteries of the Testudines (Testudinata). Bojanus (1819) named and illustrated almost all the head arteries of *Emys orbicularis*; Shindo (1914) described the cranial arteries of *Testudo graeca* and compared the place of origin of the mandibular artery in four species of turtles. Several other authors, such as Siebenrock (1897), Ogushi (1911), Nick (1913), and Parsons and Williams (1961), mention some of the larger arteries in their osteological studies of turtle skulls.

Girgis (1964) described the arteries of *Trionyx triunguis*, and McDowell (1961) has made the only other recent study of cranial arteries. By comparing the general cranial arterial patterns of the testudinids and kinosternids, McDowell established the existence of two different lines of cranial artery evolution in the Testudinoidea, and he also provided strong evidence for placing the Chelydridae in the testudinid line of evolution and the Dermatemydidae in the kinosternid line of evolution. Some of McDowell's findings concerning the smaller cranial arteries of the testudinids and kinosternids were not correct, but his conclusions were based on the general patterns of the larger arteries; hence these errors do not affect the validity of his conclusions to any great degree.

I. MATERIALS AND PROCEDURE

Among the Trionychoidea, two injected *Trionyx spinifer*, one uninjected *Trionyx muticus*, and one uninjected *Lissemys punctata* were dissected; among the Kinosternidae, one injected *Kinosternon subrubrum*,

one injected *Sternotherus*² *odoratus*, one uninjected *Sternotherus odoratus*, and one uninjected *Sternotherus minor*; and among the Testudinidae, two injected *Chrysemys (Pseudemys) scripta*. Partial dissections of another injected *Chrysemys scripta* and one injected *Terrapene carolina* were also made. All the dissected specimens were adult turtles. The dissections were performed under a dissecting microscope, and a dental drill with a very small bit was used to reveal the arteries within the bony canals.

The injected specimens of the above list were essential to a detailed study of the cranial arteries of the three types of turtles, for uninjected specimens yielded only a minimum of information concerning the larger cranial arteries and also yielded some information about the bony canals and foramina. The injected *Chrysemys* were obtained from commercial firms. I prepared the specimens of *Trionyx*, *Sternotherus*, and *Kinosternon* by injecting latex into the heart and ascending aorta of freshly killed specimens and placing the turtles in a dilute acetic acid solution for twenty-four hours to harden the latex. This procedure often produced better preparations than the commercial ones. On specimens which had been preserved for some time, however, this procedure either failed or resulted in very poor injections.

In order to extend coverage to the generic level of the detailed arterial patterns of the representative species which were dissected, the cranial arterial foramina in the skulls of

² Upon the recommendation of H. M. Smith, the spelling *Sternotherus* is retained despite Tinkle's (1958: 5-6) case for *Sternotherus*, because only "inadvertent errors" in original spellings can be corrected, whereas "incorrect transliteration" is explicitly stated in the Code *not* to be considered an inadvertent error. Furthermore the type of *Sternotherus* Bell (in Gray), 1825, must be selected from the species included in the original description ("S. odorata Gray, S. pensylvanica Gmelin"); no side-necked turtles were included. This requires that *Sternotherus* Bell, 1826, be considered a different nominal genus the type of which is determined independently from that of *Sternotherus*, which is clearly the proper name for the North American kinosternid turtles related to *S. odoratus* [unless, as suggested by Romer (1966: 365) *Kinosternon* and *Sternotherus* are considered congeneric, in which case *Kinosternon* has priority].

undissected species in each genus were examined and pertinent data from the available literature were utilized. The foramina in skulls of different genera of the Trionychidae, Kinosternidae, and Testudinidae were similarly examined and the available literature utilized to establish a basis for inference of the general arterial patterns of the three families studied. Data concerning the presence or absence, relative size, and relative position of seven externally-visible cranial arterial foramina were recorded for a series of 131 skulls of adult or subadult turtles from different parts of the United States, all in the Museum of Natural History of the University of Illinois.

The following crania were examined:

Testudinidae: 34 *Chrysemys scripta*, 26 *Chrysemys picta*, 5 *Chrysemys concinna*, 3 *Graptemys geographica*, 2 *Graptemys pseudographica*, 4 *Clemmys insculpta*, 3 *Emydoidea blandingi*, 2 *Malaclemys terrapin*, 8 *Terrapene carolina*, 3 *Terrapene ornata*, 2 *Gopherus polyphemus*.

Kinosternidae: 15 *Sternotherus odoratus*, 2 *Sternotherus minor*, 1 *Sternotherus carinatus*, 2 *Kinosternon subrubrum*, 1 *Kinosternon bauri*, 1 *Kinosternon scorpioides*, 4 *Staurotypus triporcatus*.

Trionychidae: 9 *Trionyx spinifer*, 3 *Trionyx muticus*, 1 *Trionyx ferox*.

Anatomical features described in the following accounts may be visualized by reference to Figures 1-3. New terms are indicated by boldface letters wherever they first appear in the descriptive accounts.

II. THE CRANIAL ARTERIAL FORAMINA AND BONY CANALS OF *CHRYSEMYS*, *STERNOTHERUS* AND *TRIONYX*

Many of the cranial foramina of turtles serve as passageways for arteries, and often the size of a cranial foramen or canal is directly proportional to the size of the artery which goes through it. A detailed knowledge of the position and size of the arterial foramina and canals in turtle skulls is thus very valuable in predicting the cranial arterial pattern of those turtles. As an example, the two Jurassic turtle skulls described by Parsons and Williams (1961), judged by the large foramen stapedio-temporale, the small foramen posterius ca-

nalis carotici interni, and the foramina around the basisphenoid bone, are either on the chelydrid-testudinid line of cranial arterial evolution or are on a line of arterial evolution extremely similar to that of the modern Testudinidae (of Romer, 1956) and Chelydridae (of Wermuth and Mertens, 1961).

In the discussion of the crania of *Trionyx*, *Sternotherus*, and *Chrysemys*, the standard terminology established by Parsons and Williams (1961) is used. Where Parsons and Williams do not have a name for a structure, the source of the name is indicated in parentheses. New names are coined only where no other author has given the corresponding structures suitable names, and are indicated by boldface letters.

The foramen stapedio-temporale is one of the most important of the cranial arterial foramina. In *Trionyx*, *Chrysemys*, and *Sternotherus*, the foramen stapedio-temporale is located in or at the posterior edge of the dorsal surface of the prootic bone and opens into the fossa temporalis. In all 65 of the *Chrysemys* skulls examined, the foramen stapedio-temporale was present on each side as a very large opening. According to McDowell (1961: 33) the foramen stapedio-temporale is present in *Sternotherus* as an "occasional vestige," but it is present as a greatly reduced opening in all the 18 *Sternotherus* which I examined. In *Trionyx sinensis* ("*Trionyx japonicus*" of Ogushi) and in all *Trionyx* which I examined, the foramen stapedio-temporale is present but is not reduced as much as the foramen in *Sternotherus*. Thus both *Trionyx* and *Sternotherus* have a reduced foramen stapedio-temporale, and this structure "of a large arterial foramen implies considerable rearrangement of the head arteries" (McDowell, 1961: 23). The *aditus canalis stapedio-temporalis* and the *canalis stapedio-temporalis* are present in all three genera and are reduced in diameter in *Trionyx* and *Sternotherus* in proportion to the reduction of the foramen stapedio-temporale in these same genera.

Another important arterial foramen is the foramen posterius *canalis carotici interni*.³ In *Chrysemys* and *Sternotherus* this foramen is located at the ventromedial corner of

³ Spelling courtesy Dr. Donald P. Rogers, modified from that used by Parsons and Williams.

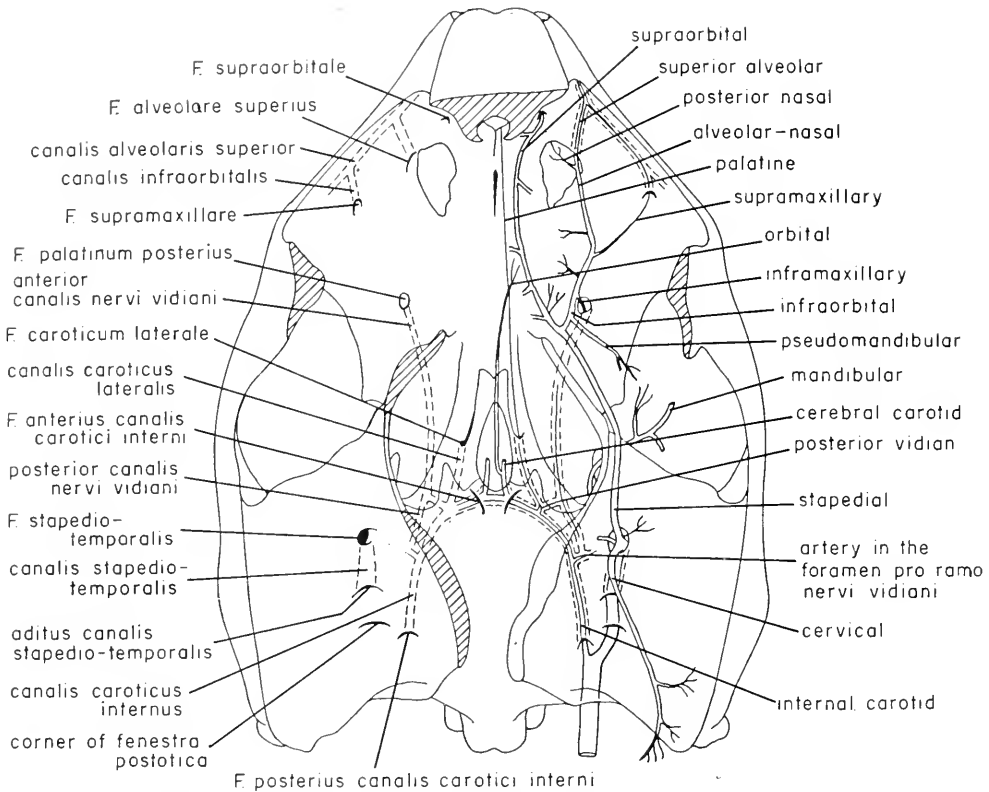


Figure 1. Semidiagrammatic dorsal view of the cranial arteries (right side) and cranial arterial foramina and canals (left side) of *Chrysemys scripta*.

the fenestra postotica, whereas in *Trionyx* the foramen posterius canalis carotici interni is separated by a broad bar of the pterygoid bone from ventrolateral fenestra postotica. The foramen posterius canalis carotici interni is very small in *Chrysemys*, but is relatively much larger in *Sternotherus* and *Trionyx*.

In all three genera, the foramen posterius canalis carotici interni leads into the canalis caroticus internus which curves anteromedially on each side of the cranium through the pterygoid and basisphenoid bones to an opening in the basisphenoid at the posterior end of the sella turcica known as the foramen anterius canalis carotici interni.⁴ As would be expected from the relative sizes of the foramen posterius canalis carotici interni, the canalis caroticus internus of *Chrysemys* is a narrow canal, whereas in

Sternotherus and *Trionyx* it is a much wider canal. The foramen anterius canalis carotici interni is located in the dorsum sellae of the basisphenoid bone medial to the processus clinoides. In *Chrysemys* and *Sternotherus* this is a fairly small foramen, but in *Trionyx* the foramen anterius canalis carotici interni is a very large foramen. Again, the relative sizes of these canals and foramina imply quite different cranial arterial patterns in this region of the skulls of the three genera.

In *Chrysemys*, *Sternotherus*, and *Trionyx*, the canalis caroticus internus on each side of the skull gives off an anterior canal in the pterygoid bone which opens into the sulcus cavernosus directly lateral to the basisphenoid. In *Chrysemys* this small canal goes for some way through the pterygoid bone and opens into the cavum cranii through an extremely small foramen lateral to the middle of the rostrum basisphenoidale. On the other hand, this canal is very

⁴ Spelling courtesy Dr. Donald P. Rogers, modified from that used by Parsons and Williams.

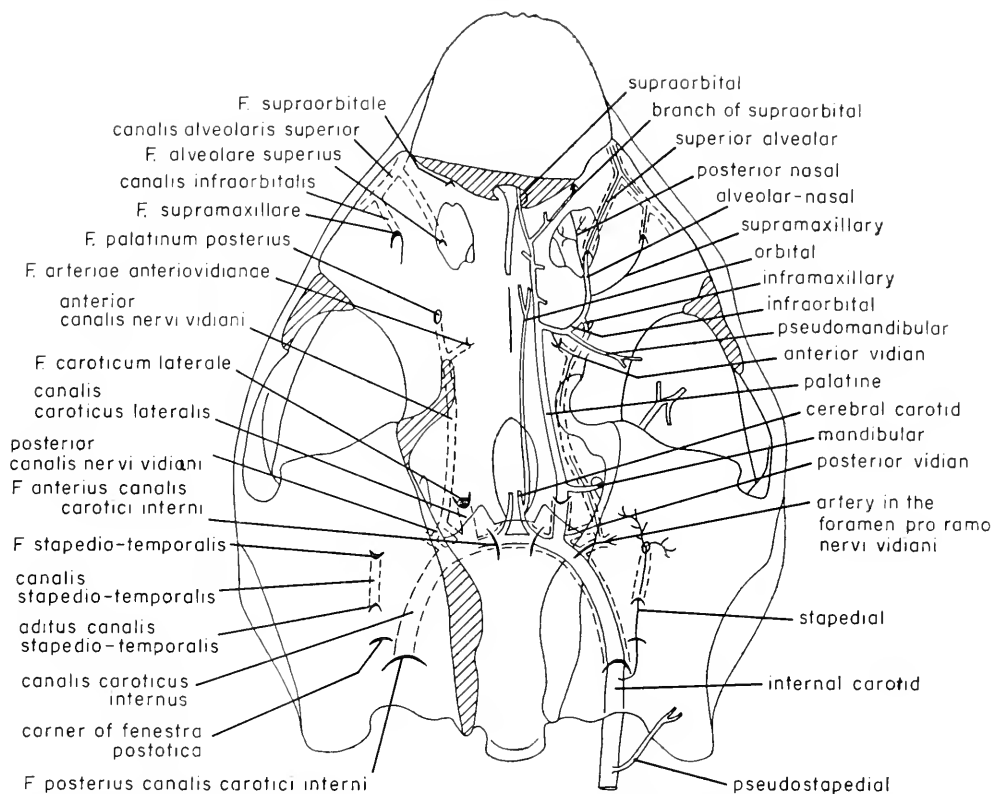


Figure 2. Semidiagrammatic dorsal view of the cranial arteries (right side) and cranial arterial foramina and canals (left side) of *Sternotherus odoratus*.

large in *Sternotherus*, and it goes only a short distance through the pterygoid bone before it opens into the cavum cranii by means of a larger foramen which is directly lateral to the dorsum sellae. Similarly in *Trionyx*, this large canal arises from the canalis caroticus internus, goes a short way through the pterygoid bone, and opens into the cavum cranii through a large foramen lateral to the dorsum sellae. This foramen in *Trionyx* may be slightly smaller than the foramen in *Sternotherus*, but in both groups it is much larger than that of *Chrysemys*. Furthermore, this foramen in the pterygoid bone of *Chrysemys* is more anteriorly-located than the foramen in the pterygoid bones of *Sternotherus* and *Trionyx*. Nevertheless, the canal in each genus is very similar in relative position in the pterygoid bone and in relation to the other canals, and hence the canal and foramen are probably homologous in *Chrysemys*, *Sternotherus*, and *Trionyx*.

The canal and foramen described above

have been given a variety of names. Siebenrock (1897) showed this foramen labeled f.c.i.' in trionychids and kinosternids and he also discussed its occurrence in the Chelidae. Ogushi (1911: 29) called this foramen and canal of *Trionyx* "die Fenestra lateralis canalis carotici." Finally, McDowell (1961) found that the palatine artery goes through this canal in testudinids and kinosternids, and he called the canal the canalis arteriopalatinus and the foramen the foramen arteriopalatinum. However, the palatine artery no longer traverses this foramen in *Trionyx*, and hence McDowell's names no longer suffice. Following Ogushi's example, I call this canal the **canalis caroticus lateralis** and its opening the **foramen caroticum laterale** in all turtle genera.

A small ventrally-directed canal is associated with the canalis caroticus lateralis in *Chrysemys* and *Sternotherus*. The canalis carotico-pharyngealis (McDowell) of *Chrysemys* is a small ventral canal which

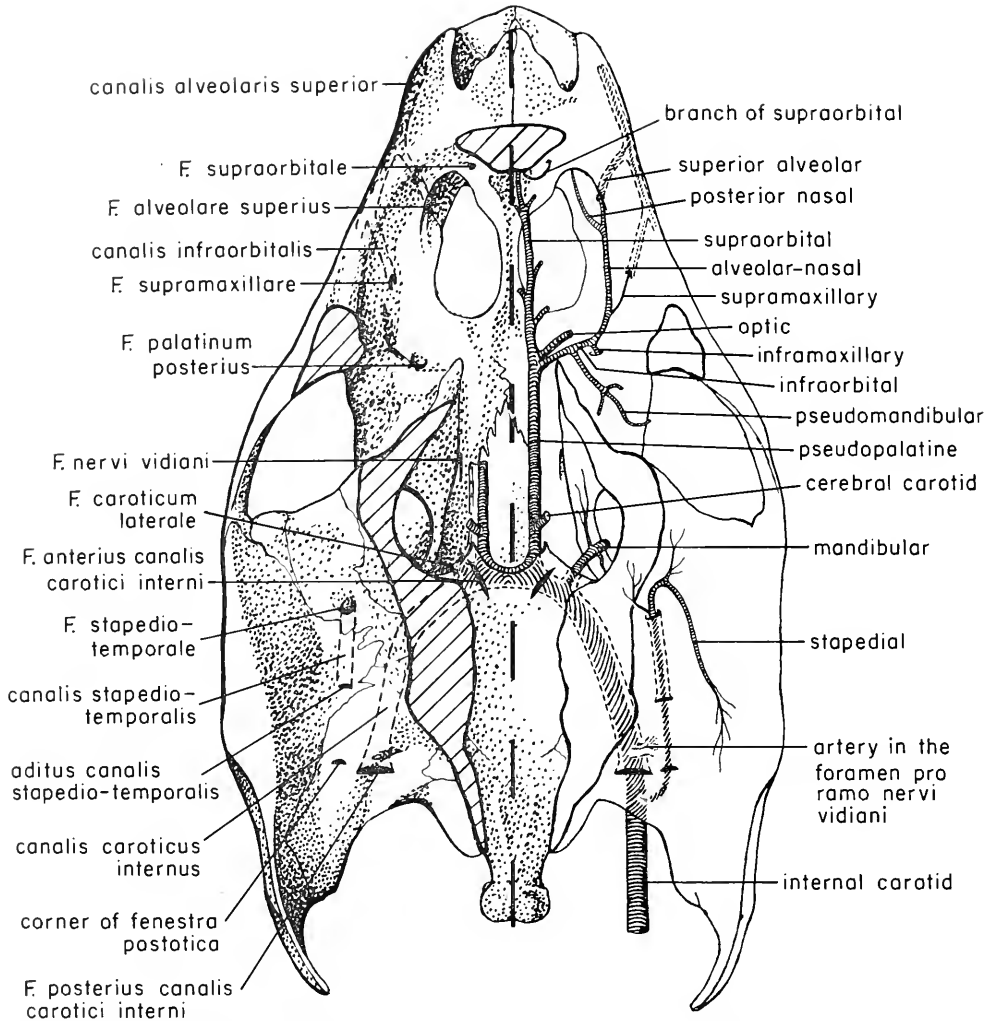


Figure 3. Semidiagrammatic dorsal view of the cranial arteries (right side) and cranial arterial foramina and canals (left side) of *Trionyx spinifer*.

arises near the posterior end of the canalis caroticus lateralis and goes ventrally through the pterygoid bone to exit through the foramen carotico-pharyngeale (McDowell). This foramen was present as a very small opening in the ventral surface of the pterygoid bone anterolateral to the middle of the ventral surface of the basisphenoid bone in all 65 of the *Chrysemys* examined. The diameters of the foramina were variable, and sometimes the foramina were barely visible; the number of foramina carotico-pharyngeale was also variable, for there often were two or three foramina on each side and in

four specimens the foramen was not visible on one side of the skull. In *Sternotherus*, the canalis carotico-pharyngealis arises directly at the origin of the canalis caroticus lateralis and goes ventrally in the pterygoid bone to open at the foramina carotico-pharyngeale. This foramen and canal are usually slightly larger than those of *Chrysemys*, and the foramen carotico-pharyngeale of *Sternotherus* is located in the pterygoid bone lateral to the anterior tip of the ventral surface of the basisphenoid, anteriorly in relation to the foramen in *Chrysemys*. Although they were present in all the

Chrysemys and *Sternotherus* examined, the foramina carotico-pharyngeale were absent in all the *Trionyx* examined.

The canalis carotico-pharyngealis of *Chrysemys* and *Sternotherus* is associated with the canals for the vidian nerve. In *Chrysemys*, the vidian nerve enters the canalis caroticus internus by means of the foramen pro ramo nervi vidiani, which connects the canalis caroticus internus with the canalis cavernosus and is visible as a large opening in the dorsal wall of the canalis caroticus internus medial to the condylus mandibularis. From this foramen, some nerves enter a small, anterolaterally-directed canal in the pterygoid which goes lateral and parallel to the canalis caroticus internus anteriorly to the region of the canalis carotico-pharyngealis; for convenience, I call this nerve canal the posterior canalis nervi vidiani. Other nerves exit from the foramen pro ramo nervi vidiani and traverse the canalis caroticus internus anteriorly to enter the canalis caroticus lateralis. These nerves then divide; some branches go through the canalis caroticus lateralis and exit on the dorsal surface of the pterygoid bone whereas other nerves go ventrally, entering the canalis carotico-pharyngealis and finally joining the nerves of the posterior canalis nervi vidiani by means of an anterolateral canal which connects the canalis carotico-pharyngealis with the posterior canalis nervi vidiani. These nerves in the bony canals then enter the anterior canalis nervi vidiani which goes through the pterygoid and palatine bones from the region of the canalis carotico-pharyngealis to the foramen palatinum posterius; the nerves then traverse this foramen to enter the orbit. The vidian canal pattern is thus much more complicated than indicated by McDowell.

The canals for the vidian nerve of *Sternotherus* are very similar to those of *Chrysemys*. The posterior canalis nervi vidiani, connection of the canalis nervi vidiani with the canalis carotico-pharyngealis, anterior canalis nervi vidiani, and the connection of the anterior canalis nervi vidiani with the foramen palatinum posterius are present. However, there are some differences from the bony canal pattern of *Chrysemys*. First of all, the foramen pro ramo nervi vidiani is smaller in diameter and is located near the base of the canalis caroticus lateralis, therefore farther anterior than in *Chrysemys*.

Furthermore, the anterior canalis nervi vidiani connects with another anterior canal in the pterygoid bone just posterior to its connection with the foramen palatinum posterius. This anterior canal angles anterodorsally to open on the dorsal surface of the pterygoid bone through a small foramen anterior to the anterior end of the crista pterygoidea, posteromedial to the dorsal foramen palatinum posterius. This short anterior canal connects with very small canals opening in the ventral surface of the palatine bone medial to the ventral foramen palatinum posterius; I call these ventral openings the **foramina arteriaevidianae** and the larger opening on the dorsal bone anteroventral from the processus inferior parietalis I call the **foramen arteriae arteriovidianae**. The extremely small, variable foramina arteriaevidianae were present in all 18 of the *Sternotherus* skulls examined. These foramina are lacking in *Chrysemys* and *Trionyx*.

The vidian nerve pattern of *Trionyx* is very simple in comparison with the complex patterns of *Chrysemys* and *Sternotherus*. The nerves enter the canalis caroticus internus through the foramen pro ramo nervi vidiani, which is similar in size and position to the foramen of *Chrysemys*. The nerves then continue on from the canalis caroticus lateralis and exit into the sulcus cavernosus by means of the foramen caroticum laterale; the nerves go a short way over the dorsal surface of the pterygoid bone to enter the foramen nervi vidiani (Siebenrock) at the medial base of the crista pterygoidea ventral to the anterior edge of the foramen nervi trigemini. The foramen nervi vidiani leads to the canalis nervi vidiani which goes through the pterygoid and palatine bones to another canal in the palatine bone which in turn carries the vidian nerves to the foramen palatinum posterius. From the foramen palatinum posterius, the vidian nerves of *Trionyx* enter the orbit, as in *Chrysemys* and *Sternotherus*. Thus *Trionyx* differs from *Chrysemys* and *Sternotherus* in having no canalis carotico-pharyngealis, no posterior canalis nervi vidiani, and no connection between the canalis nervi vidiani and the canalis caroticus lateralis. The vidian nerve canals of *Chrysemys* and *Sternotherus* contain small arteries, but no artery was found in the vidian canal of *Trionyx*.

The foramen palatinum posterius is pres-

ent in all the skulls of the three genera as an opening on the posterior floor of the orbit, anterior to the crista pterygoidea. In *Trionyx*, the foramen palatinum posterius is connected by a small, posteromedially-directed canal in the palatine bone which opens ventrally through a variable number of small foramina. These foramina are located in the palatine bone posteromedial from the ventral opening of the foramen palatinum posterius, and I call these the **foramina palatinum accessorium**. The canal connecting the foramina palatinum accessorium with the foramina palatinum posterius is called the canalis palatinus major et minor by Ogushi, but I shall use the simpler term **canalis intrapalatinus**. The canalis intrapalatinus transports arteries and nerves and also serves as the anterior opening of the canalis nervi vidiani. The foramina palatinum accessorium and the canalis intrapalatinus were present in all the *Trionyx* examined, but they were not present in any of the *Sternotherus* or *Chrysemys* crania.

Besides the foramen palatinum posterius, there are also a number of other arterial foramina in the orbital region of the three genera. The foramen orbito-nasale is a large foramen on the anterior floor of the orbit in *Trionyx*, *Chrysemys*, and *Sternotherus*. The smaller foramen alveolare superius is located at the lateral edge of the foramen orbito-nasale; the foramen alveolare superius leads into the anterolaterally-directed canalis alveolaris superior which goes through the maxillary bone, branching into the lateral canalis alveolaris superior which goes anteriorly and posteriorly along the ventrolateral edge of the maxillary bone.

Posterolateral from the foramen alveolare superius there is a small foramen located in the maxillary bone of the floor of the orbit. This small foramen, the **foramen supra-maxillare** (new term, adapted from Bojanus) leads into a narrow, anterolaterally-directed canal, the canalis infraorbitalis (Ogushi), which connects with the lateral canalis alveolaris superior. The foramen supra-maxillare was present in all 96 of the *Chrysemys*, *Sternotherus*, and *Trionyx* skulls examined.

Another extremely small arterial foramen is located on the prefrontal bone in the anterodorsal part of the orbit, dorsolateral from the dorsal edge of the fissura ethmoi-

dal. This opening, the **foramen supra-orbitale**, leads into an extremely narrow canal which goes anteriorly through the prefrontal bone and terminates by opening into the fossa nasalis. In *Chrysemys*, the canal leads to the anterior end of the dorsal part of the prefrontal bone, and its openings there are often visible on dry skulls. Despite its small size, the foramen supraorbitale was present in all 96 of the *Chrysemys*, *Sternotherus*, and *Trionyx* skulls examined. Thus the arterial foramina and canals of the orbit are nearly identical in *Chrysemys*, *Sternotherus*, and *Trionyx*.

There are also a number of other cranial arterial foramina common to the three genera, such as the foramen nervi trigemini, the fossa meckelii, and the fissura ethmoidalis, but these are very large openings which contain much more than arteries and are fairly similar in *Trionyx*, *Chrysemys*, and *Sternotherus*. The foramina praepalatinum also transports arteries; these foramina are present as paired, very small openings in *Chrysemys* and *Sternotherus*, but in *Trionyx* the two foramina praepalatinum are fused to form a very large opening into the fossa nasalis.

In general, the differing cranial arterial foramina of *Trionyx*, *Sternotherus*, and *Chrysemys* were found to be quite constant in all the skulls of each genus examined, and only the smallest foramina were subject to minor individual variations. To summarize, the larger cranial arterial foramina and canals of *Trionyx* are very similar to those of *Sternotherus*, as evidenced by the reduced foramen stapedio-temporale, the large foramen posterius canalis carotici interni, the large canalis caroticus internus, the large canalis caroticus lateralis, and the large foramen caroticum laterale. *Chrysemys* differs from *Trionyx* and *Sternotherus* in having a very large foramen stapedio-temporale, a small foramen posterius canalis carotici interni, a small canalis caroticus internus, and a very small canalis caroticus lateralis with more anteriorly-located foramen caroticum laterale. *Chrysemys* and *Sternotherus* have a complex vidian nerve canal complex and foramina carotico-pharyngeale which are not present in *Trionyx*, and *Trionyx* has a very large foramen arterius canalis carotici interni which is small in *Chrysemys* and *Sternotherus*. The foramen supraorbitale, foramen supra-maxillare, canalis infraorbit-

alis, foramen alveolare superius, canalis alveolaris superior, foramen palatinum posterius, and foramen orbito-nasale are very similar in all three genera. The foramina arteriaevidianae and foramen arteriae arteriovidianae are peculiar to *Sternotherus*, and the foramen palatinum accessorium and canalis intrapalatinum are peculiar to *Trionyx*. Finally, it should be re-emphasized that all the above facts concerning foramina and canals are directly related to the different cranial arterial patterns of *Chrysemys*, *Sternotherus*, and *Trionyx*.

III. CRANIAL ARTERIAL FORAMINA AND CANALS ON A FAMILIAL LEVEL

McDowell (1961) described the general foramina and canals of the Testudinidae, with emphasis on the large foramen stapedio-temporale, small canalis caroticus internus, and very small canalis caroticus lateralis. From the studies of Siebenrock and McDowell and my own studies of the crania of seven testudinid genera, I conclude that the above are constant features in the Testudinidae. Furthermore the foramen palatinum posterius, foramen praepalatinum, foramen supramaxillare, foramen supraorbitale, and the foramen carotico-pharyngeale were present in all the testudinid skulls which I examined. The foramina carotico-pharyngeale seemed to be most variable in the testudinids, for they were very small in *Chrysemys*, *Graptemys*, and *Malaclemys* and fairly large in *Clemmys*, *Emydoidea*, *Terrapene*, and *Gopherus*. In *Gopherus*, there was a single large foramen carotico-pharyngeale located in the basisphenoid, and a peculiar foramen arteriomandibulare (McDowell) was also present. The other arterial foramina studied also differed slightly in size and position in the different genera. McDowell failed to note the connection between the vidian canals and the canalis carotico-pharyngealis and he was not correct in stating that the canalis carotico-pharyngealis is a branch of the canalis caroticus internus (1961: 27).

Siebenrock and McDowell also described some of the foramina and canals of the Kinosternidae, emphasizing the large canalis caroticus internus, the large canalis caroticus lateralis, and the greatly reduced foramen stapedio-temporale. McDowell stresses the

reduced or "absent" foramen stapedio-temporale and states that it is present as an occasional vestige in the Kinosternidae (1961: 33). On the other hand, Siebenrock disagrees with this viewpoint and states that the foramen stapedio-temporale "fehlt aber bei keiner Art" (1897: 266). The foramen is present in all the 26 skulls I examined, except in one large skull of *Kinosternon scorpiodes*, and its absence in this specimen may have been due to old age. Hence McDowell's statement should be changed to say that the foramen stapedio-temporale is occasionally absent in the Kinosternidae. Examination of the three genera of Kinosternidae also revealed the presence of the foramen palatinum posterius, foramen supramaxillare, foramen supraorbitale, foramen arteriaevidianae, and foramen carotico-pharyngeale in all specimens; the foramen praepalatinum was not present in *Stawotyphus*.

The foramina and canalis of the other genera of the Trionychidae have not been described in as much detail as they have for different genera in the other two families. Siebenrock noted the large foramen posterius canalis carotici interni and the large foramen caroticum laterale, and he made an important observation about the "besondere Grösse" (1897: 262) of the foramen anterius canalis carotici interni which by his system separated the trionychids from all other turtles. From the illustrations of the skulls of the Trionychidae in Wermuth and Mertens (1961) it can also be concluded that the reduced foramen stapedio-temporale is a constant feature of the trionychids.

To generalize from the above facts, the relative sizes and presence of the foramen stapedio-temporale, the canals and foramina of the basisphenoid region, and the foramina of the orbital region were found to be constant characteristics of the testudinids and kinosternids. From this it follows that the general arterial pattern of these two families can be validly inferred from the detailed arterial patterns of *Chrysemys* and *Sternotherus*. Less is known about the other genera of the Trionychidae, but it can be inferred that the general arterial patterns in the basisphenoid region and in the foramen stapedio-temporale are constant in all the trionychids and that the arterial pattern in these regions is the same as that of *Trionyx*.

IV. THE CRANIAL ARTERIES OF *CHRYSEMYS*

The common carotid artery courses up the side of the neck, giving off small branches into the adjacent muscles. Behind the skull, the common carotid artery branches into the ventral arteria carotica externa (external carotid artery), which supplies the tissue around the hyoid apparatus under the tongue, and the arteria carotica interna (internal carotid artery). The internal carotid artery goes anteriorly a short way to the region directly posterior to the fenestra postotica, where it gives rise to a large, dorso-lateral branch, the arteria stapediaлис (stapedial artery). The internal carotid artery then continues on into the foramen posterius canalis carotici interni.

The stapedial artery gives off a fairly large branch which goes around the posterior part of the skull to supply the tissue of the incisura columellae auris, and then the stapedial artery enters the fenestra postotica. In the cavum acustico-jugulare anterior to the columella, the stapedial artery gives rise to a ventral branch, the arteria mandibularis (mandibular artery). Contrary to McDowell, the mandibular artery is large and not "minute" (1961: 28) in size. The mandibular artery goes through the canalis cavernosus and into the muscles of the fenestra subtemporalis by means of the foramen cavernosum and the foramen nervi trigemini. The mandibular artery goes ventrally through the muscles of the fenestra subtemporalis, giving off many branches, and then enters the fossa meckelii. In this fossa, the mandibular artery gives off branches which remain in the canalis cartilaginis meckelii, branches which exit from the bone through a large medial foramen ventral to the processus coronoideus, and small branches which go posteroventrally to exit from the mandible through small foramina in the lateral bone near the area articularis mandibularis.

From the cavum acustico-jugulare, the large stapedial artery enters the aditus canalis stapedio-temporalis and goes through the canalis stapedio-temporalis to the foramen stapedio-temporale. In the temporal fossa, the stapedial artery gives rise to a large posterior branch, the arteria cervicalis (cervical artery), which supplies muscles of the temporal fossa and dorsal neck muscles behind the head. The stapedial artery curves anterodorsally in a groove in the lateral sur-

face of the parietal bone and branches into the arteria supraorbitalis and the arteria infraorbitalis under the postorbital bone.

The arteria supraorbitalis (supraorbital artery) is usually the smaller of the two branches of the stapediaლ artery. It curves over the dorsomedial part of the eyeball, giving off many branches to the eyeball, small branches into the prefrontal bone, and a small branch into the foramen supra-orbitale. This last branch goes through its foramen and canal in the prefrontal bone to supply the anterior tissue of the fossa nasalis. In one *Chrysemys* which I dissected, the supraorbital artery was larger than the infraorbital artery and was divided into two large branches. One branch formed a loop on the posteromedial surface of the eyeball, sending many branches to the adjacent tissue. The other branch went anteromedial to the eyeball and was located in the middle of the orbit, not in the dorsal part of the orbit as in the normal supraorbital artery. Furthermore, this anterior branch of the supraorbital artery sent a small dorsal branch into the foramen supraorbitale, but it also sent a large branch into the fissura ethmoidalis.

The arteria infraorbitalis (infraorbital artery) runs ventrally in the posterior part of the orbit, supplying the eyeball and also giving rise to the small arteria pseudo-mandibularis (pseudomandibular artery) which supplies the anterior muscles of the fenestra subtemporalis. On the floor of the orbit, the infraorbital artery gives rise to three branches, the arteria supramaxillaris (supramaxillary artery) the **arteria infra-maxillaris** (inframaxillary artery) and the **arteria alveolare-nasalis** (alveolar-nasal artery).

The largest of the three arteries, the alveolar-nasal artery, goes anteriorly on the ventral surface of the eyeball across the floor of the orbit and into the membrane covering the foramen orbito-nasale. Here the alveolar-nasal artery branches into the lateral arteria alveolaris superior (superior alveolar artery) and the anterior arteria posterior nasalis (posterior nasal artery). The posterior nasal artery goes through the foramen orbito-nasale to supply the tissue of the posterior part of the fossa nasalis. The superior alveolar artery goes through the foramen alveolare superius and into the canalis alveolaris superior, where it sends

small branches into the maxillary bone, to the lateral skin, and to the tissue of the nasal capsule.

The supramaxillary artery is a very small artery passing anteriorly on the lateral floor of the orbit and entering the canalis infraorbitalis by way of the foramen supra-maxillare. Its function probably is that of supplying the branches of the trigeminal nerve within the canalis infraorbitalis and canalis alveolaris superior.

The inframaxillary artery runs directly ventrad through the foramen palatinum posterius to emerge on the roof of the mouth. The inframaxillary artery then goes anteriorly in the tissue medial to the border of the triturating surface, sending many small branches into the adjacent tissue and into the maxillary bone. The arteries of each side anastomose, forming the "U-shaped artery" of McDowell, and a branch on each side, the arteria anterior nasalis (anterior nasal artery) extends from the anastomosis into the foramen praepalatinum and then into the tissue of the fossa nasalis.

The small internal carotid artery enters the canalis caroticus internus and curves anteromedially to the foramen arterius canalis carotici interni. Shortly after entering its canal, the internal carotid artery gives off an extremely small dorsal branch which goes into the foramen pro ramo nervi vidiani and supplies some of the tissue in the canalis cavernosus. Anteriorly in its canal, the internal carotid artery gives off a small branch which enters the canalis caroticus lateralis; this branch is the base of the arteria palatina (palatine artery). This base of the palatine artery gives rise to two other arteries, the **arteria carotico-pharyngealis** (pharyngeal carotid artery) and the **arteria posterior vidiana** (posterior vidian artery). The small pharyngeal carotid artery arises as a ventral branch of the base of the palatine artery; it goes through the canalis carotico-pharyngealis and out the foramen carotico-pharyngeale to supply the adjacent tissue on the roof of the mouth. The very small posterior vidian artery arises at the same place on the base of the palatine artery and goes through the canal which connects the canalis carotico-pharyngealis with the canalis nervi vidiani. Then the posterior vidian artery sends extremely small branches into the posterior canalis nervi vidiani and

into the anterior canalis nervi vidiani. Contrary to McDowell, the posterior vidian artery does not extend the length of the vidian canal, for it ends in the canal and probably supplies only the tissue within the canal. McDowell also erred in stating that the pharyngeal carotid artery arises as a branch of the internal carotid artery (1961: 29). After giving off the above two arteries at its base, the minute palatine artery exits from the foramen caroticum laterale into the cavum cranii and runs lateral to the rostrum basisphenoidale and lateral to the cartilage which fills the sulcus vomeri to the tissue which fills the fissura ethmoidalis. There is no anastomosis of the palatine artery in the cavum cranii with the posterior vidian artery as found by McDowell, and the palatine artery anteriorly appears to be a functionless vestige.

After giving off the base of the palatine artery, the internal carotid artery on each side goes out the foramen arterius canalis carotici interni to form a large anastomosis in the dorsum sellae of the basisphenoid. Contrary to McDowell (1961: 31), this anastomosis is not the circle of Willis, for the circle of Willis is formed dorsal to it on the ventral surface of the brain. The arteria carotica cerebialis (cerebral carotid artery) extends dorsally from each side of the anastomosis. Before entering the brain, each cerebral carotid artery gives off a small artery, the arteria orbitales (orbital artery), which goes anteriorly under the brain, dorsally through the interorbital tissue, and into the orbit to supply the ocular muscles (*vide* Burda).

The cerebral carotid arteries go on to the ventral surface of the brain lateral to the pituitary body. There the cerebral carotid arteries on each side give off a posterior branch and an anterior branch. The anterior branch on each side gives rise to a large arteria cerebri media (middle cerebral artery), which angles anterodorsally up the middle of the cerebrum; the middle cerebral artery on each side has small branches which anastomose in front of the optic chiasma, and other more anterior branches are the arteria cerebri anterior (anterior cerebral artery) and the arteria olfactoria (olfactory artery). The posterior branch of the cerebral carotid artery gives rise to a large arteria cerebri posterior (posterior cerebral artery) which goes along the pos-

terior margin of the cerebrum and sends branches dorsally to terminate in the choroid plexus of the third ventricle. The posterior branches of the cerebral carotid artery on each side then anastomose under the medulla oblongata to form the arteria basilaris (basilar artery); the basilar artery also receives blood from spinal arteries. The anastomosis for the basilar artery and the anterior anastomosis together form the circle of Willis.

V. THE CRANIAL ARTERIES OF *STERNOTHERUS*

The common carotid artery goes up the side of the neck and gives rise ventrally to external carotid artery, as in *Chrysemys*. Just anterior to the external carotid artery, the internal carotid artery gives rise to a large dorsal branch which goes through the neck muscles to supply the muscles above the fossa temporalis. This branch takes over the function of the cervical branch of the stapedia artery in *Chrysemys*, and hence I call it the **arteria pseudostapedialis** (pseudostapedial artery).

Before entering the foramen posterius canalis carotici interni, the internal carotid artery gives off a small dorsolateral branch which goes around the posterior part of the skull to supply the tissue of the incisura columellae auris; this branch is extremely similar to the branch from the stapedia artery of *Chrysemys*. McDowell found no stapedia artery in the canalis stapedio-temporalis and foramen stapedio-temporale of the one injected *Sternotherus* which he dissected, and he concludes that the foramen stapedio-temporale is "purely venous" in function (1961: 33). Contrary to that statement, a minute stapedia artery is present in *Sternotherus*. The stapedia artery arises as a minute branch of the larger dorso-lateral branch mentioned above, and it goes through the fenestra postotica, cavum acustico-jugulare, aditus canalis stapedio-temporalis, canalis stapedio-temporalis, and foramen stapedio-temporale, just as in *Chrysemys*. The stapedia artery emerges from the foramen stapedio-temporale, sending extremely small branches into the epithelium under the muscles of the temporal fossa, and it also sends one small branch into the supraoccipital bone. The stapedia artery of *Sternotherus* does not give rise to the man-

dibular artery and is greatly reduced in comparison with the stapedia artery of *Chrysemys*. McDowell's one specimen of *Sternotherus* may have been poorly injected, causing him to completely miss this evolutionarily-important artery.

The very large internal carotid artery curves anteromedially through the canalis caroticus internus to the foramen anterius canalis carotici interni. The internal carotid artery gives off an extremely small branch, smaller than that of *Chrysemys*, into the foramen pro ramo nervi vidiani. More anteriorly, the internal carotid artery gives rise to the large palatine artery in the canalis caroticus lateralis. The palatine artery immediately gives rise to the ventral pharyngeal carotid artery; this artery is much larger than that of *Chrysemys*, and its ventral branches run anteriorly and posteriorly to supply much of the tissue of the roof of the mouth. In fact, these branches of the pharyngeal carotid arteries are sometimes visible when a live *Sternotherus* opens its mouth. In the pterygoid bone, the pharyngeal carotid artery gives rise to a very small posterior vidian artery which goes only a short way into the anterior and posterior canalis nervi vidiani, as in *Chrysemys*.

The internal carotid arteries anastomose in the dorsum sellae and give rise to the cerebral carotid arteries and orbital arteries which proceed to the eye and to the brain, just as in *Chrysemys*; the branches of the cerebral carotid arteries in the brain are also similar to those of *Chrysemys*. My injected specimen of *Sternotherus* had no anastomosis between the internal carotid arteries, but this was clearly an individual variation, for the anastomosis was present in the other dissected *Sternotherus*.

The large palatine artery emerges from the foramen caroticum laterale and immediately gives rise to a large lateral branch, the mandibular artery, which exists through the foramen nervi trigemini to supply the muscles of the fenestra subtemporalis and the mandible as in *Chrysemys*. In the cavum cranii, the mandibular artery on each side gives off a fairly large artery which goes posterodorsally to connect with the basilar artery on the brain; these branches are not found in *Chrysemys*.

The palatine artery continues on in the cavum cranii medial to the ventral processus

inferior parietalis and divides into the supra-orbital artery and infraorbital artery just as it leaves the cavum cranii. The supraorbital artery is very similar to the large supra-orbital artery of the aberrant *Chrysemys*. The supraorbital artery runs anteromedial to the eye in the middle of the orbit, sending many branches to the eye; after sending a small dorsal branch into the foramen supraorbitale, the supraorbital artery sends branches into the fissura ethmoidalis.

The infraorbital artery, pseudomandibular artery, supramaxillary artery, inframaxillary artery, anterior nasal artery, alveolar-nasal artery, superior alveolar artery, and posterior nasal artery are so similar to the same arteries in *Chrysemys* that a redescription is not necessary. However, one small branch of the infraorbital artery in *Sternotherus* was not observed in *Chrysemys*. This small branch, the **arteria anterior vidiana** (anterior vidian artery) enters the foramen arteriae anterovidianae and goes postero-ventrally through the palatine bone to the region of the foramina arteriaevidianae. The anterior vidian artery in this region sends a very small branch into the anterior canalis nervi vidiani, and it also sends a variable number of branches through the foramina arteriaevidianae to supply a small area of tissue on the dorsal roof of the mouth.

To generalize, the cranial arteries in the brain region, orbital region, nasal region, and mandibular region are very similar in *Sternotherus* and *Chrysemys*. The major arterial differences in the two genera involve the size and function of three major arteries and the place of origin of three additional arteries. In *Chrysemys*, the stapedia artery is large, the internal carotid artery is small, and the palatine artery is minute; in *Sternotherus*, the stapedia artery is minute, the internal carotid artery is large, and the palatine artery is large. In *Chrysemys*, the mandibular artery, supraorbital artery, and infraorbital artery arise from the stapedia artery; in *Sternotherus*, these same three arteries arise from the palatine artery. *Sternotherus* also has pseudostapedial arteries, anterior vidian arteries, and branches from the mandibular arteries to the brain which are not present in *Chrysemys*.

VI. THE CRANIAL ARTERIES OF *TRIONYX*

The common carotid artery goes up the side of the neck and gives off the external carotid artery, as in *Sternotherus* and *Chrysemys*. Directly behind the skull, the large internal carotid artery gives off a smaller dorsolateral branch, the stapedia artery. Before entering the fenestra postotica, the stapedia artery gives rise to a branch which goes around the posterior part of the skull to the tissue of the incisura columellae auris, just as in *Chrysemys* and *Sternotherus*. In *Trionyx*, the stapedia artery is smaller than the internal carotid artery, but it is not greatly reduced as in *Sternotherus*. After traversing the dorsolateral corner of the fenestra postotica, the cavum acusticojugulare, the aditus canalis stapedio-temporalis, the canalis stapedio-temporalis, and the foramen stapedio-temporale, the stapedia artery enters the temporal fossa as a medium-sized artery which supplies only the muscles of the temporal fossa.

Shortly after entering the canalis caroticus internus, the large internal carotid artery sends a small branch dorsally into the foramen pro ramo nervi vidiani; this branch is similar to that of *Chrysemys* and is larger than that of *Sternotherus*. The internal carotid artery curves anteromedially in its canal and gives off a large branch into the canalis caroticus lateralis. This branch exists from the foramen caroticum laterale and from the foramen nervi trigemini to supply the muscles of the fenestra subtemporalis and to enter the fossa meckelii, where arteries are distributed as in *Chrysemys* and *Sternotherus*. In short, the mandibular artery arises as a branch of the internal carotid artery and utilizes the canalis caroticus lateralis, which conducts the palatine artery in *Sternotherus* and *Chrysemys*.

The internal carotid artery directly posterior to the foramen antierius canalis carotici interni is much larger than the internal carotid artery in the same region of *Sternotherus* and *Chrysemys*. Because of this, the anastomosis in the dorsum sellae of *Trionyx* is also larger than the anastomosis in the other two genera. From each side of the anastomosis, an artery emerges into the cavum cranii; this artery is much larger than the cerebral carotid artery of *Sternotherus* and *Chrysemys*. In the cavum cranii, this large artery goes anteriorly lateral to the pi-

tuitary body a short distance and then gives off a dorsal branch on each side which is clearly the cerebral carotid artery. The cerebral carotid arteries branch on the anterior and posterior ventral surface of the brain, giving rise to the middle cerebral artery and its branches, the posterior cerebral artery, the basilar artery, and the circle of Willis, just as in *Sternotherus* and *Chrysemys*.

After giving off the cerebral carotid artery, the large artery runs anteriorly in the cavum cranii medial to the ventral processus inferior parietalis, and just as it leaves the cavum cranii, the large artery branches into the orbit. Except for its origin, this large artery of *Trionyx* is very similar to the palatine artery of *Chrysemys* and *Sternotherus*. However, the position of origin from the internal carotid artery is an important point which very likely indicates that the large artery of *Trionyx* is not homologous with the palatine artery of the other two genera. Hence I call this artery the **arteria pseudopalatina** (pseudopalatine artery). To recapitulate, the pseudopalatine artery of *Trionyx* is a branch of the internal carotid artery which goes through the foramen anterius canalis carotici interni and gives rise to the cerebral carotid artery and the arteries of the orbit. In contrast, the palatine artery of *Sternotherus* is a large branch of the internal carotid artery which goes through the foramen caroticum laterale and gives rise to the mandibular artery and the arteries of the orbit; the palatine artery of *Chrysemys* is a minute branch of the internal carotid artery which goes through the foramen caroticum laterale and terminates without branching.

Medial to the anterior end of the crista pterygoidea, the pseudopalatine artery branches into three arteries which run anteriorly, anterodorsally, and ventrolaterally in the orbit. The fairly large anterior branch is the supraorbital artery, which runs anteromedially in the middle of the orbit, sending many branches to the eye and adjacent tissues. The main branch of the supraorbital artery then enters the fissura ethmoidalis, where it branches extensively to supply the tissue of the fossa nasalis. One of the anterior branches of the supraorbital artery a short distance inside the fissura ethmoidalis gives rise to a small posterior branch which arises from the posterior part of the fissura ethmoidalis and goes dorsally to enter the

foramen supraorbitale. From the foramen, the small supraorbital branch enters its own canal in the prefrontal bone to supply the anterior nasal tissue.

The fairly large anterodorsal branch of the pseudopalatine artery is situated in the dorsal part of the posteromedial part of the orbit. This artery becomes associated with the optic nerve, and it supplies the eye. There is no orbital artery branching from the cerebral carotid artery of *Trionyx*, but this anterodorsal artery probably has approximately the same function as the orbital artery of the other two genera. I call this artery the **arteria optica** (optic artery); there is no optic artery in *Sternotherus* or in *Chrysemys*.

The ventrolateral branch of the pseudopalatine artery in the orbit is the infraorbital artery. In the posterior part of the orbit, the infraorbital artery gives rise to the pseudomandibular artery which goes dorsally to supply the muscles under the postorbital bar and then ventrally to supply the tissue of the lateral part of the mandible; the pseudomandibular artery of *Trionyx* is much larger than the same artery in *Sternotherus* and *Chrysemys*. The infraorbital artery continues ventrolaterally and gives rise to the infra-maxillary artery, which enters the foramen palatinum posterius. In the ventral foramen palatinum posterius, the inframaxillary artery gives rise to a small branch which goes through the canalis intrapalatinus, exits from the foramen palatinum accessorium, and supplies the adjacent tissue on the roof of the mouth. The inframaxillary artery itself exits from the foramen palatinum posterius and runs anteriorly in the tissue medial to the border of the triturating surface, giving off many small branches to the adjacent tissue and to the maxillary bone. The arteries of each side then form a narrow anastomosis which sends small branches dorsally to the mouth tissue. The anterior nasal artery on each side extends from the anastomosis into the foramen praepalatinum and then into the nasal tissue.

The infraorbital artery goes a short distance anteriorly in the orbit and divides into the supramaxillary artery and the alveolar-nasal artery. The very small supramaxillary artery enters the foramen supramaxillare and supplies the tissue within the canalis infraorbitalis and canalis alveolaris superior. The alveolar-nasal artery goes an-

teriorly on the orbit floor and divides into two arteries in the foramen orbito-nasale; the smaller posterior nasal artery goes through the foramen orbito-nasale to supply the posterior nasal tissue, whereas the superior alveolar artery enters the canalis alveolaris superior to supply the lateral side of the maxillary bone and adjacent tissue.

To compare and summarize, the major arterial differences between *Trionyx* and the other two genera occur in the basisphenoid region of the skull. In *Trionyx*, the anastomosis of the internal carotid arteries in the dorsum sellae gives rise to the very large pseudopalatine artery, whereas in *Chrysemys* and *Sternotherus* the small anastomosis in the dorsum sellae gives rise to the cerebral carotid artery. The cerebral carotid artery of *Trionyx* is a branch of the pseudopalatine artery. In *Chrysemys* and *Sternotherus*, the palatine artery is a branch of the internal carotid artery which exits through the canalis caroticus lateralis, but in *Trionyx* the mandibular artery is a branch of the internal carotid artery which exits through the canalis caroticus lateralis. The mandibular artery of *Chrysemys* is a branch of the stapedial artery, and the mandibular artery of *Sternotherus* is a branch of the palatine artery. A branch from the mandibular artery to the brain is present only in *Sternotherus*. In spite of their different origins, the mandibular artery of each genus exits from the foramen nervi trigemini, goes through the fenestra subtemporalis, enters the fossa meckelii, and branches similarly in the mandible. Furthermore, the branches of the cerebral carotid arteries in the brain are very similar in the three genera.

The origin of the arteries of the orbital and nasal regions is a direct consequence of the rearrangement of the arteries in the basisphenoid region. In *Trionyx*, the pseudopalatine artery gives rise to the infraorbital and supraorbital arteries, and the stapedial artery supplies only the muscles of the temporal fossa. In *Chrysemys*, the large stapedial artery gives rise to the infraorbital and supraorbital arteries and to the cervical artery, which supplies the muscles of the temporal fossa; the palatine artery of *Chrysemys* is minute. In *Sternotherus*, the large palatine artery gives rise to the infraorbital and supraorbital arteries, and the stapedial artery is minute; only *Sternotherus*

has a pseudostapedial artery which supplies the muscles of the temporal fossa.

The arteries of the orbit are surprisingly similar in the three genera, but there are minor differences. The supraorbital artery of *Chrysemys* is often smaller and more dorsally located than the supraorbital artery of the other two genera, and the branch of the supraorbital artery into the foramen supraorbitale arises more anteriorly in *Trionyx*. The infraorbital artery of *Sternotherus* gives rise to the anterior vidian artery, which is lacking in the other two genera, and the inframaxillary artery of *Trionyx* has a small branch into the canalis intrapalatinus which is absent in the other two genera. But the supramaxillary artery, inframaxillary artery and its anastomosis, anterior nasal artery, pseudomandibular artery, alveolar-nasal artery, superior alveolar artery, and posterior nasal artery are present in *Trionyx*, *Sternotherus*, and *Chrysemys*.

The internal carotid arteries are large in *Sternotherus* and *Trionyx* but small in *Chrysemys*. The branches from the internal carotid arteries into the foramen pro ramo nervi vidiani are larger in *Trionyx* and *Chrysemys* than in *Sternotherus*. The pharyngeal carotid artery of *Sternotherus* is larger than that of *Chrysemys*, and this artery is not present in *Trionyx*. The posterior vidian arteries of *Chrysemys* and *Sternotherus* are very similar and are not present in *Trionyx*. Finally, the orbital arteries of *Chrysemys* and *Sternotherus* are alike and are not present in *Trionyx*, which has a peculiar optic artery.

VII. THE GENERAL ARTERIAL PATTERNS ON A FAMILIAL LEVEL

Variations in cranial arteries within a genus seem to be very minor. The cranial arteries of the two *Trionyx spinifer* and the one dissected *Trionyx muticus* were nearly identical, and agree in most details with those of *Trionyx triunguis* described by Girgis (1964) except for the anastomosis he described between the mandibular and stapedial arteries. With the exception of the supraorbital artery, the arterial pattern was the same in all three dissected *Chrysemys*. The cranial anastomoses are somewhat variable, for one *Sternotherus* had no anastomosis between the internal carotid arteries, and one *Kinosternon* had no anas-

tomosis between the inframaxillary arteries.

However, there may be characteristic variants in cranial arterial pattern among the genera of one family. Within the Testudinidae, the arteries of *Testudo graeca* (according to Shindo) seem to be nearly the same as those of *Chrysemys*, but in the other genera the following variations have been noted: in *Gopherus* and *Geochelone*, the mandibular artery arises from the stapedia artery, but it sometimes exits into the temporal fossa through its own foramen arterio-mandibulare and not through the foramen cavernosum as in *Chrysemys* (according to McDowell); in *Emys orbicularis*, the mandibular artery arises from the infraorbital artery and only a small vestige remains of the mandibular artery which arises from the stapedia artery (according to Bojanus and Shindo); in some other genera such as *Terapene*, the pharyngeal carotid artery is larger than that of *Chrysemys*, and still other genera have a larger palatine artery (according to McDowell). Within the Kinosternidae, the *Kinosternon subrubrum* which I dissected differs from *Sternotherus* in the following ways: the alveolar-nasal artery arises as a branch of the inframaxillary artery and runs dorsally through the foramen orbito-nasale to divide into the posterior nasal and superior alveolar arteries; the anterior vidian artery is slightly larger than that of *Sternotherus*, and it extends the full length of the anterior vidian canal. Within the Trionychidae, the uninjected *Lissemys punctata* which I dissected appeared to have branches of the infraorbital artery different from those of *Trionyx*. From the above, the arteries of the orbit and their branches seem to be variable in the different genera of each family, and hence these arteries cannot be included in considerations of the general arterial pattern at the family level, as seen in the Testudinidae, Kinosternidae, and Trionychidae.

In summary, many cranial arteries are, or appear to be, variable in occurrence among the different genera. Until more information is available, these arteries must be excluded from a description of the general arterial patterns at the family level. From the dissections and crania examined by myself and other authors, it can be seen that the general cranial arterial patterns of the three families can be characterized by the following:

Testudinidae: The large stapedia artery exits from the foramen stapedio-temporale, gives rise to the arteries of the orbit and often gives rise to the mandibular artery. The small internal carotid artery in the canalis caroticus internus gives rise to the minute, vestigial palatine artery which exits through the foramen caroticum laterale; the internal carotid arteries anastomose in the dorsum sellae and give rise to the cerebral carotid arteries.

Kinosternidae: The stapedia artery is a minute vestige which exits through a greatly reduced foramen stapedio-temporale. The large internal carotid artery in the canalis caroticus lateralis gives rise to the large palatine artery, which exits from the foramen caroticum laterale, gives rise to the arteries of the orbit and also gives rise to the mandibular artery; the internal carotid arteries anastomose in the dorsum sellae and give rise to the cerebral carotid arteries.

Trionychidae: The stapedia artery is smaller than the testudinid stapedia artery but is much larger than the stapedia artery of kinosternids. The large internal carotid artery in the canalis caroticus internus gives rise to the fairly large mandibular artery, which exits from the foramen caroticum laterale; the internal carotid arteries anastomose in the dorsum sellae and give rise to the large pseudopalatine artery. The pseudopalatine arteries give rise to the cerebral carotid arteries and to the arteries of the orbit.

VIII. POSSIBLE EVOLUTIONARY IMPLICATIONS

McDowell hypothesized a primitive cranial arterial pattern in which there is both a large stapedia artery and a large palatine artery (1961: 34). The testudinids may have evolved from this primitive pattern by enlarging the stapedia artery and greatly reducing the palatine artery, whereas the kinosternids possibly evolved in such a way that the stapedia artery was greatly reduced and the palatine artery was enlarged. This is all quite easy to understand, but the trionychid arterial pattern is much more difficult to derive from this primitive pattern, for trionychids have a reduced stapedia artery with no palatine artery.

The cranial arteries of the testudinids and kinosternids seem to give clear evidence for

the separate evolution of these two families of turtles. The different sizes of the palatine and stapedial arteries, the different origins of the mandibular artery and the arteries of the orbit, the presence of the kinosternid pseudostapedial artery and anterior vidian artery, and the branches from the mandibular arteries to the brain in kinosternids all point toward a long, separate evolution of the Kinosternidae and Testudinidae. As McDowell pointed out, the arterial pattern of each of these two families cannot be derived from the other arterial pattern. However, cranial arteries also provide evidence for the placement of these two families in a common superfamily. The presence of a palatine artery in the canalis caroticus lateralis, the origin of the cerebral carotid arteries, the presence of the orbital arteries, the similar arteries of the orbit, brain, and mandible, the presence of pharyngeal carotid arteries, and particularly the similar canals, foramina and arteries of the vidian nerve complex all point toward a common origin of these two types of testudinoid turtles.

Trionyx resembles *Chrysemys* and *Sternotherus* in having similar arteries of the brain, orbit, and mandible. Trionychids in general have followed the kinosternid type of cranial arterial evolution as opposed to the testudinid type, for soft-shelled turtles possess a large internal carotid artery and a stapedial artery which is not as large as the stapedial artery of testudinids. This similarity in basic cranial arterial patterns in the Kinosternidae and Trionychidae may be a case of parallel evolution, but it also may lend support to the opinion that these two families "are relatively closely related" (Webb, 1962: 443).

The presence of the pseudopalatine artery in the dorsum sellae, the origin of the mandibular artery from the internal carotid artery and its presence in the canalis caroticus lateralis, and the complete absence of the palatine and orbital arteries all point toward a trionychid arterial evolution which is extremely different from the arterial evolution of *Chrysemys* and *Sternotherus*. It seems very possible that the trionychids and kinosternids evolved in a parallel manner insofar as they enlarged the internal carotid artery, and a branch of the enlarged internal carotid artery gave rise to the arteries of the orbit. However, the trionychids evolved

completely separately from the kinosternids thereafter, for they acquired a pseudopalatine artery in the foramen arterius canalis carotici interni, whereas the kinosternids developed a palatine artery in the canalis caroticus lateralis. This completely separate evolution of the three families from a common ancestor requires a primitive arterial pattern different from that hypothesized by McDowell, but I do not know what that primitive pattern would be.

On the other hand, the trionychids and kinosternids may have arisen from a common ancestor or from similar ancestors in which the internal carotid artery was large, the palatine artery in the canalis caroticus lateralis was large, the cerebral carotid arteries near the dorsum sellae gave rise to the orbital arteries, and the stapedial artery was similar to that of modern trionychids. From this hypothetical, primitive pattern, the kinosternids might have evolved by reducing the stapedial artery but retaining the other arteries. An anastomosis between the primitive mandibular artery and the palatine artery, and the degeneration of the primitive posterior mandibular artery may have resulted in the origin of the mandibular artery from the palatine artery.

The trionychids hypothetically could have evolved from this primitive pattern in a complex manner. For some reason, the palatine artery of the trionychid ancestor perhaps began to degenerate, and this degeneration could have caused the orbital artery to enlarge, for the orbital arteries of some recent turtles anastomose with the supraorbital and infraorbital arteries. As this degeneration and subsequent enlargement took place, an anastomosis may have developed between the palatine artery and mandibular artery, which primitively probably exited from the foramen cavernosum as a branch of the stapedial artery. This anastomosis resulted in the complete disappearance of the anterior part of the primitive palatine artery, causing the orbital arteries to supply all the blood to the orbital and nasal regions. The posterior, primitive mandibular artery then completely degenerated, and the anastomosis allowed blood to flow from the internal carotid artery to the mandible. Thus the hypothetical formation of the generalized trionychid arterial pattern was complete. It thus may be the case that the pseudopalatine artery of trionychids is homologous with the

orbital artery of kinosternids, and the base of the trionychid mandibular artery may be homologous with the base of the kinosternid palatine artery.

It should be noted that the arterial pattern of *Trionyx* and the general arterial pattern of the trionychids can be derived in the above manner from the cranial arteries of *Sternotherus* and the general arterial pattern of the kinosternids. Furthermore, as Shindo noted, the mandibular artery of modern turtles is quite variable, and thus its different origins from the palatine artery, internal carotid artery, or stapedial artery of different turtles is not too surprising.

In my opinion, the similar small arteries, foramina, and canals associated with the vidian nerves of *Chrysemys* and *Sternotherus* show that the testudinids and kinosternids are fairly closely related, and these two families probably evolved from a common ancestor, as hypothesized by McDowell. Perhaps earlier, this common ancestor of the testudinids and kinosternids gave rise to a branch of turtles which evolved a cranial arterial pattern similar to the pattern the kinosternids would later acquire. In other words, the ancestor of the trionychids may have evolved in a manner parallel to the cranial arterial evolution later taken by the kinosternids. The trionychids may have arisen from this older branch in the manner described above.

In order to determine the closeness of the relationship between kinosternids and trionychids and the cranial arterial patterns of the ancestors of the trionychids, kinosternids, and testudinids, many more detailed descriptions of the arterial foramina and bony canals of fossil skulls must become available. From these descriptions, the general arterial patterns can validly be inferred, as was done earlier for the Jurassic skulls described by Parsons and Williams. Much more work also needs to be done with the cranial arteries of all the genera in a single turtle patterns of the sea turtles and side-necked turtles have never been described in detail, and a detailed description of the cranial arteries of all the genera in a single turtle family has never been published.

IX. CONCLUSION

In this paper, the cranial arterial foramina and bony canals of *Chrysemys*, *Sternotherus*, and *Trionyx* are described and

compared, and the cranial arteries which utilize these foramina and canals in the three turtle genera are also described and compared. Skull studies and published knowledge show that cranial arterial variation within a genus is slight and permit inference of the general cranial arterial patterns characteristic of the Testudinidae, Kinosternidae, and Trionychidae. Detailed knowledge of the cranial arteries gives evidence for assuming a long, separate evolution of the Kinosternidae and Testudinidae from a common ancestor, and evolution of the Trionychidae from an earlier branch of turtles which had evolved parallel to the evolutionary path later taken by the kinosternids. Finally, it should be re-emphasized that the cranial arteries of turtles are indeed evolutionarily significant, and more work in this field may help to clear up many of the current problems of turtle taxonomy.

X. TERMINOLOGY

The anatomical terms used in this paper which are not used by Parsons and Williams (1961) are listed below. The oldest source used by this author for each term is cited, and those terms for which no author is cited are original. Cited sources are not necessarily the first in which the terms were used.

- arteria alveolare-nasalis
- arteria alveolaris superior (Shindo, 1914)
- arteria anterior nasalis (Shindo, 1914)
- arteria anterior vidiana
- arteria basilaris (Bojanus, 1819)
- arteria carotico-pharyngealis
- arteria carotica cerebralis (Siebenrock, 1897)
- arteria carotica externa (Bojanus, 1819)
- arteria carotica interna (Siebenrock, 1897)
- arteria cerebri anterior (Shindo, 1914)
- arteria cerebri media (Shindo, 1914)
- arteria cerebri posterior (Shindo, 1914)
- arteria cervicalis (Bojanus, 1819)
- arteria inframaxillaris
- arteria infraorbitalis (Shindo, 1914)
- arteria mandibularis (Shindo, 1914)
- arteria olfactoria (Bojanus, 1819)
- arteria optica
- arteria orbitalis (Shindo, 1914)
- arteria palatina (Shindo, 1914)
- arteria posterior nasalis (Shindo, 1914)
- arteria posterior vidiana

arteria pseudomandibularis (McDowell, 1961)
 arteria pseudopalatina
 arteria pseudostapedialis
 arteria stapedialis (Parsons and Williams, 1961, but not listed)
 arteria supramaxillaris (Bojanus, 1819)
 arteria supraorbitalis (Bojanus, 1819)
 canalis carotico-pharyngealis (McDowell, 1961)
 canalis caroticus lateralis
 canalis infraorbitalis (Ogushi, 1911)
 canalis intrapalatinus
 foramen arteriae anteriovidianae
 foramen arteriae vidianae
 foramen arteriomandibulare (McDowell, 1961)
 foramen carotico-pharyngeale (McDowell, 1961)
 foramen caroticum laterale
 foramen nervi vidiani (Siebenrock, 1897)
 foramen palatinum accessorium
 foramen supramaxillare
 foramen supraorbitale

XI. ACKNOWLEDGMENTS

My sincere thanks go to Dr. Hobart M. Smith, who gave me the opportunity to do this research and contributed to publication of the results. I would also like to thank Tom Fritts, who provided indispensable aid and materials; Mike Jones and Alice Boatright, who made the illustrations; and Dr. Donald P. Rogers, who checked the form of the anatomical terms used in this paper. Without the typing of Mrs. Paul Dauten and the assistance of Tyra Eppler, the completion of this paper would have been much more difficult.

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NOTES ON THE DISTRIBUTION AND ECOLOGY OF THE HIGHER
PRIMATES OF RIO MUNI, WEST AFRICA

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ABSTRACT

Data taken from preliminary observations of distribution and ecology are presented and summarized for twelve species of primates from Rio Muni, West Africa. Three basic patterns of ecologic distribution are apparent. Nine taxa of primates occur mainly in dense and defective forests, two species occur primarily in regions of hygrophilic and litoral vegetation, and one species occurs typically in plantation areas. The most widely distributed species are those that occur in many rather than few plant communities. The influence of man has resulted in a reduced range for nine species of primates and an increased range for one species. Two species seemingly are unaffected.

INTRODUCTION

Little information has been published on the ecology and distribution of primates in Rio Muni, a part of the Equatorial Region of Spain (Spanish Guinea). Information on gorillas in Rio Muni has been contributed by Sabater Pí and Lassaletta (1958) and Sabater Pí (1960, 1964, 1966a, 1966b). Basilio (1962), while presenting general information on some vertebrates of Spanish Guinea, mentioned the ecology and distribution of primates. Information on primates in areas adjacent to Rio Muni in West Africa has been presented by Malbrant and Maclatchy (1949).

The purpose of this report is to furnish information on the geographic and ecologic distributions of the higher primates (Anthropoidea) of Rio Muni and to discuss briefly some of the factors that influence these distributions.

METHODS AND MATERIALS

Procedures.—Reconnaissance of Rio Muni and the compilation of data for this report were accomplished mostly during 50 days in July and August, 1966; we spent 35 days, 221.5 hrs., observing and studying primates. It must be noted, however, that Sabater Pí has been publishing results of observations of gorillas since 1958 (Sabater Pí and Lassaletta, 1958).

Information on centers of abundance of primates was obtained from natives and then field expeditions were made into the areas that were selected. All major sections of the country have been visited. Distributions of gorillas and chimpanzees were determined by sightings and by locating recent beds, droppings, and feeding areas. General ecologic conditions of the localities and vicinity where primates were seen and identified by us were noted.

No attempts have been made to review thoroughly the literature or to summarize completely data from specimens in museums. Some specimens have been examined in order to corroborate identifications.

Description of the area.—The Spanish province of Rio Muni is a region of approximately 26,000 km² located in West Africa between 1° and 2° 30' N lat and 9° 30' and 11° 30' E long. From the coast, the elevation rises to 1,200 m at the highest peak, Mt. Mitra. Much of the interior plains of the area has an elevation of 500 to 600 m. Three major river systems provide drainage and influence the biota of this geographic region, the Rio Campo and the Rio

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Mbia in the north, the system of the Rio Benito in the central section, and the estuaries and tributaries of the Rio Muni in the south.

The climate is characterized throughout the year by rather uniform temperature and humidity, but variable rainfall. The mean annual temperature is 24.8° C, with a recorded maximum of 33.2° C in April and a recorded minimum of 15.5° C in August. Temperatures in the interior high plains average 2 to 3° C lower than temperatures in the lowland regions. The mean annual relative humidity is 90.3% with a minimum of 88.0% recorded in August and February. Typically, cloud cover is present at night over much of the area. Over the lowland areas, clouds are relatively high, but over the higher inland regions, clouds prevail as ground fog about 80% of the time. The cloud cover usually disperses about 10:00 AM. Because of these differences in cloud cover, relative humidity and rainfall are greater in the highland areas than in lowland sections of the country. Rainfall varies from a recorded high of 492.3 mm in October to a recorded low of 1 mm in July. The mean annual rainfall varies from 2,250 mm to 2,500 mm. Most precipitation occurs from September to December and the least rain falls during June to September. These climatic data were taken mostly from records of the airport observatory in Bata, but are complete for only one entire year (1962) and merely indicate general climatic conditions of the area.

The soils, typical of many tropical regions, are laterites formed by the decomposition of granite and gneiss. These soils are slightly acidic and the pH of surface water is 5.5 to 6.0. The plains and old playas near the present coast are deposits of sand and sandstone.

Approximately 200,000 humans live in Rio Muni, a density of about 7.5 inhabitants km². The distribution and the influence of the human inhabitants upon the distribution and ecology of other primates are discussed later in this report.

The vegetation of Rio Muni was categorized generally as dense forest by Clark (1965). Sabater Pi (1964) recognized that three major types of vegetation were important with regard to the distribution of gorillas. Because of the complexity of the vegetation and because of the influence of

human cultures on the natural vegetation and on the primates in the area studied, further descriptions and discussions of vegetation are warranted.

In the following descriptions of vegetation and characterizations of ecologic communities, some names of plants were taken from the publications by Emilio Guinea (1946) and Saint Aubin (1963). In addition, some plants from Rio Muni were identified by various persons at the Museum National d'Histoire Naturelle de Paris, the Koninklijk Museum Voor Midden-Afrika, Tervuren, Belgium, the Royal Botanical Gardens, Kew, England, and the New York Botanical Garden, New York. Personnel of the Forest Service of Rio Muni also aided in the identifications of plants.

In accordance with the varied topography of the study area, the distributional limits of the many types of vegetation are irregular and interdigitating, resulting in many complex ecotones. In addition, the composition of a given vegetation varies from one locality to the next. Herein, we attempt only to describe and characterize the types of vegetation that seem important with regard to the distribution of primates in Rio Muni. Four types of vegetation are distributed over large areas and four other types are relatively limited in distribution (Fig. 1).

Dense forests.—These primary forests represent the most stable and mature forests within the study area. For discussions and some dates of early disturbances of some forested regions of West Africa, see Clark and Fagan (1965). Dense forests occupy about 20% of Rio Muni, and are typically found in the interior high plains, but occur in some lowland and coastal parts of the country. These forests are characterized by a rather uneven canopy, nearly completely closed, and 50 to 60 m high. In some areas it is possible to distinguish three strata. Low-growing vegetation is rather sparse. Light and visibility at ground level are generally poor. Some plants typical of this type of forest include *Terminalia altissima*, *T. superba*, *Erythroleium ivorensis*, *Baillonella toxisperma*, *Copaifera tessmanni*, *Lophira alata*, *Desbordesia glaucescens*, *Entandiodaphragma cylindricum*, *Piptadeniastrum africanus*, *Anthrocaryon klaineanus*, and *Uapaca* sp.

Defective forests.—These forests occur in approximately 20% of the study area ad-

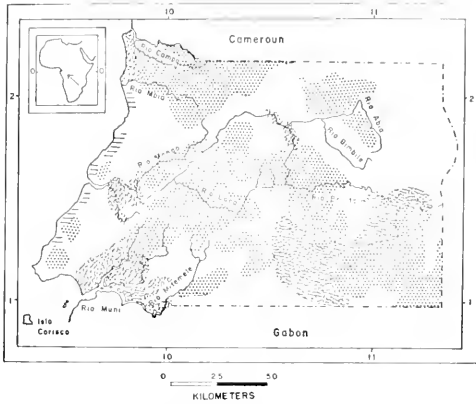


Figure 1. Map of the study area showing the distribution of the major types of vegetation. Dense and defective forests are represented by stippled areas, agroligic forests and plantations are represented by white areas, hygrophilic forests are represented by mottled areas, and meadows are represented by lined areas. This map of vegetation was modified according to our observations and records from a map of the Army Geographical Service of Spain, first edition, May, 1951. In addition, many data were obtained from the office of the Forest Service of Rio Muni.

adjacent to and merging with the dense forests. Because of the absence or the lesser development of some plant species in the defective forests, physiognomy differs from that of the dense forests. The defective forests exhibit a fairly even canopy about 40 m high and closed as much as 75 to 80% in some regions. Generally, two strata are distinguishable. Vegetation growing near the ground is more abundant here than in the forest described above. As in the dense forests, light and visibility near the ground are rather poor. Tree species present in the dense forests occur in this formation as well, but they attain greater heights in the dense forest than in the defective forests. Some plants obvious in the lower strata in the defective forests include *Oncocalamus manni*, *Ancistrophyllum acutiflorum*, *Eremospatha macrocarpa*, *Sarcophrynium velutinum*, *Trachypogon violaceum*, *Palisota hirsuta*, *Dichapetalum* sp., and *Funtumia* sp. In addition, some epiphytes such as *Polypodium* sp., *Platycterium* sp., and *Rhoktophyllum* sp., are common.

Agroligic forests.—These regenerating forests occur in areas that were once partly

cleared for cultivation or for lumber; they presently include an estimated 40% of Rio Muni. Regenerating forests are not uniform throughout the study area, but are present in various stages of development. Descriptions and discussions of seral stages of regeneration of forests of similar types were presented by Emlen and Schaller (1960) and Sabater Pi (1964), and need not be repeated here. In Rio Muni, agroligic forests have a main canopy 10 to 12 m high, but because of the presence of large trees that were not removed in the original clearing, the canopy is uneven, broken, and has many openings for penetration of light. Many young trees and a well developed ground cover usually are present, thus limiting visibility. The most important species of plants are *Musauga cecropioides*, *Veronica conferta*, *Harungana paniculata*, *Anthoecista nobilis*, *Aframomum* sp., *Costus lucanusianus*, *Alchornea cordifolia*, *Sclerosperma manni*, *Albizzia* sp., *Combretum latilatum*, *Ficus mucosus*, and *F. exasperata*. This type of forest is the main habitat of the five species of lower primates (Prosimii) that occur in Rio Muni. Some primates occur in defective forests and plantations as well. Because of the secretive habits of the animals, few ecologic data are available. The species are *Perodicticus potto*, *Arctocebus calabarensis*, *Galago alleni*, *G. demidovi*, and *Eutotius elegantulus*.

Plantations.—Plantations occupy about 20% of the region and due to extensive development in some areas, especially in the northeast section, are important factors in primate distribution. We distinguish two categories of plantations based on the systems of maintenance and the plants utilized. One type is recultivated each year and is utilized for the production of food items. Cultivated plants are *Manihot utilissima* (yuca), *Ipomea batatas* (sweet potatoes), *Colocasia esculentum* (Malanga), *Zea mays* (corn), *Arachis bipogea*, (cacaohuate), *Musa sapientum* (banana), *M. paradisiaca* (plantanos), *Cucumeropsis edulis* (calabaza), *Saccharum officinarum* (sugar cane), and *Solanum* sp. (tomato). The other type of plantation is more stable and plants are cultivated on a long-term basis for the production of commercial items: these include *Coffea robusta*, *C. liberica* (coffee), *Theobroma cacao* (cacao), *Elaeis guineensis* (palm oil trees), and *Cocos nucifera* (coconut).

Hygrophilic forest.—This formation often adjoins the defective forest and these communities are frequently inundated by water. They are found in three to six percent of Rio Muni. They are confined to inland swamp areas as well as river margins, and are frequently affected by changing water levels due to runoff, or in coastal areas, due to tides. This forest type exhibits a low, dense, almost closed canopy 10 to 12 m high. There is no low ground vegetation between the clumps of large plants. Visibility is poor. Plants typical of the inland swamps include *Raphia vinifera*, *R. bookeri*, *Sclerosperma manni*, *Myrtagine ciliata*, *Oxytenanthera abyssinica*, and *Cyrtosperma senegalense*. Stands of *Pandanus* sp., *Raphia vinifera*, *R. bookeri*, and *Sclerosperma manni* are common along river margins not affected greatly by tides. In the areas that are influenced by tides, dense growths of *Rhizophora mangle* and *Laguncularia* sp. occur.

Littoral screen.—This type of vegetation is represented in a rather narrow, but distinct, band bordering the coast and near the mouths of river systems. Most obvious plants include *Phoenix reclinata*, *Cocos nucifera*, *Canavalia ensiformis*, *Urena lobata*, *Pennisetum purpureum*, and *Terminalia cattapa*.

Domed peaks.—These geologic formations are restricted to some of the steep, high hills of the southeastern portion of the study area and generally support two obvious zones of vegetation. Thickets of *Triumfetta cordifolia*, *Euphorbia camerunensis*, and *Strophantus* sp., as well as herbaceous forms such as *Virecta* sp., *Habenaria* sp., and *Orquideas* sp. are present. In some cases, there are exposures of almost barren granitic materials.

Meadows.—These communities are located near the coast and are confined to disjunct regions of sand, which is remnant of Quaternary playas. The low-growing vegetation, usually one meter and less in height, includes numerous representatives of the families Gramineae, Cyperaceae, and Compositae.

ANNOTATED LIST OF SPECIES

Excluding man, the higher primates of Rio Muni include representatives of 2 families, 3 subfamilies, 7 genera, and 12 species representing 13 races. In the following ac-

counts, species are listed according to the order following by Simpson (1945).

Cerocebus albigena albigena (Gray).—This species was found only in limited areas of dense forests and in some marginal formations that have well developed tall vegetation. This form appeared to be confined mostly to several disjunct regions (Fig. 2), but was often associated with *Cercopithecus cephus*, *C. nictitans*, and *C. mona*.

Cerocebus galeritus agilis (Milne Edwards).—The only known example of this species from Rio Muni, an adult female, was trapped in a local marsh area that supports a stand of *Pandanus* (Fig. 2).

Cerocebus torquatus torquatus (Kerr).—This species especially occurred in lowlands adjacent to the confluences of the major river systems and the sea, but also occurred in limited areas in the interior. It also was found in some areas of littoral vegetation near the coast (Fig. 2).

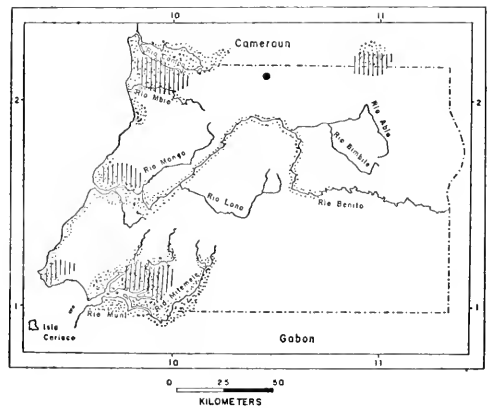


Figure 2. Map showing the general distribution of *Cerocebus torquatus* (stippled areas) and *C. albigena* (lined areas) in Rio Muni. The dot represents the locality for *C. galeritus*.

Papio sphinx (Linnaeus).—This animal seemed common, especially in regenerating forests, but may be locally abundant in nearly all parts of Rio Muni, except in areas of extensive cultivation near some of the larger villages. This form has been seen in fairly open areas on some of the domed peaks and in the meadows. For a depiction of distribution of this species, see Fig. 3.

Cercopithecus cephus cephus (Linnaeus).—This form was found in dense, defective, and agrological forests in most parts of Rio Muni (Fig. 4). It occurred in areas with

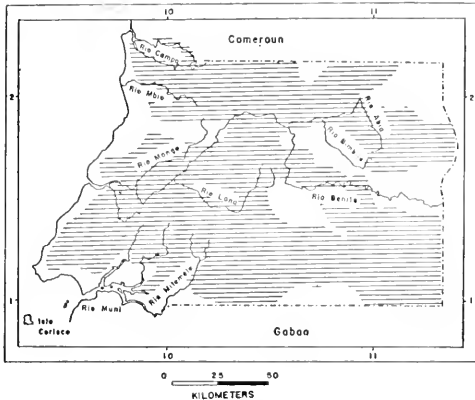


Figure 3. Map showing the general distribution of *Papio sphinx* (lined areas) in Rio Muni.

C. nictitans, but *C. cephus*, was more abundant and was seen more often in margins of plantations near pueblos than *C. nictitans*. In some areas, *C. cephus* occurred with *C. neglectus* and sometimes with *Colobus*.

Ceropithecus mona Schreber.—This form occurred in dense, defective, and agrological

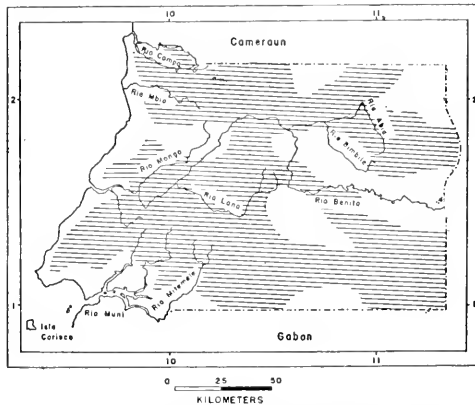


Figure 4. Map showing the general distribution of *Cercopithecus cephus* and *C. nictitans* (lined areas) in Rio Muni. For more discussions of the distributions of these species, see comments in the text.

forests in the study area (Fig. 5). This species is under study by Pierre Dandelot of the Museum National d'Histoire Naturelle de Paris, who currently recognizes two subspecies on the basis of morphological features. *Ceropithecus mona grayi* Fraser was frequently associated with *Colobus*, *Ceropithecus nictitans*, *C. cephus*, *C. neglectus*, and occasionally with *Miopithecus talapoin*; *C.*

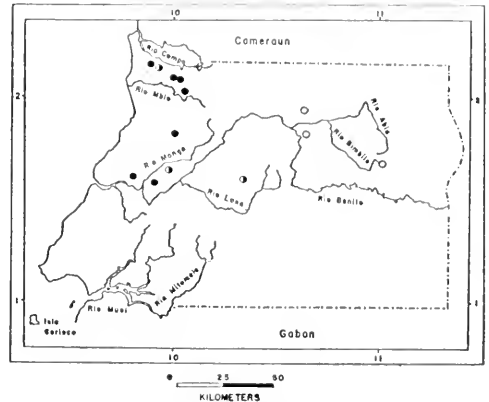


Figure 5. Map showing the distribution of *Cercopithecus mona* in Rio Muni. Open circles represent localities for *C. m. grayi*, dots represent localities for *C. m. nigripes*. Half-closed circles represent localities where intermediate forms were taken, but these forms are referred to *C. m. nigripes* on the basis of distribution. All specimens were collected by Sabater Pi and are deposited in the Museum National d'Histoire Naturelle de Paris and information was furnished by Pierre Dandelot.

mona nigripes du Chaillu was often found along with *C. nictitans*, *C. cephus*, *C. neglectus*, *C. albigena*, and in some regions, with *Miopithecus talapoin*.

Ceropithecus neglectus Schlegel.—The typical habitat for this species was the dense vegetation adjacent to rivers. It also occurred in some limited areas in the interior, as well as in some parts along the coast. It was more common in lowland coastal regions than in the interior. In some communities, this species exists with *C. nictitans*, *C. cephus*, and *C. mona*. Distribution of this form is shown in Fig. 6.

Ceropithecus nictitans nictitans (Linnaeus).—In general, this species was found in dense, defective, and agrological forests throughout most of the area studied (Fig. 4). It was absent from well developed plantations. These animals were seen often with or near groups of *C. cephus*, but *C. nictitans* was seemingly more shy than the former species. In addition, *C. nictitans* occurred occasionally with *C. mona* and *Colobus*.

Miopithecus talapoin talapoin (Schreber). This was an abundant species in agrological forests and plantations near the habitations of humans. It also occurred in marginal vegetation along rivers and was the only

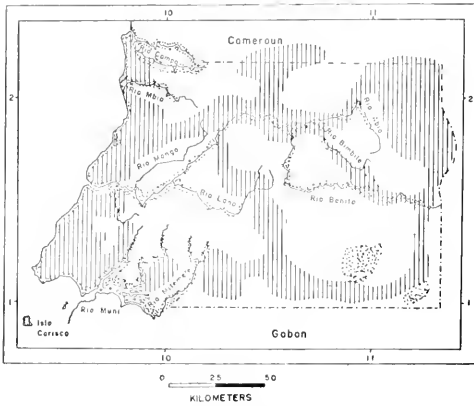


Figure 6. Map depicting the general distribution of *Cercopithecus neglectus* (stippled areas) and *Miopithecus talapoin* (lined areas) in Rio Muni.

form present on the island of Corisco (Fig. 6). In some limited areas, it occurred occasionally with *Cercopithecus nictitans*, *C. cephus*, and *C. mona*.

Colobus satanas anthracinus Leconte.—Animals of this species occurred mostly in rather restricted areas of high, dense forests, usually away from human habitation. It has been seen with *Cercopithecus nictitans*, *C. cephus*, and *C. mona*. The geographic distribution of this form (Fig. 7) is discussed later in this report.

Pan troglodytes (Linnaeus).—This species was present in extensive areas of dense forests, in defective forests, and in agrological forests near plantations. Evidence of its feeding activities was frequently seen in small agricultural areas, especially in plantations near agrological or dense forests. *Pan*

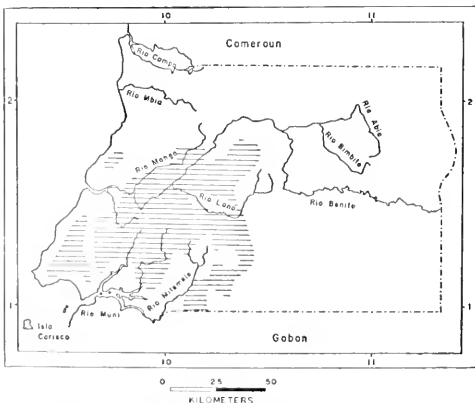


Figure 7. Map showing the distribution of *Colobus* (lined areas) in Rio Muni.

occupies an area slightly larger than the area inhabited by *Gorilla*, and the former probably is more abundant than the latter (Fig. 8).

Gorilla gorilla gorilla (Savage and Wyman).—This primate typically occurs in the thick vegetation of the dense forests, defective forests, and agrological forests, but also frequently enters plantation areas for food. In addition, this animal has occasionally been seen in open areas of the domed peaks. Sabater Pi (1964) estimated that a population of approximately 5,000 animals was dispersed in four major local populations with a maximum density of about 1.3 ani-

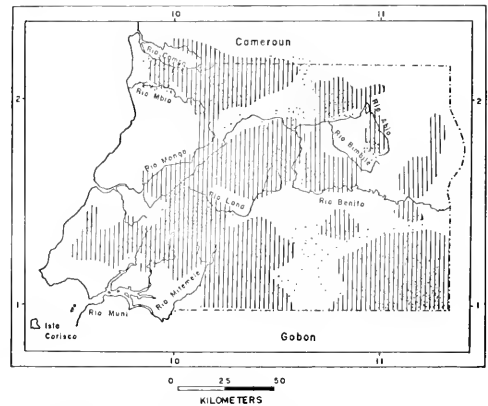


Figure 8. Map showing the general distribution of *Pan troglodytes* (lined areas) and *Gorilla gorilla* (stippled areas) in Rio Muni.

mals km² in the southeast portion of the area. For additional discussions of various aspects of the ecology of gorillas in Rio Muni, see Sabater Pi and Lassaletta (1958) and Sabater Pi (1960, 1964, 1966a, 1966b). The distribution of this species depicted in Figure 8 is a modification of the map of Sabater Pi (1964). Recent changes in the distribution of gorillas are due to activities of man in expanding areas of agriculture and lumbering in parts of Rio Muni.

DISCUSSION

In the preceding accounts of the higher primates of Rio Muni, the conspicuous absence of *Papio leucocephalus* (F. Cuvier) warrants brief explanation. This animal was recorded from Rio Muni by Basilio (1962), but we have been unable to satisfactorily corroborate its presence in Rio Muni. In the field and especially in the native villages, we have observed many ex-

amples of *P. sphinx* of several age classes, but we have seen no *P. leucocephalus*. In addition, the records of the Centro de Ikunde of the Barcelona Zoo show that 205 *P. sphinx* have been handled in the past several years, but not a single *P. leucocephalus* was recorded. Milbrant and Maclatchy (1949) state that the drill coexists in similar habitats with the mandrill in most of French Equatorial Africa, but the distribution of the drill is irregular in some parts of the range.

The ecologic distributions of the species of primates listed in this report are summarized in Table 1. Nine forms (*Cercocebus albigena*, *Papio*, *Cercopithecus cephus*, *C. mona grayi*, *C. m. nigripes*, *C. nictitans*, *Colobus*, *Pan*, and *Gorilla*) occur mainly in dense and defective forests. Of these nine forms, all except *Cercocebus albigena* and *Colobus* inhabit agrolological forests and three (*Papio*, *Pan*, and *Gorilla*) occur rather frequently in some plantation areas. In addition, *Papio* occurs very occasionally in some of the meadows, and *Papio* and *Gorilla* have been observed in the open areas of some of the domed peaks. Two species (*Cercocebus torquatus* and *Cercopithecus neglectus*) typically occur in dense vegetation near rivers. On infrequent occasions, these species may be found in vegetation of the littoral plain, and also occur rarely in forests near rivers, but usually within about 2 km of the water. *Miopithecus talapoin* typically lives in agrolological forests and plan-

tations, but is found commonly in riverside vegetation as well. For one species (*Cercocebus galeritus*), ecologic data are insufficient.

Of the 12 species of higher primates in Rio Muni, two (*Cercocebus albigena* and *Colobus*) exhibit a narrow range of ecologic tolerance and occur in only two major types of vegetation. *Papio sphinx*, in contrast, has a rather broad ecologic range and occurs in six zones of vegetation. In general, those forms with narrow ecologic ranges (*Cercocebus albigena*, *C. torquatus*, *Cercopithecus neglectus*, and *Colobus*) are distributed in small geographic areas, but the species with broad ecologic ranges (*Papio*, *Pan*, and *Gorilla*) have extended geographic distributions.

For some groups of primates that coexist in areas of similar habitat, limited data with regard to vertical stratification are available (Fig. 9). A few general statements on ecologic relationships may be drawn from these data. The level of the upper stratum (Fig. 9), occupied mainly by *Cercopithecus* and *Colobus*, reflects the habits of these species and the height of the vegetation. This stratum also supports populations of the white crested hornbill (*Tropicranus albocristatus*). This form is frequently seen in the presence of primates and the ecologic relationships between these forms were mentioned by Chapin (1932) and Malbrant and Maclatchy (1949). The lower stratum is frequented by *Papio* and *Gorilla*. *Pan* was observed in this

TABLE 1

The ecologic distributions of the higher primates of Rio Muni arranged with respect to the major types of vegetation. Because of inadequate data, *Cercocebus galeritus* is not included.

	Dense forests	Defective forests	Agrolological forests	Plantations	Hygrophilic forests	Domed hills	Littoral screen	Meadows
<i>Colobus satanas</i>	X	X						
<i>Cercocebus albigena</i>	X	X						
<i>Cercopithecus mona grayi</i>	X	X	X					
<i>Cercopithecus mona nigripes</i>	X	X	X					
<i>Cercopithecus nictitans</i>	X	X	X					
<i>Cercopithecus cephus</i>	X	X	X					
<i>Pan troglodytes</i>	X	X	X	X				
<i>Gorilla gorilla</i>	X	X	X	X		X		
<i>Papio sphinx</i>	X	X	X	X		X		X
<i>Miopithecus talapoin</i>			X	X				
<i>Cercopithecus neglectus</i>					X		X	
<i>Cercocebus torquatus</i>					X		X	

stratum nearly as frequently as in the upper levels.

Distributions of primates in Rio Muni are correlated with the presence of and interaction with man.

Species that occur on the ground or below 15 m, the height of the upper limit of the placement of traps by the natives, are captured frequently and utilized mostly for food. The total impact of human pressures upon the various species of primates of the lower strata is not known fully at this time. An example of the influence of man's activities on a primate is illustrated by the distribution of *Colobus*, an inhabitant of ecologic strata not frequented by man (Fig. 9).

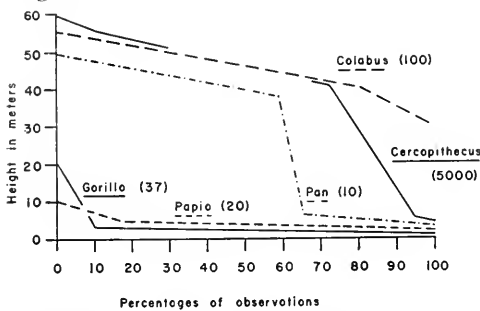


Figure 9. Vertical stratification of several groups of primates in Rio Muni. The number of observations is given in parentheses by the name of each animal; the numbers given for *Colobus* and *Cercopithecus* are approximate. The line under the name of each species identifies the graph line for that species.

This species, which is highly territorial, and is localized in small areas probably occupied all of Rio Muni a century ago but now is restricted to an area of less than 1/3 of the original habitat. In earlier years, the pelts were highly prized, but now *Colobus* is killed mostly for food.

The effects of the molestation of vegetation by man also are very important factors that influence the distributions of most of the primates of the study area. Disturbances of vegetation by man have been occurring in various degrees for some time. There is ample evidence that cultivation by Neolithic cultures, dating to ± 450 A.D. in Fernando Po (Clark and Fagan, 1965), had a sizeable role in the destruction of natural vegetation in some areas and influenced the distribution of certain species of plants.

Current disturbances of vegetation in Rio Muni are considerable. Due to the traditional system of progressive clearing of forests for purposes of agriculture and an ever-increasing demand for food materials, the areas of distribution of plantation and agrological forests are being expanded in geometric fashion. For example, on the basis of data gathered from interviews with inhabitants and from personal examinations of cleared and regenerating forest areas near the pueblo of Ayaminken, we estimate that approximately 50 km² of forest has been cut in the past 50 years (the approximate age of the pueblo). The population of Ayaminken includes 150 persons, but 25 years ago only 50 inhabitants were present. Because of severe degeneration of soils after a few years of human disturbance, many areas exploited previously and located typically adjacent to pueblos support only grasses, a habitat that is unsuitable for non-human primates.

The distributions of only two species (*Cercocebus torquatus* and *Cercopithecus neglectus*) of primates in Rio Muni possibly are not influenced greatly by current activities of man. These species occur in areas that are relatively impenetrable to man, including inundated riverside regions and inland swamps that are characterized by the presence of perennial mud, tangles of *Rhizophora*, and stands of *Pandanus*.

Only one species, *Miopithecus talapoin*, is common in the much disturbed sections of agrologic forests and plantations near the presence of man. This reduction of species in exploited areas is exemplified vividly in the extensive agricultural area of the northeast section of Rio Muni where only *Miopithecus talapoin* and man are found.

SUMMARY AND CONCLUSIONS

Preliminary determinations of ecologic and geographic distributions of some of the primates that occur in Rio Muni were made by conducting general surveys of the major types of vegetation in all sections of the country and by noting, whenever possible, the presence of representative plants in each major community.

Three basic patterns of ecologic distribution are obvious. Nine taxa of primates occur mainly in dense and defective forests; seven of them also occur in agrologic forests, but only three are found in agricultural

regions. Two species of primates occur principally in regions of hygrophilic vegetation, but do occur occasionally in vegetation of the litoral screen. One primate occurs typically in plantation areas, in agrologic forests, and in hygrophilic forests. Species that inhabit a greater range of plant communities are distributed more widely than those species that occur in a few communities.

The data indicate that as a result of the influences of man, the ranges of nine species of primates are reduced, the distributions of two forms seemingly are not greatly affected, and one species has an increased range of distribution.

ACKNOWLEDGMENTS

Many people have been of great service to us during the course of this preliminary study. We thank Dr. Arthur Riopelle, Director of the Delta Regional Primate Research Center of Tulane University, Covington, Louisiana, Señor Antonio Jonch, Director of the Barcelona Zoo, and Señor Rindor of the Service of Parks and Gardens, Barcelona for their cooperation and support. We appreciate the considerations given us by Señor Jose Diaz de Villegas, Director General of the African Provinces, Madrid. Padre Emilio Aguirre helped make many arrangements in the early phases of this project. Sincere thanks are due Señor Simon Ngomo, Civil Governor of Rio Muni, and Señor Hevia, Director of the Forest Service of Rio Muni, for their cooperation and hospitality. Various associates of the firm of Transportes Africanos of Bata were helpful to us in many ways. Señora Nuria Coca de Sabater Pí performed many services and provided much encouragement during the preparation of this report. We are indebted especially to numerous Fang and Pigmy guides who not only performed many helpful services, but who were our constant and loyal companions in the field.

This study received financial support from the National Geographic Society and the National Institutes of Health (FR00164).

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REDESCRIPTION OF TWO GULF COAST DIPLOCARDIANS
(OLIGOCHAETA: MEGASCOLECIDAE)

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ABSTRACT

Redescription of two megascolecid earthworms, *Diplocardia eiseni* and *D. alba*, based upon extensive collections throughout the southern portions of the United States. Substantial structural differences occur in these species including spermathecal form, prostatic duct structure, (height and number of calciferous gland lamellae), pigmentation, and ecology. Both appear to belong to a group which share the following in varying degree:

(1) quadrithecate condition, (2) variable position of spermathecal pores, (3) vestigial prostatic setae, (4) anterior doubling of the dorsal vessel, and (5) internal lamellar edges of the calciferous gland not connected. These earthworms occur throughout the Gulf Coast area and Florida; *D. alba* is not now known to exist west of Louisiana. Both species tolerate very sandy soils but *D. eiseni* is more likely to be found in submerged, or very wet soils.

These descriptions are based upon extensive collections of two species of diplocardian earthworms, both widely distributed throughout Florida and the Gulf Coast region. For one of these, *Diplocardia alba* Gates, 1943, I have been able to examine the types; for the other, *D. eiseni* (Michaelson, 1894) specimens collected near the type locality have been available.

Both species are variable in structure. Substantial differences have been noted among individuals from a single population. From present indications, *Diplocardia alba* is more common in the eastern Gulf Coast region, especially in Florida, while *D. eiseni* ranges at least from the northern Mexican border area into southern Florida and parts of eastern Georgia. These earthworms have not been collected together in the same

habitats although their ranges overlap. For both, local population density may be quite high, depending upon prevailing soil conditions, essentially soil moisture.

Morphologically, *Diplocardia eiseni* and *alba* differ substantially; unfortunately, reliance upon a few characteristics which these and other diplocardian species have in common, has obscured the differences. Thus, both species are quadrithecate, possess vestigial prostatic setae, anterior doubling of the dorsal blood vessel, and a tendency for the spermathecal pores to vary in position. Among the more obvious differences are pigmentation, structure of the spermathecae, calciferous gland, prostate glands and ecology.

Diplocardia eiseni (Michaelson, 1894)
Geodrilus eiseni (Michaelson), 1894
Diplocardia eiseni Ude, 1895
D. eiseni Eisen, 1899
D. eiseni Eisen, 1900
D. eiseni Macnab and McKey-Fender,
1955

Specimens available for this study include:

Lake Eola, Florida March
1896 A Hempel 11 specimens
Lake Placid, Highlands County, Florida
April 3, 1950 D. E. Beck 32 specimens
Lake Placid, Highlands County, Florida
April 5, 1950 D. E. Beck 38 specimens
Suwanee River, Florida
April 15, 1950 D. E. Beck 2 specimens
Bayou de Loutre, Union Parish, Louisiana
June 14, 1959 W. R. Murchie 11 specimens
Encinal, Webb County, Texas October
13, 1962 W. R. Murchie 16 specimens

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- Nuttall Rise, Taylor County, Florida August 15, 1963 W. R. Murchie 58 specimens
- El Campo, Wharton County, Texas August 20, 1964 W. R. Murchie 6 specimens
- Sinton, San Patricio County, Texas August 20 1964 W. R. Murchie 46 specimens
- Port Lavaca, Jackson County, Texas August 22, 1964 W. R. Murchie 1 specimen
- Edna, Jackson County, Texas August 22, 1964 W. R. Murchie 13 specimens
- Melville, Landry Parish, Louisiana March 24, 1965 R. Tandy 4 specimens
- Campus, LSU, East Baton Rouge Parish, La. April 8, 1965 J. T. Tafare 16 specimens
- Providence, Union County, Florida August 6, 1965 W. R. Murchie 4 specimens
- Frost Proof, Polk County, Florida August 7, 1965 W. R. Murchie 9 specimens
- Donaldsonville, Ascension Parish, La. April 28, 1966 R. E. Tandy 1 specimen
- Springhill, Webster Parish, Louisiana August 22, 1966 R. E. Tandy 10 specimens
- 16 mi. west Holly Beach, Cameron Parish, La. September 20, 1966 R. E. Tandy 7 specimens
- 11 mi. west Holly Beach, Cameron Parish, La. September 20, 1966 R. E. Tandy 9 specimens
- Grand Chenier, Cameron Parish, La. September 22, 1966 R. E. Tandy 12 specimens
- The Lake Eola specimens, collected by A. Hempel in March, 1896, were apparently sent to Professor Frank Smith. It is likely that Smith separated these into two groups; one of these was kept at the University of Illinois and has been described by Macnab and McKey-Fender (1955). The other portion was stored in the University of Michigan Zoology Department, Ann Arbor, Michigan. It is these specimens, bearing Smith's accession numbers 845 and 847, which I report here.

Professor W. Michaelsen (1894) appears to have had specimens from at least nine populations available when he wrote the original description. Some of this material still exists in the collections of the Hamburg

Museum, East Germany (Dr. M. E. Thiel, personal communication). Unfortunately, anterior ends of these worms were sectioned; these slides were destroyed by fire (1943). Designation of a lectotype from this material is not presently feasible; the following specimens of the Hamburg Museum collections are designated as syntypes inasmuch as all were available at the time Michaelsen prepared his description but none was singled out as the type:

- V. 377 Arcadia, DeSoto County, Florida E. Lönnberg
- V. 378 Lake Leonore, Orange County, Florida September 5, 1892 E. Lönnberg
- V. 379 Lake Eola, Florida February 20, 1893 E. Lönnberg
- V. 380 Sanford, Seminole County, Florida March 31, 1893 E. Lönnberg
- V. 381 Savannah, Chatham County, Georgia March 1889 E. Lönnberg

The following collection, also deposited in the Hamburg Museum, was used by Ude (1895) in his emendation of the original description:

- V. 5022 Lake Gatlin, Orange County, Florida 1892/93 E. Lönnberg

Description

Elongate, often robust, normally tapering over the posterior 50 somites so that the diameter of the penultimate segment does not exceed one-half the greatest diameter of the worm. Pigmented, reddish brown to brown or dark amber, darkest in posterior fifth of the body, lightest in color in middle portion of the body. Clitellum yellowish to flesh-colored. Size 112 mm (average of 203 measurable specimens) with expected range from 63 to 157 mm in length and 1.8 to 3.0 mm (average 2.5 mm) in width. Average segment number 135 (193 specimens) with range from 111 to 190.

Prostomium pro-epilobic one half length of first segment, tongue narrow. Annulations, simple in I through V, multiannulate VI to clitellum. First dorsal pore in 10/11. Setal formula: $aa:ab:bc:cd = 20:8:15:11$ (post-clitellar). Clitellum XIII-XVII, XVIII; cingulum, absent ventrally posterior to 16/17. Tubercula pubertatis absent. Seminal gutters nearly straight to convex from $\frac{1}{2}$ XVIII to $\frac{1}{2}$ XX; edges of gutters glandu-

lar. Male field flat with supernumerary annulations. Male pore on anterior $\frac{1}{2}$ of XIX, on small papilla in gutter. Prostatic pores equatorial in XVIII and XX, at ends of gutters. Female field slightly developed elliptical zone of XIV anterior to equator; female pores closely paired ($\text{♀♀} = ab$) antero-median to *ab*. Genital tumescences occur as papillae at *ab* on VIII and IX and often appearing in ventral area (*a-a*) of XXI; normally post-setal or nearly inter-segmental. Prostatic setae small (0.15 mm), modified, hidden in body wall of XVIII and XX. Setae *a* and *b* of segment XIX are present and normal in size. Spermathecal pores two pair in VIII and IX; variable in position, most commonly in anterior part of VIII and at equator in IX or equatorial to post-equatorial in VIII and post-equatorial in IX. Spermathecal setae *a* and *b* modified; distal one-third of shaft with fine spines (*ca* 10 rows); arcuate, about 0.4 mm in length. Somatic setae *ca.* 0.35 mm in length. Nephridiopores on anterior edge of somite in setal line *d*.

Pharyngeal gland masses end in IV. Gizzard in V and VI, strongly developed. Esophagus VII through XIII, straight with internal lining papillose. Esophagus of XIV and XV expanded to form calciferous gland with approximately 20 free lamellae. Gland-like ridges may extend into XIII or XIV. Intestine begins abruptly in XVII. Typhlosole begins in XX; simple fold, diminishes gradually posteriorly, disappearing in XCV. Last hearts in XIII. Dorsal vessel doubled intrasegmentally from XVII forward into VIII. Supra-esophageal vessel free and visible X-XII. Parieto-esophageal vessel joins esophageal wall in XIII; passes into esophageal wall from which it emerges in XI, passing forward to disappear in VII.

Testes two pair on ventro-anterior wall of X and XI, small to medium in size, manicate. Male funnels rather box-like, folded, with iridescence. Sperm duct direct, passing posteriorly on inner parietal wall at setal line *b*; ducts of each side contiguous, join in XIX. No atrium. One pair of ovaries in XIII; multiple strand. Ovarian funnel rather simple, auriculate. Oviduct direct, enter parietes immediately anterior to seta *a*. Ovisac very small, from 13/14, dorso-median to funnel. Seminal vesicles two pair in IX, from 9/10, and in XII from 11/12; larger pair in XII. Prostate glands

two pair, elongate to U-shaped; duct shorter than gland proper. Prostate glands of XVIII extend into XIX, those of XX extend into XXI. Prostatic setae of XVIII and XX very small, embedded in ectal portion of duct wall. Spermathecae two pair in VIII and IX, duct as long as large ampulla; finger-like diverticulum from extreme ental end of duct near junction of duct and ampulla; duct narrow and of uniform width. Meganephridial, avesciculate. Septa 7, 8, 8/9, and 9/10 thickened; 10/11 somewhat thickened.

Remarks

In the most recent emendation of Michaelson's description, Macnab and McKey-Fender (1955) make the following observations:

"There are indications that Michaelson may have had more than one species or subspecies in his material. The fact that *D. eiseni*, judging from the Lake Eola material, actually must be a variable species complicates matters." Whether Michaelson did or did not have a mixed collection before him may never be known. The work of Ude (1895) does confirm that some of Michaelson's worms most certainly were *D. eiseni* as we know it.

Because of the substantial variation in some characters, the present analysis had as one of its primary objectives, the identification of somatic features showing structural constancy. The following characters appear to have the greatest stability in *Diplocardia eiseni*: (1) vestigial condition of the prostatic setae, (2) constant occurrence of setal couple *a-b* in segment XIX, (3) quadrithecate condition, (4) form of the spermathecae, (5) modification of the spermathecal setae (setae *a* and *b* of VIII and IX), (6) intrasegmental doubling of the dorsal blood vessel, (7) last hearts in XIII, (8) very sharp postero-ventral clitellar margin, and (9) free internal lamellar edges of the calciferous gland.

The prostatic setae (Figure 1-D) do vary somewhat in shape from one population to the next but are characteristically so small that they do not normally extend into the coelomic cavity. Instead, they are closely applied to the terminal portion of the prostatic duct and with it, are embedded in the body wall. An exception was found in one aprostatic population in which instance the setae, while vestigial, did extend into the

body cavity, although slightly. The spermathecae (Figure 1-F) are characterized by a distinct ampulla and a diverticulum that arises at the junction of the ampulla and duct. The posterior boundary of the clitellum is decidedly sharper than frequently obtains for diplocardian species. The rather flat male field is bound by seminal gutters with strongly glandular lips (Figure 1-A); this glandular development does not extend anteriorly beyond intersegmental furrow 17-18. The nine characters listed in the previous paragraph, provide the most adequate basis for recognition of this species.

The more important areas of variation in *D. eiseni* include: (1) size, (2) disposition of the spermathecal pores, (3) pigmentation, and (4) condition of the prostate gland. A sample obtained by Dr. D. E. Beck at Lake Placid, Highlands County, Florida, April 5, 1950, contained eight exceedingly small specimens in a collection of 38 worms. The larger individuals average 104 by 3.0 mm in length and width with 157 segments (average of 30 specimens); the eight smaller animals averaged 39 by 1.2 mm, length and width, and 81 segments. The clitellum, as well as the internal reproductive structures showed full sexual development in each specimen. In every particular, except dimension, they answered the description of *Diplocardia eiseni*. It must be recognized that size *per se* is not a reliable feature of earthworm anatomy inasmuch as a variety of environmental conditions can act to change body size. Thus, while the averages and ranges given in the diagnosis may be considered as probable values, populations do vary with respect to size. Causal mechanisms cannot be assigned as yet; genetic factors might be suggested but parthenogenecity is a strong probability for *D. eiseni*. An amber or dark brown pigmentation is normal for most of the populations seen, but it is not an invariable attribute of *D. eiseni*. Of the North American representatives of the family Lumbricidae, the species *Eiseniella tetraedra* (Savigny), 1826, is very close in pigmentation to *D. eiseni* and it is interesting to note that these two species are very similar in habitat preference.

Disposition of the spermathecal pores has been given considerable weight in diplocardian systematics. For *D. eiseni*, the pattern is generally regular, but variable between

populations, sometimes even within a single population. The pores in segment VIII may be close to the setal arc (equatorial), in line with seta *b*, or slightly median to same, or the pores may be found at varying distances anterior to the equator, shifting at times to the extreme anterior edge of the segment, nearly in 7-8. In IX, the pore may be similarly nearly equatorial but more often is shifted posteriorly in varying degree, sometimes to the extreme posterior edge of the segment at 9-10. One pattern is shown in Figure 1-A. The precise position of the spermathecal pores is so variable as to be of little value in identification; the variability itself is undoubtedly of greater phylogenetic significance than the patterns expressed.

Another collection made by Dr. D. E. Beck at Lake Placid, Florida, on April 3, 1950, contained 32 specimens of *D. eiseni*, unique in that every specimen lacked the entire battery of prostate glands. In all other particulars these worms agree with descriptions of *D. eiseni*. The aprostatic condition has been recorded for this genus previously (*Diplocardia eglestoni* Murchie, 1958). It should be noted that while the prostatic battery as described and figured (Figure 1-C) is to be expected, populations may be encountered in which the prostate glands are missing.

In habitat preference, *D. eiseni* is the most nearly limnic of the known diplocardians. The heaviest populations were encountered in poorly drained situations. In several instances, great numbers were collected from water-covered soils, in ditches, or the margins of lakes or streams. Throughout much of the region inhabited by *D. eiseni* the water table is quite high; in addition, soils are often very sandy so that free water is readily available. Wherever these is sufficient moisture, soil type is of little consequence in controlling population density; equally large numbers of *D. eiseni* have been found in such diverse soil types as sand, loam, or heavy mucky clay. Similarly, vegetational type is not a limiting factor in determining habitat occupancy by diplocardians. In view of the preference of *D. eiseni* for low, wet areas, considerable similarity is to be expected in tree and shrub cover.

Present distributional evidence for *D. eiseni* would suggest a coastal species, with

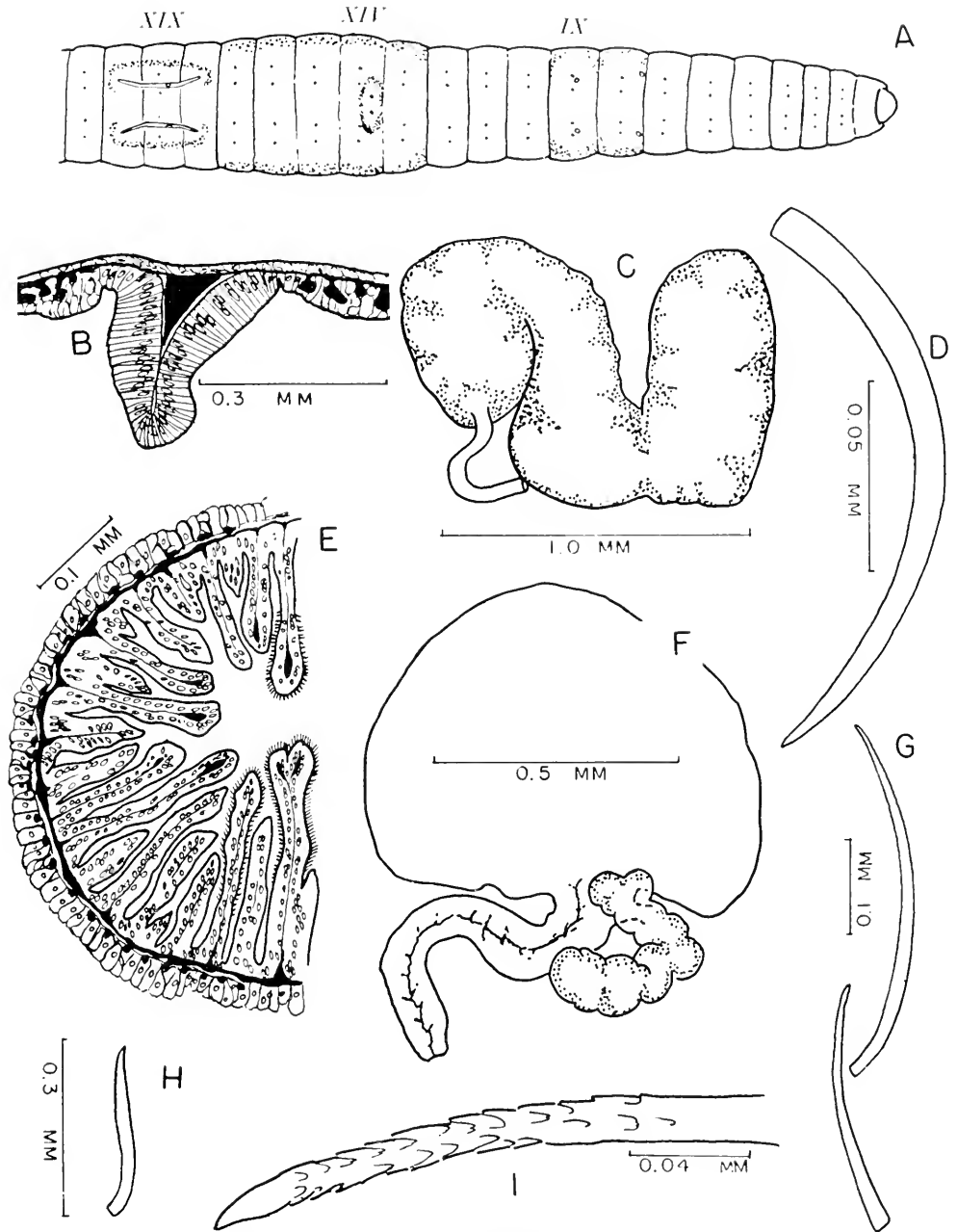


Figure 1. Anatomical features of *Diplocardia eiseni*. **A.** Ventral view of anterior 21 segments. **B.** Cross section of typhlosole, segment XXI. **C.** Prostate gland of XX. **D.** Prostate seta of XVIII. **E.** Cross section of calciferous gland of XIV. **F.** Spermatheca of VIII. **G.** Spermathecal seta *a* of VIII; normal and reserve. **H.** Seta *b* of segment XIX. **I.** Tip of spermathecal seta of VIII.

a range from an unknown point along the Mexican east coast, into the entire peninsular Florida region, and northward at least to South Carolina. Insofar as currently known, the species has not extended its range very far up the Mississippi Valley; it can be expected that scattered populations may be encountered in poorly drained soils adjoining any of the major rivers draining south and eastward across the Gulf and Atlantic coastal plains.

Diplocardia alba Gates, 1943

Specimens available for this study include:

Gainesville, Alachua County, Florida

April 14, 1950 D. E. Beck 1 specimen

Tallahassee, Leon County, Florida July

23, 1959 W. R. Murchie 17 specimens

Naples, Collier County, Florida August

9, 1963 W. R. Murchie 27 specimens

Naples, Collier County, Florida August

9, 1963 W. R. Murchie 11 specimens

Naples, Collier County, Florida August

10, 1963 W. R. Murchie 14 specimens

Tice, Charlotte County, Florida August

11, 1963 W. R. Murchie 5 specimens

La Belle, Glades County, Florida August

11, 1963 W. R. Murchie 9 specimens

Lake Wales, Polk County, Florida August

12, 1963 W. R. Murchie 16 specimens

Clyo, Effingham County, Georgia August

18, 1963 W. R. Murchie 20 specimens

West of El Campo, Wharton County,

Texas August 20, 1964 W. R. Murchie

8 specimens

Bogalusa, Washington Parish, Louisiana

January 21, 1965 R. E. Tandy 2 speci-

mens

Torrey State Park, Liberty County, Florida

January 25, 1965 R. E. Tandy 3 speci-

mens

Bonita Springs, Collier County, Florida

August 8, 1965 W. R. Murchie 17

specimens

Bowling Green, Hardee County, Florida

August 7, 1965 W. R. Murchie 21

specimens

20 miles north of Okeechobee, Okeecho-

bee County, Florida August 10, 1965

W. R. Murchie 56 specimens

Newberry, Alachua County, Florida Au-

gust 11, 1965 W. R. Murchie 21

specimens

Camp Blanding, Clay County, Florida Au-

gust 12, 1965 W. R. Murchie 21 speci-

mens

Specimens were placed in the U. S. National Museum by Professor G. E. Gates and designated co-types as follows:

Yellow Fern Creek, Fort Myers, Lee County, Florida January 21, 1941 W. M.

Barrows USNM 20967 1 specimen

Fort Myers, Lee County, Florida February

19, 1941 W. M. Barrows USNM 20630

72 specimens

I designate the Yellow Fern Creek specimen (USNM 20967) as the lectotype for this species.

A subspecies *Diplocardia alba mexicana* was described by Gates (1955) on the basis of a single specimen intercepted at the Mexican border (Brownsville, Texas), February 20, 1950; the description is somewhat incomplete.

Description

Elongate, slender, without noticeable swelling of extremities. Unpigmented, clitellum yellowish to brown (formalin fixation). Size 26 to 160 mm with averages of 67 by 2.0 mm in length and width respectively (204 specimens). Somite numbers, 96 to 199; average 145 (205 clitellate specimens). Prostomium epilobic one-half, tongue broad. First dorsal pore at 9/10. Annulations simple in I through V, multiannulate VI to clitellum, weakly multiannulate posterior to clitellum. Setal formula $aa:ab:bc:cd = 12:3:9:6$ (posterior to clitellum). Tubercula pubertatis absent. Clitellum XIII, XIV, to XVI and dorsally on XVII; cingulum. Genital tumescences weakly developed, may involve combinations of VII, VIII, IX, possibly X, and sometimes XXI in *ab*, usually paired or may include the entire ventral area *b-b*. Spermathecal pores on VIII, and IX, variable in terms of antero-posterior position; most commonly in anterior VIII and equatorial in IX, usually midway between *a* and *b* regardless of other variations. Spermathecal setae modified, 0.53 by 0.02 mm in length and width respectively; distal one third of shaft with *ca.* eight rows of fine sculpturing; sometimes setae of IX are unmodified. Male field strongly glandular. Seminal grooves straight or curved from $\frac{1}{2}$ XVIII to $\frac{1}{2}$ XX, often with convexity directed mesiad. Male pore equatorial or immediately anterior to equator on XIX, in groove. Prostatic pores at ends of gutters in XVIII and XX. Prostatic setae modified, virtually confined to

body wall adjacent to prostatic duct, involve setae *a* and *b*; primary setae of couple are 0.25 by 0.005 mm in length and width, variously bent, without sculpturing. Female field slightly developed elliptical area antero-medial to *a*. Nephropores at anterior edge of somite in *d*.

Pharyngeal glands end in IV. Gizzards in V and VI. Esophagus straight, narrow, without diverticula, from VII; walls papillose and ridged. Calciferous gland development in XIV, XV-XVI; about 18-20 lamellae, without fusion of lamellar ends internally. Intestine begins in XVII or XVIII. Typhlosole a simple fold, beginning in XX, ends LXX. Last hearts in XIII. Dorsal vessel intrasegmentally doubled from XVIII forward into VIII. Supra-esophageal vessel free in X-XII. Parieto-esophageal joins esophagus in XIII.

Testes two pair from 9 10 and 10 11 into X and XI; manipulate, male funnels moderately large, folded, with iridescence. Sperm ducts of each side on internal parietes, highly convoluted, especially from XIV through XVII; ducts of each side contiguous, joining in XIX. Prostatic glands two pair in XVIII and XX; U-shaped with free limbs directed dorsad. Prostatic ducts as long as gland proper, strongly coiled, first coil often contiguous with ectal limb of gland proper; anterior or posterior limb of the gland may penetrate adjacent segments. Seminal vesicles acinous, in IX and XII, from 9 10 and 11 12; those of XII the larger pair. Ovaries one pair, multiple strands of ova, from 12 13 in ventral portion of XIII. Ovarian funnel simple, oviduct direct. Ovisac in XIV, small, dorsal to oviduct on 13 14. Spermathecae two pair, in VIII and IX; ampulla oval to cordate and nearly as long as the stout duct; diverticulum pear-shaped to digitiform, on narrow, folded stalk arising from the antero-lateral aspect of the main spermathecal duct, usually near center of latter. Holonephric, avesciculate. Septa 7 8 and 8 9 thickened; 6 7 and 9 10 somewhat thickened.

Remarks

The following are the specific anatomical features which, when correctly analyzed and considered in combination with all others in this list, provide the pattern with least variability in describing *D. alba*: (1) shape of the prostatic duct, (2) vestigial prostatic

setae, (3) last hearts in segment XIII, (4) intrasegmental doubling of the dorsal blood vessel, (5) internal edges of the calciferous gland lamellae are free, and (6) structure of the spermathecae.

The prostatic duct is at least as long as the gland itself, but is characteristically coiled (Figure 2-H). This condition was found to obtain in co-type specimens. The prostatic setae as in *D. civeni* are very small (Figure 2-I) and can only be isolated with difficulty. They are appressed to the ectal portion of the prostatic duct, within the body wall. Spermathecal structure is reasonably constant (Figure 2-G). An expanded ampulla is set apart in size from the duct; the diverticulum arises by means of a narrow stalk about midway along the length of the duct proper. The diverticulum itself is rather pear-shaped, or may be generously expanded, and in one instance, was bifurcated.

While these characters are constant, there are several other features which are useful but subject to variation. The spermathecal setae (*a* and *b* of segments VIII and IX) of segment VIII, for example are invariably modified (Figure 2-C and D). Similar setae in segment IX may or may not be modified (Figure 2-E). In like fashion, the opening of the spermathecal pores is not constant. The pattern figured (Figure 2-A) is common but the pores in VIII may be closer to or on the equator; those of IX may be closer to the posterior edge of the segment, near 9 10.

In writing of the male field, Gates (1943) states:

"A male genital shield is not definitely marked off but an area between the setal arcs of XIII (= XVIII) and XX may be very slightly protuberant. Seminal grooves are nearly straight, fairly deep—the median margins especially tumescent, in *ab*, between setal arcs of XVIII and XX."

In some populations of *D. alba* I have examined, the male field is very strongly developed. In the specimen figured (Figure 2-A), the mid-ventral portion of XVIII-XX is quite glandular, forming a flat shield between the seminal grooves which are then forced outward at the center instead of remaining straight as described by Gates. This condition is not constant, even among members of a single population; both patterns have been studied during this investi-

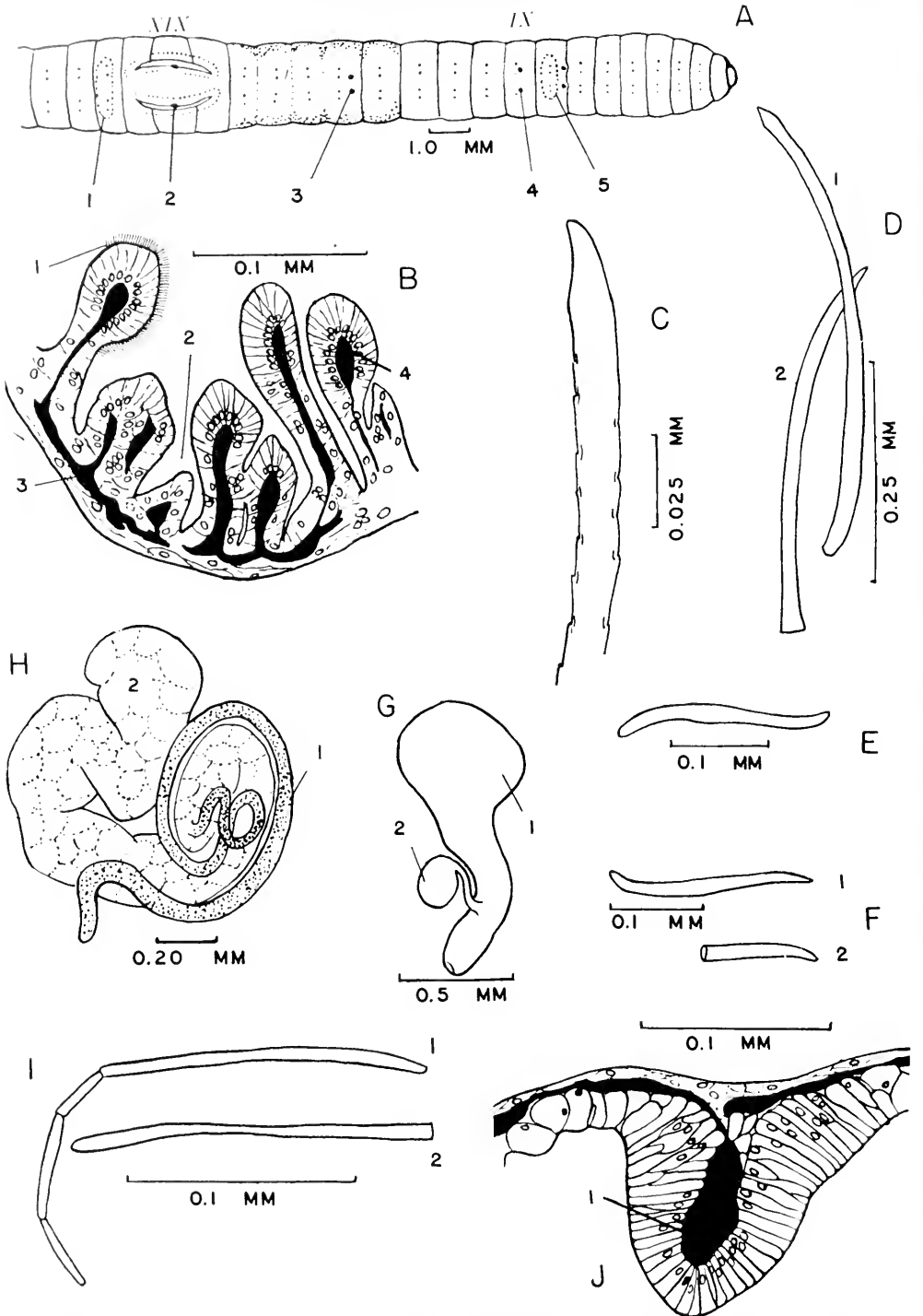


Figure 2. Anatomical features of *Diplocardia alba*. **A.** Ventral view of anterior 23 segments, 1. Glandular tumescence of XXI, 2. Male pore, 3. Female pore, 4. Spermathecal pore, 5. Glandular tumescence of VIII. **B.** Cross section of calciferous gland in XIV: 1. Ciliated border of lumen, 2. Lumen of esophagus, 3. Peripheral blood sinus, 4. Intralamellar blood sinus. **C.** Tip of spermathecal seta *b* of VIII. **D.** Spermathecal seta *b* in VIII: 1. Normal seta, 2. Reserve seta. **E.** Unmodified spermathecal seta of IX. **F.** Somatic seta of XIII: 1. Regular seta, 2. Reserve seta. **G.** Spermatheca of VIII: 1. Duct, 2. Gland. **H.** Prostate gland of XVIII: 1. Duct, 2. Gland. **I.** Prostatic seta of XX: 1. Regular seta, 2. Reserve seta. **J.** Typhlosole of segment XXIII: 1. Typhlosole, 2. Typhlosole sinus.

gation. It can be considered as one of the anatomical variables in *D. alba*.

Size is known to be an inconstant feature, even within a single population of earthworms. In this instance, three populations showed striking differences from what might be considered "average": animals from Effingham County, Georgia (20 specimens), Newberry, Alachua County, Florida (21 specimens), and Washington Parish, Louisiana (2 specimens) had average lengths of 38, 32, and 41 mm respectively. Segment numbers in like order were 130, 110, and 106. Dimensions in *D. alba*, as with *D. eiseni*, must be used with caution in describing the species.

One population of *D. alba* from Okechobee County, Florida, collected August 10, 1965, resembled Beck's Lake Placid specimens of *D. eiseni* in having no prostatic glands. As noted for that species, aprostatic populations are to be expected for *D. alba* if not, indeed, for many other diplocardian earthworms.

Ecologically, *Diplocardia alba* has been collected only from sandy soils in what could be considered well-drained situations. Most often, grass, pine, and palmetto were the dominant vegetational forms. The species is highly tolerant of open, sunny situations such as roadside fill areas, trails, and old roadways. Soil temperatures at the depth occupied by these worms were measured as high as 32°C and commonly at 30°C. This species casts freely on the soil surface and normally lives in the upper five to ten centimeters of soil.

Diplocardia alba ranges throughout the Florida peninsula and along the Gulf Coast; limits of distribution are unknown as yet. The species is certainly to be expected on lighter (sandy) soils along the entire Gulf Coast. Greater structural variance than that described here can also be expected for *D. alba*: in view of the current lack of knowledge of genetic mechanisms in most oligochaetes, the significance of this variance cannot be fully evaluated.

Discussion

The affinities of *Diplocardia alba* and *D. eiseni* with each other, and with *D. mississippiensis*, Smith, 1924, *D. floridana*, Smith, 1924 and *D. michaelseni*, Eisen, 1899 have been noted by Gates (1943) and Macnab and McKey-Fender (1955). As pointed out

by these authors, *D. mississippiensis* and *floridana* are characterized by a large T-shaped typhlosole and by the fact that the lamellae of the calciferous gland are joined internally. Neither *D. eiseni* nor *D. alba* would be confused with those species if typhlosole and calciferous gland characteristics alone were considered. With respect to *D. michaelseni*, Macnab and McKey-Fender have contrasted it with *D. eiseni* as follows (1955):

"It follows that if the Smith material is *D. eiseni*, *D. michaelseni* may be no more than subspecifically distinct from *D. eiseni* and in any case the two species are very close".

Smith (1923) and Stephenson (1937) have reviewed and revised the description of *Diplocardia michaelseni*. I have examined several collections of what I recognize as *D. michaelseni*: from these sources and observations, it is clear that *D. eiseni* and *D. michaelseni*, while similar, are distinct species. The following conditions in *D. michaelseni* are substantially different from the situation obtaining in *D. eiseni*: (1) tanylobic prostomium, (2) absence of setae *a* and *b* in XIX, and (3) the location of the last hearts in XII.

The simplex condition of the dorsal vessel in *D. udei* Eisen, 1899 and *D. gracilis* Gates, 1943, has been cited as clear evidence of the distinctness of *D. eiseni* from these two species (Macnab and McKey-Fender, 1955). The points of similarity and difference between *D. alba* and *D. eiseni* have been reviewed earlier in this paper. The differences are constant and by no means obscure; there can be no doubt about the distinctness of both species.

Variability in earthworm species, particularly among members of the family Lumbricidae, has long been recognized. By designating these variants as morphs, forms, subspecies, and the like, a cluster of "kinds" has been created in some instances. Subsequent systematic treatment has tended either to bind these variants together by enlarging the species definition, or at the other extreme, the diverse elements have been formalized as distinct species. In at least one diplocardian species, *D. singularis*, some of these variants have been given subspecific names (*D. singularis fluviatilus* Smith, 1915 and *D. s. caroliniana* Eisen, 1899); another variant, *Diplocardia eggles-*

toni Murchie, 1958, has been established as a species but may prove to be an aprotatic morph of *D. singularis*.

Among the several populations of *Diplocardia eiseni* examined, several were evidently male-sterile because parasitism had removed most of the contents of the seminal vesicles and quite often virtually destroyed the testes. This situation, or natural parthenogenecity in the genus, means that those diplocardian species with significant geographic distribution are likely to show a degree of clonal structure in the total population. In the absence of selection based upon bisexual reproduction, variations in structure, or disposition of such structures as prostate glands, spermathecal pores, and genital setae can scarcely be treated in a formal taxonomic fashion. This approach must prevail even when populations rather than single individuals are involved until such time as earthworm reproduction is more adequately understood. Accordingly, the descriptions of *Diplocardia eiseni* and *D. alba* need not be expanded beyond the point of usefulness by itemizing all probable points of difference likely to be encountered from place to place. It must be recognized, however, that certain non-adaptive features can be variable, or missing, in these species. It can be hoped that laboratory experimentation will eventually prove the significance as well as the causes of this variation.

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BEHAVIOR OF THE LONGEAR SUNFISH, *LEPOMIS MEGALOTIS*
(RAFINESQUE)

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ABSTRACT

Longear sunfish, *Lepomis megalotis* (Rafinesque) consistently exhibit aggressive behavior when placed in small aquaria in the laboratory. Apparently there is less aggressive behavior in wild populations in their natural Louisiana stream environments. Of the many longear sunfish collected from their natural habitat, few had any fin damage and none had extensive fin damage or body scars. A comparison of field observations with laboratory experiments showed that aggressive behavior in the longear sunfish increases markedly due to laboratory conditions, especially when the fish are confined to smaller areas, or volumes, than they normally occupy in nature.

Field experiments and observations are included for year-to-year occupancy of home range, spawning in the home range, reproductive behavior, feeding behavior, and aggressive behavior, as well as laboratory work on aggressive behavior.

INTRODUCTION

The longear sunfish (*Lepomis megalotis*) is a member of the exclusively North American freshwater family Centrarchidae. The species ranges from Minnesota east to Ontario, Ohio, and western Pennsylvania southward through the Mississippi Basin to the Gulf states and Mexico (Blair *et al.*,

1957) and east to the Apalachicola River (Dr. R. D. Suttkus, personal communication). The longear sunfish treated here is the southern subspecies (*Lepomis megalotis megalotis*).

Data on the behavior of the longear sunfish are limited. Kirsch (1895) reported longear sunfish on spawning beds in northern Indiana during July. Hankinson (1919) stated that the breeding season for the longear sunfish in Illinois dates from May 25 to June 17 in streams and from July to as late as August 23 in ponds. He also reported that longear sunfish appear to nest in small colonies. The nest of the longear sunfish has been described by Hubbs and Cooper (1935). They also give data on age and growth and report that male longear sunfish grow faster than females. Witt and Marzolf (1954) described one incident of spawning of the longear sunfish. The home range of the longear sunfish and the phenomenon of homing have been defined and discussed by Gerking (1950, 1953), Gunning (1959), and Gunning and Shoop (1963).

Miller (1963) investigated the behavior of the pumpkinseed and the orangespotted sunfish kept in aquaria. She found the behavior of the two species to be similar and compared their behavior with that of other species of *Lepomis*. In comparing the pumpkinseed (*L. gibbosus*) to other *Lepomis*, Miller found that paired pumpkinseeds were not aggressive in a 50-gallon tank but that it was not possible to maintain more than one individual *L. megalotis* or *L. auritus* in

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the same size tank because one individual would become dominant and attack the others until they died.

Tinbergen (1953) stated that most inter-specific fighting is done in the breeding season and appears as a consequence of gonadal growth, which in its turn, through the pituitary gland, depends on rhythmic factors such as day-lengthening in the case of many animals of the north temperate zone. Some fighting is related to the dominance relationship in the group and is not linked with the breeding season. Greenberg (1947) studied social hierarchy in the green sunfish and found that immature green sunfish maintain hierarchies, territories, or both in small aquaria. Considering that Greenberg did not make field observations, we propose that it is possible that his observations were merely artifacts resulting from laboratory conditions.

METHODS

The field experiments and observations were conducted on Warner Creek, a gravel-bottomed creek near Enon in Washington Parish, Louisiana. The water was clear except after rains; therefore, the creek was excellent for field observations. The width of the stream in the area studied ranged from 1.8 to 4.8 meters. The study area was divided as follows: Section A (upstream), 23.5 m; Section B (middle), 35.4 m; and Section C (downstream), 49.1 m.

The stream was checked once a week from April 11, 1964, to May 25, 1964, and every other day from May 25, 1964, until June 19, 1964, to observe reproductive behavior when it first commenced. The study area was visited daily from June 19, 1964, to June 24, 1964, at which time reproductive activity was at its peak. Spawning was observed on four occasions. Thereafter, the stream was checked every other day until August 18, 1964, at which time there was no further spawning activity.

Observations were made from the bank with the aid of 7 x 50 binoculars and notes were recorded on a portable tape recorder. Observations were made at numerous intervals during the day for 10-minute periods during which time all of the activities of the fish were recorded. Temperature readings in $^{\circ}\text{C}$ were taken at intervals during the day. All nests were measured after they were deserted by the male longear sunfish.

Single pairs of fish were placed in a battery of ten to twelve five-gallon tanks in the laboratory and observations were made for 10-minute periods recording: (1) time for dominance to become established, (2) number of chases per 10-minute period, (3) number of nips per 10-minute period and area nipped, and (4) length of time required to kill the subordinate fish. The tanks were bare except for gravel on the bottom; they were aerated and the temperature was maintained at 25 $^{\circ}\text{C}$. The fish were fed daily with mealworm larvae (*Tenebrio*). After the subordinate fish was killed, both fish were removed, measured for standard length and body depth, and cut open and sex determined.

OBSERVATIONS AND RESULTS

Year-to-Year Occupancy of Home Range

During July of 1963, a total of 80 longear sunfish in Section B was marked by removing a pelvic fin from each fish; all fish were returned to this section following fin-clipping. The entire study area was sampled by electrical shocking on four occasions during June and July, 1964. A total of 24 longear sunfish bearing pelvic fin-clips was taken. No multiple recaptures were involved since all fish lacking a pelvic fin were re-marked by clipping another fin. The 24 recaptures were distributed as follows: 2 in Section A, 20 in Section B, and 2 in Section C. Twenty of the 24 recaptures were thus found in their respective home ranges after one year had elapsed. The recapture rate one year subsequent to marking was 25 percent. The number of recaptures diminishes with the passage of time due to several factors (Gunning and Shoop, 1963): (1) natural mortality, (2) fishing mortality, (3) mortality resulting from electrical shock, and (4) emigration of fishes to other parts of the stream. A 25 percent recapture rate is excellent under these conditions. Ricker (1945) studied the mortality of the bluegill in two Indiana lakes and reported an annual rate of natural mortality of 46 percent for one lake and 56 percent for the other. Natural mortality rates are not known for the longear sunfish, but they are probably equally as high. On the basis of these data, it is concluded that a stable population was studied.

Spawning in the Home Range

Twelve fish were observed on nests during this study. Four occupied nests before fish were marked for future recognition on June 26, 1964 by the fin-clipping method. Of the eight fish occupying nests after June 26, 1964, five were marked; therefore, 62.5 percent of the fish observed bore marks. This is good evidence that the longear sunfish spawn in their home range since only 41 fish were marked and this was probably less than half of the total population of the section.

Territoriality

In the upstream portion of Section C, there was a cluster of 7 nests, ranging from 12.7 to 45.7 cm apart. The defended area was practically restricted to the nest and 5 to 7 cm beyond in all directions. In the downstream portion of Section C, one nest was 1.2 to 1.5 m from the surrounding nests and consequently the territory consisted of an area described by a 1-meter radius from the center of the nest.

The inter-specific territoriality relationships varied. Males guarding their territory were seen to chase away small and large (17-22 cm total length) *Hypentelium nigricans* and *Moxostoma poecilurum* (up to 30 cm total length). Witt and Marzolf (1954) reported that the behavior of the longear sunfish toward *Fundulus notatus* was quite different from that toward other fishes; at no time did the sunfish attempt to chase them even though they passed over the nest. They concluded that *Lepomis megalotis* does not defend against surface-feeding fishes but rather against those that may feed from the bottom. Nesting longear sunfish in Warner Creek were observed chasing *Fundulus olivaceus*, which is a surface-feeding fish. Therefore, our findings are in conflict with their hypothesis.

Longear sunfish were never seen to chase largemouth bass (*Micropterus salmoides*) in this study even though the latter passed across their nests. Witt and Marzolf (1954) hypothesized that the longear sunfish may be able to recognize differences in form between predacious and non-predacious fishes in the same manner as birds are presumably able to differentiate between silhouettes of predacious and non-predacious birds (Tinbergen, 1951).

Intra-specific territorial relationships were consistent. All longear sunfish, regardless of size, were chased away from the nests except females ready to spawn. Occasionally there was chasing between holders of adjacent territories, or more often two males of adjacent territories would meet at the territory line, face each other and back off.

There was no actual physical contact in any of these defensive attacks and no threatening posture was observed. Defense in the natural environment consisted of a sudden rush on the part of the defender and retreat by the intruder.

Nest Construction

The males alone constructed the nests. Nests were built on a gravel-bottom area in shallow water ranging from 20.3 to 59.7 cm deep. The nests are circular excavations and the depression is made by vigorous action of the tail. The diameter of the nest is usually about equal to twice the length of the fish. At the onset of occupying a territory and constructing a nest, the male swims into shallow water and remains over an area, circles the area, chases away other fish, tail-wags, and circles back out to the deep water and remains there for a short time. The male assumes a position at a 45° angle with the bottom and moves the whole caudal peduncle area vigorously from side to side, thus hollowing out a depression in the gravel; this activity is called "tail-wagging." For example, on June 20, 1964, the construction of nest 5 was observed. In nine observation periods of 10 minutes each there were 145 tail-wags in the center of the nest, 128 tail-wags along the edge, and 22 tail-wags across the nest. In addition the male circled the nest 14 times, circled back to the deep pool 39 times, chased off other longear sunfish 36 times, and chased off other species of fishes 3 times.

There were twelve nests in the study area. The dimensions of the nests are given in Table 1.

On five occasions a male was observed to occupy a deserted nest. The fish were differentiated from each other by markings, such as the presence of clipped fins or dark pigmented spots. In these cases the new male would simply clear the debris from the bottom of the old nest by tail-wagging.

Sex Recognition and Courtship

The sex of a longear sunfish is somewhat difficult to determine on the basis of external features. During the spawning season the males usually are more brightly colored. The female may also be brightly colored but upon entering a male's territory, she usually shows a number of dusky, vertical bars on the body. The pattern of the female is similar to that of a longear sunfish that has been badly frightened or like the "fear pattern" of the subordinate fish in the laboratory experiments.

Noble (1934) believed that sex recognition on the part of male *Lepomis gibbosus* is based on the differential behavior of males and females. He stunned adult males and females and pulled them slowly toward a male guarding a nest and both were welcomed in the same manner. Noble concluded that males are unable to distinguish sex of quiescent adults of their own species by appearance alone. Males recognize males by their rapid movement and displays. Similar experiments were conducted by Breder (1936) for *Lepomis gibbosus* and *Lepomis auritus*. From our field observations the same conclusions were drawn about sex recognition in the longear sunfish. The male longear sunfish guarding a nest leaves the nest to chase off approaching longear sunfish of either sex. Approaching male longear sunfish will turn and flee and are chased by the guarding male; female longear sunfish ready to spawn will remain in the territory. The male longear sunfish then displays violently, dashing to the surface of the water and back to the bottom of the

nest, turning on his side and displaying his bright orange ventral surface to the female. The female then enters the nest and circles with the male.

Spawning

In the process of spawning, the male and the female circled the nest side by side. The female was always between the male and the center of the nest. Both circled in an upright position and every 50 to 60 seconds the female turned over on her side at a 20 to 30 degree angle with the bottom and brought her vent close to the male's. This spawning posture lasted from 2 to 20 seconds while both fish circled slowly and quivered rapidly, thus releasing their gonadal products.

If another fish came near the nest while the male was spawning, he immediately left to chase the intruder away and then returned to circle with the female either in the same or opposite direction. After spawning was completed the male chased the female from the nest and then returned to fan the eggs and guard the nest.

Spawning was first observed on June 21, 1964, at 11:00 A.M. in nest 8. A 17 cm male guarded the nest and a 12 cm female, with vertical bars and a slightly orange ventral surface, entered the nest. The male circled the nest with the female and they spawned five times in five minutes. The male left the nest to chase off another male longear sunfish and the female left also. The temperature at the time of spawning was 29°C.

At 11:35 A.M., a 12 cm longear sunfish

TABLE 1
Nest data for *Lepomis megalotis* of Warner Creek, Louisiana.

Nest	Diameter of Nest Floor in cm	Width of Nest Rim in cm	Depth of Nest in cm	Water Depth in cm
1	45.7	10.2	7.0	21.1
2	45.7	10.2	3.8	35.6
3	45.7	12.7	4.4	39.4
4	35.6	7.6	3.8	21.6
5	38.1	7.6	5.7	59.7
6	40.6	7.6	4.4	38.4
7	40.6	10.2	2.9	36.8
8	33.0	10.2	2.8	26.0
9	35.6	12.7	6.4	22.9
10	40.6	7.6	3.8	20.3
11	45.7	7.6	5.1	25.4
12	35.6	12.7	4.4	35.6
Mean	40.2	9.0	4.5	31.9

female entered nest 8. It was not possible to determine if it was the same female that spawned in the nest previously. This female remained in the nest for twenty minutes. The male and the female circled in the nest and spawned 20 times in 20 minutes; the male left the nest 15 times during this period to chase off other longear sunfish. The male chased the female from the nest after 20 minutes and returned to guard it. The following day the nest was full of small longear sunfish, 5 to 10 cm in length. These fish had invaded the nest and were feeding on the eggs deposited the previous day. The male which had been guarding the nest moved into the area, chased a few fish from the nest, and left. The small longear sunfish returned and ate the bulk of the eggs.

Spawning was observed in nest 5 on June 21, 1964, at 1:30 P.M. The water temperature was 31°C. A 10 cm female entered nest 3, which was 1.2 meters from nest 5. The male guarding nest 5 became very excited when the female moved into nest 3 and dashed back and forth to the surface of the water, turned over on his side, and displayed the bright orange on his ventral side. The female only circled with the male in nest 3 and then left to enter nest 5 where she spawned seven times in 5 minutes with the 22 cm male there. During this time, the male from nest 5 left the nest once to chase away the male from nest 3. After five minutes the male from nest 5 chased the female away.

At 1:40 P.M., a 12 cm female entered nest 5 and spawned five times in five minutes, during which time the male left twice to chase off another longear sunfish. The water temperature was 31°C when spawning took place in nest 5. The nest was guarded by the male until three days later when it was left unguarded and was invaded by 15 small longear sunfish. The male returned, made an attempt to chase a few of the fish away,

and then left the nest unguarded again. The small longear sunfish returned and ate the bulk of the eggs.

The following conclusions can be drawn relevant to the spawning acts observed: (1) the female was smaller than the male, usually 5 cm or more; (2) the female had vertical bars while in the male's territory; (3) the female circled and spawned toward the center of the nest with regard to the male's position; (4) the female spawned while slanting horizontally at a 20 to 30 degree angle to the bottom and with her vent next to that of the male's; (5) the male remained in an upright position while spawning; (6) there was an average of one spawning act per minute; (7) a spawning act lasted from two to 20 seconds; and (8) the males did not always guard the nest sufficiently and allowed small longear sunfish to enter and feed on the eggs.

Guarding the Nest

After spawning, the males chased the females from the nests and fanned the eggs by moving the pectoral fins and the caudal peduncle rapidly. This behavior is similar to the tail-wagging activity associated with nest construction. The aggressiveness of the males increased after the eggs and young were present in the nest and decreased subsequent to the departure of the young fish. (Table 2).

Behavior of the Young

Eggs were present in nest 6 on July 20, 1964. The actual spawning in this instance was not observed. Some of the rocks, with the eggs adhering to them, were removed from the nest and placed in an aquarium in the laboratory. Acriflavin was added to the tank to prevent fungus growth and the temperature was maintained at 25°C. The eggs hatched on July 22, 1964, both in the laboratory and in the stream. When the young hatched out they remained hidden

TABLE 2
Aggressiveness of male longear sunfish on nests under various conditions.

	Nest 5		Nest 6	
	No. of observation periods	Chases per 10 minutes	No. of observation periods	Chases per 10 minutes
Prior to egg laying	9	5.5	7	3.0
Eggs present in nest	9	6.2	6	11.0
Young present in nest	—	—	22	12.0
After young left nest	—	—	12	1.0

among the rocks in the bottom of the nest. They had large yolk sacs and remained stationary on their sides in the bottom of the nest. On July 23, 1964, eyespots were noticeable and the fishes exhibited more movement. On July 24, 1964, the young could not swim, but were propelled by quick flexing actions in the bottom of the nest. The behavior and development of laboratory-hatched young corresponded closely with that of those in the stream. The male guarding the nest would remain within 60 cm of the observer while the nest was being checked for young. The young were present in the nest on July 27, 1964. Due to rain and muddy water, the nest could not be checked again until July 31, 1964, at which time the young were no longer present in the nest. The young probably left the nest between the 29th and the 31st of July, 1964, since the young in the laboratory did not lose their yolk sacs and become free-swimming until July 29, 1964.

The young in the laboratory swam around jerkily at a 45-degree angle with the bottom before the yolk sac was completely absorbed. They could swim only a distance of approximately 2.5 cm before they would start to sink, frequently resting on the bottom. After the young were free-swimming, they were placed in a 20-gallon tank. The fish dispersed over the entire tank and showed no sign of schooling.

Length of Time the Male Defends the Nest

In nest 6, the only one in which the eggs hatched successfully in this study out of 12 nests, the male remained on the nest from the time the young left (between July 29, 1964, and July 31, 1964) until August 13, 1964, or 15 to 16 days after the young had left. Occasionally he chased fish from the nest and left periodically to spend more and more time in an adjacent deep pool.

Feeding Behavior

Longear sunfish in pools were observed eating dragonflies and other insects which touched the surface of the water. Those fish defending their territory, nest, or young were never observed to feed.

An interesting form of commensalism with the sucker, *Hypentelium nigricans*, was noted on two different days. On July 12,

1964, from 9:30 A.M. to 9:50 A.M., two 17 cm and three 12 cm longear sunfish were seen following a 30 cm *Hypentelium nigricans*. The sucker was moving along the bottom shoving gravels around and picking them up with its mouth. The longear sunfish moved along beside the sucker, picking around and feeding in the gravel after it had been stirred up. From 12:25 P.M. to 1:00 P.M. on the same day, one 17 cm, three 10 cm, and a group of 5 cm longear sunfish followed a 30 cm and a 22 cm *Hypentelium*, feeding beside them in the gravel. On July 22, 1964, two 17 cm longear sunfish were seen following a 25 cm *Hypentelium* and feeding beside it.

Inter-Specific Relationships

Inter-specific relationships were studied in longear sunfish which were not occupying territories. They were not disturbed by the presence of any of the large suckers (Catostomidae) or by any of the other sunfish or minnows (Cyprinidae). They were frightened by the largemouth bass and occasionally were chased by them. On one occasion a large largemouth bass swam by a group of about twenty-five small longear sunfish which were resting quietly in the open water of a pool, and they immediately formed a small, compact group. A school of large sharpfin chubsuckers (*Erimyzon tenuis*) moved into the same group of sunfish without disturbing them.

Intra-Specific Relations

Observations were made on behavioral reactions between longear sunfish which were not guarding territories. A total of 16 hours of observations were made in 10-minute periods from April 16, 1964, through August 18, 1964. No nipping or chasing was observed during this time, and on only five occasions were fish seen to even dash a short distance toward each other. Frequently as many as 20 fish were seen swimming together in pools and grouped together near the surface as close together as two cm, and yet no aggressive action was observed. Absence of damaged fins in 245 longear sunfish collected for laboratory experiments suggested that there was not the type of aggressive behavior noted in small tanks.

TABLE 3
Aggressive experiments on the longear sunfish during the period
April 10, 1964 to May 5, 1964.

Dominant		Subordinate		Sex	S.L. in cm	B.D. in cm	Time to Establish Dominance*	Average Number/ 10 Min. Interval	
Sex	S.L. in cm	B.D. in cm	Chases					Nips	
Male	3.8	1.8	4.0	Male	1.5	3 hrs. 10 min.	9.8	1.3	
Male	4.4	1.6	3.2	Male	1.1	5 hrs. 10 min.	17.8	1.1	
Male	4.6	2.2	4.5	Male	1.9	4 hrs. 20 min.	9.1	2.3	
Male	5.4	2.0	5.3	Male	2.0	2 hrs. 15 min.	6.1	7.3	
Male	5.9	2.8	5.2	Male	2.1	4 hrs. 15 min.	3.1	2.4	
Male	6.6	2.6	5.7	Male	2.5	30 min.	20.2	21.2	
Male	6.6	2.6	6.3	Male	2.4	5 hrs. 30 min.	17.0	5.8	
Male	7.0	2.8	6.6	Male	2.6	20 min.	35.3	2.3	
Male	7.9	3.3	6.6	Male	2.6	5 min.	23.3	7.9	
Male	10.3	4.4	10.0	Male	4.4	2 hrs. 45 min.	15.8	3.3	
Male	5.9	2.8	5.6	Female	2.2	13 hrs. 30 min.	0.3	0.1	
Male	5.0	2.0	4.6	Female	1.9	3 hrs. 50 min.	22.4	3.1	
Female	10.5	4.5	10.0	Male	4.4	7 hrs. 45 min.	3.2	1.4	
Female	10.5	4.5	7.0	Male	2.8	1 hr. 35 min.	2.0	0.3	

* Time elapsed from the time of placing the pair in the tank until the subordinate fish assumed the striped "fear pattern".
S.L. = standard length B.D. = body depth

TABLE 4
Aggressive experiments on the longear sunfish during the period
July 16, 1964 to August 5, 1964.

Dominant		Subordinate		Sex	S.L. in cm	B.D. in cm	Time to Establish Dominance	Average Number/ 10 Min. Interval	
Sex	S.L. in cm	B.D. in cm	Chases					Nips	
Male	5.6	2.3	5.2	Male	2.1	85 hrs. 35 min.	2.5	3.6	
Male	7.6	3.2	6.7	Male	2.6	18 hrs. 25 min.	15.5	1.8	
Male	13.5	6.7	12.4	Male	5.5	1 hr. 15 min.	0	0.6	
Female	9.4	3.8	9.1	Female	3.6	13 hrs. 20 min.	13.6	15.3	
Female	9.4	3.8	7.9	Female	3.1	11 hrs. 25 min.	2.2	2.3	
Male	6.7	2.5	5.4	Female	2.3	34 hrs. 20 min.	12.0	1.1	
Male	12.4	5.5	9.7	Female	3.9	24 hrs.	1.6	1.2	
Female	6.0	2.4	5.1	Male	2.1	14 hrs. 45 min.	22.8	5.0	
Female	9.3	4.3	8.2	Male	3.6	17 hrs. 50 min.	17.9	1.3	
Female	9.1	3.6	8.9	Male	3.9	10 hrs. 45 min.	5.6	3.6	

S.L. = standard length B.D. = body depth

Results of Laboratory Investigations

A. General Experiments on Aggressive Behavior

When two longear sunfish were placed in a five-gallon tank (Tables 3-6), they remained side by side in one of the bottom corners for a period of time, usually one hour or longer. They then began to move around and investigate the tank. Suddenly one fish chased the other but no fighting occurred. Soon the subordinate fish became barred or assumed the so-called "fear pattern" and remained near the top of the tank. When this happened dominance had definitely been established.

The eye of the subordinate fish turned dark. The iris is normally lightly pigmented with a variable amount of red around the pupil. If a fish lost in an encounter, black pigment spread to the rest of the iris and the red was obscured.

After dominance was established, the dominant fish began to nip the fins, caudal peduncle area, and sides of the subordinate fish and did not cease the aggressive behavior until the subordinate fish turned ventral side up and died.

From 55 experiments (Tables 3-6), the following data were obtained with regard to the role of sex: (1) 10 females were dominant over 10 males, (2) 10 males were dominant over 10 females, (3) 25 males were dominant over 25 males, and (4) 10 females were dominant over 10 females. As many females were dominant over males as there were males dominant over females; therefore, sex plays no role in the determination of dominance. By way of confirmation, Hale (1956) noted no sex difference in levels of aggression in *Lepomis cyanellus*.

In 48 out of 50 experiments in which there was a size difference, the dominant fish was the largest. The results of these experiments indicate that dominance is influenced by the size of the fish, the larger usually establishing dominance. Hale (1956) found that size was an important factor in dominance relations in the green sunfish, the larger fish usually dominating the smaller fish.

The size of the fish used in the experiments ranged from 3.8 to 13.5 cm in standard length. All fish were equally aggressive,

but it took longer for the smaller-sized fish to kill the subordinate fish.

The average length of time for dominance to be established was 5 hours and 18 minutes with a range from 5 minutes (Table 3) to 85 hours and 35 minutes (Table 4).

Observations were made in the laboratory during April, May, July, and August (Tables 3-4), as well as during October, November, and December (Tables 5-6), to compare aggressive behavior during the spawning period with that during other months of the year. There was no significant difference between intensity of aggression during the winter months and the spawning season.

There was no preference in the order of which fins were nipped first, but some fins and parts of the body were nipped more than other parts. The areas nipped the most are listed in descending order of frequency: pectorals, caudal, side, anal, caudal peduncle, head, dorsal, pelvics, and opercle.

B. Experiments on Tank Size as a Factor Affecting Aggressive Behavior

Eighteen pairs of fish ranging in standard length from 4.0 cm to 10.3 cm were placed in 50-gallon tanks (120 x 41 x 41 cm) and observed for aggressive behavior. If dominance was not established after a period of 4 to 5 days, the pairs were moved to 20-gallon tanks (76 x 32 x 32 cm).

Nine fish ranging in standard length from 6.3 cm to 10.3 cm established dominance over the other member of the pair in the 50-gallon tanks.

Nine pairs of fish ranging in size from 4.0 cm to 6.1 cm did not exhibit aggressive behavior in 50-gallon tanks; instead each fish maintained a separate territory at opposite ends of the tank. Upon placing these pairs in 20-gallon tanks, the larger one immediately established dominance over the smaller.

It was not necessary to move the fish to smaller tanks since even the smallest pair showed aggressive behavior in 20-gallon tanks. The 50-gallon tanks were not large enough for fish over 6.3 cm (standard length) to maintain separate territories. Fish under 6.3 cm (standard length) were able to maintain separate territories in 50-gallon tanks, but when they were confined to a smaller area they immediately displayed aggressive behavior. These experiments

TABLE 5
Aggressive experiments on the longear sunfish during the period
October 24, 1964 to November 29, 1964.

Sex	Dominant		Sex	Subordinate		Time to Establish Dominance	Average Number/ 10 Min. Interval	
	S.L. in cm	B.D. in cm		S.L. in cm	B.D. in cm		Chases	Nips
Male	6.5	2.7	Male	6.4	3.0	5 hrs. 40 min.	12.6	3.7
Male	6.7	2.7	Male	5.7	2.7	1 hr.	23.4	2.8
Male	6.9	3.2	Male	6.6	3.1	1 hr. 10 min.	32.5	4.6
Male	7.3	3.1	Male	5.9	2.6	11 hrs. 20 min.	27.0	8.7
Male	9.3	4.4	Male	9.3	3.8	9 hrs. 30 min.	16.0	1.6
Male	9.3	4.4	Male	9.3	4.4	30 min.	13.6	4.1
Male	12.5	5.9	Male	12.3	4.6	7 hrs. 40 min.	0.3	0.9
Male	8.1	3.5	Male	7.7	3.4	71 hrs.	2.7	3.7
Male	11.0	4.6	Male	9.1	3.7	8 hrs. 45 min.	7.9	0.5
Male	12.2	5.9	Male	11.0	4.6	19 hrs. 20 min.	3.8	0.1
Female	5.5	2.4	Female	4.9	2.2	6 hrs.	15.3	3.4
Female	6.9	3.1	Female	6.3	2.6	21 hrs. 50 min.	7.7	1.6
Female	7.5	3.2	Female	8.1	3.5	5 hrs. 30 min.	13.9	4.6
Female	9.1	3.9	Female	8.7	3.9	1 hr. 10 min.	15.4	1.4
Female	4.9	2.0	Female	4.5	1.8	27 hrs. 30 min.	26.0	3.8
Male	7.5	3.2	Female	7.4	3.1	22 hrs. 10 min.	8.1	2.2
Male	8.5	3.4	Female	8.5	3.4	3 hrs. 20 min.	16.3	2.8
Male	9.7	4.1	Female	9.1	3.9	10 hrs. 30 min.	17.2	5.9
Male	10.2	4.1	Female	10.0	3.9	4 hrs. 10 min.	1.8	2.6
Female	6.0	2.7	Male	5.9	2.4	3 hrs. 30 min.	28.0	1.0
Female	6.0	2.7	Male	5.7	2.4	1 hr. 10 min.	13.1	4.3
Female	7.5	3.2	Male	7.5	3.2	1 hr. 40 min.	7.7	5.0
Female	6.8	3.0	Male	6.4	2.4	4 hrs. 10 min.	13.4	8.9

S.L. = standard length B.D. = body depth

TABLE 6
Aggressive experiments on the longear sunfish during the period
November 13, 1964 to December 14, 1964.

Sex	Dominant		Sex	Subordinate		Time to Establish Dominance	Average Number/ 10 Min. Interval	
	S.L. in cm	B.D. in cm		S.L. in cm	B.D. in cm		Chases	Nips
Male	5.8	2.5	Male	5.3	2.5	2 hrs.	14.0	5.4
Male	5.8	2.5	Male	5.3	2.4	2 hrs.	25.3	7.1
Female	4.6	1.8	Female	4.3	1.8	5 hrs. 10 min.	5.1	6.8
Female	6.8	3.0	Female	6.6	2.7	1 hr. 50 min.	11.8	11.0
Female	7.0	3.2	Female	7.0	3.2	2 hrs.	1.6	0.9
Male	6.9	3.0	Female	6.1	2.5	1 hr. 30 min.	33.3	6.2
Female	5.0	2.0	Male	4.7	1.9	1 hr. 10 min.	42.8	4.2
Female	5.6	2.4	Male	5.0	2.3	1 hr. 10 min.	27.0	5.2

S.L. = standard length B.D. = body depth

show that the consistent aggressive behavior of pairs of fish in 5-gallon tanks is due to fish being confined to such a small area or volume. Investigators studying sunfish behavior in the laboratory should do preliminary work in order to determine the importance of tank size in determining the extent of aggressiveness in each species studied.

DISCUSSION

The stated purpose of this study was to observe the behavior of the longear sunfish, with primary emphasis on the reproductive and aggressive behavior of the species.

The reproductive behavior of the longear sunfish is characteristic of the Family Centrarchidae. Our observations are generally in agreement with those in the literature summarized by Breder (1936) for *Lepomis*. However, there was a marked difference with regard to the effect of sunshine on nesting fish. Breder (1936) reported that the pumpkinseed sunfish was so sensitive to changes in illumination that the male left the nest during the passage of a cloud over the sun and retreated to deep water. Breder (1936) also reported the same observation for the redbreast sunfish. Longear sunfish were never observed to leave their nests during the passage of a cloud over the sun and even remained over their nests during heavy rains.

Aggressive intensity in the laboratory, that is intolerance to confined aquarium conditions, was the same during the winter months as it was during the spawning season. One can collect longear sunfish from the natural environment at any time of the year and observe aggressiveness in aquaria after the fish have been in the laboratory aquaria for a short time.

Aggressive behavior in the natural environment is intensified after the male longear sunfish builds a nest and establishes his territory. In fact, aggressive behavior in the form of chasing was not observed in nature except for those males guarding nests.

In the laboratory, sex appears to play no role in the determination of dominance relationships. In the natural environment the male dominates the female to the extent that he chases her from the nest after spawning is completed.

It appears that confining longear sunfish to small aquaria causes more serious dam-

age to the fish as a result of aggressiveness than occurs in nature. As stated previously, of the 245 longear sunfish collected in the natural environment and returned to the laboratory, none had damaged fins. In laboratory aquaria, the typical result of placing two large longear sunfish together is damage to the fins from nipping and ultimately death of the subordinate member as a result of aggressiveness by the dominant member of the pair. An artifact situation is created in the laboratory that would not ordinarily obtain in nature. The physical contact between fishes that was observed during laboratory investigations on aggressiveness was not seen in the natural environment.

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MARVIN L. WASS

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DISPERSION OF THE DARK RED CHROMATOPHORIC PIGMENT IN THE DWARF CRAYFISH, *CAMBARELLUS SHUFELDTI*: A QUANTITATIVE ANALYSIS OF THE HOGBEN AND SLOME STAGES¹

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ABSTRACT

The areas of the pigment in the dark red chromatophores of adult dwarf crayfish, *Cambarellus shufeldti*, were determined at each of the five stages of the Hogben and Slome scale. The increase in area as the pigment proceeded from the maximally concentrated position (stage 1) through the intermediate stages to the final, maximally dispersed condition (stage 5) was statistically significant at each interval. The area of the pigment in a stage 5 chromatophore was 5.0 times that of a stage 1 chromatophore. No such simple relationship existed with the other stages. The chromatophores of adults compared with juveniles were larger but fewer in number per unit area in the portion of the epidermis where the chromatophores were observed. The increase in area offset the decrease in density, resulting in a constant contribution by the dark red chromatophores to the total coloration of the dwarf crayfish regardless of the size of the crayfish.

Several methods of staging the degree of dispersion or concentration of the pigment in chromatophores have been utilized. These have been reviewed by Fingerman (1963). The most commonly employed method is that of Hogben and Slome (1931) who divided the range of pigment migration into five stages. Stage 1 represents maximal concentration, stage 5 maximal dispersion, and stages 2, 3, and 4 the intermediate conditions. Although this system is subjective, trained investigators have no difficulty in duplicating each other's readings with precision. In this laboratory the mean chromato-

phore stage of the same 10 animals determined by two investigators will not differ by more than 0.2 of a stage. However, the Hogben and Slome system is open to criticism because it is subjective and more importantly because the numbers obtained are not additive, *a priori*. For example, stage 4 was not intended to represent twice as much dispersion as seen in stage 2. On the other hand, the advantages of the Hogben and Slome system are its inherent simplicity and the opportunity to examine individual chromatophores, especially in an animal that has more than one type of chromatophore and where one pigment may be dispersing while another is concentrating as the result of changing the animal from a light to a dark background.

The present investigation was undertaken to obtain an objective basis for the Hogben and Slome stages with the dark red chromatophores of the dwarf crayfish, *Cambarellus shufeldti*. The actual area of the pigment in the chromatophores at each of the five stages was determined in order to calculate the relative extent of spreading of the pigment. In this manner the true mathematical relationships of the five stages could be calculated for this particular chromatophore. In addition, the areas of the pigment in chromatophores of two different sizes of crayfish were determined with the objective of learning whether or not the chromatophores increase in size when the crayfish does. Finally, the chromatophores were counted in

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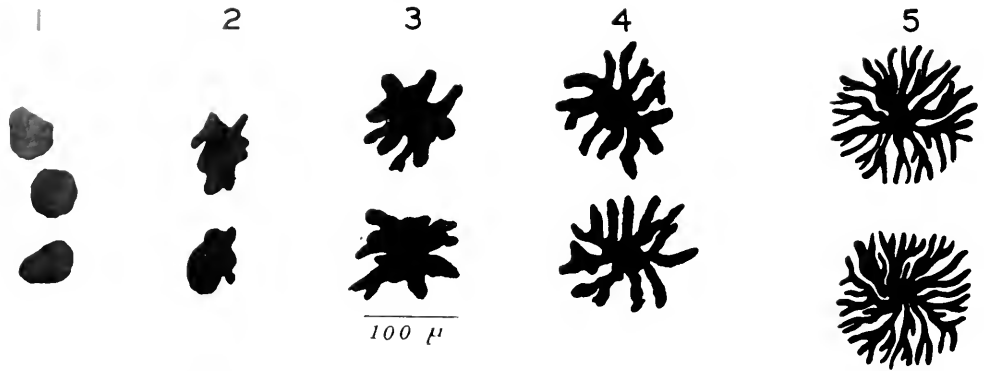


Figure 1. The five stages of the dark red chromatophores of *Cambarellus shufeldti* according to the Hogben and Slome method.

a unit area of the epidermis from juveniles and adults in order to determine whether or not the density changes as the crayfish grows.

MATERIALS AND METHODS

Specimens of the dwarf crayfish, *Cambarellus shufeldti*, were collected periodically from a pond near the town of Pearl River, Louisiana. The crayfish were kept in the laboratory in aquaria containing aerated tap water about 2.5 cm deep and maintained at a temperature of 22-24°C under a constant illumination of 3.25 meter-candles.

For all of the observations only the dark red chromatophores dorsal to the heart were used. This crayfish also has smaller light red chromatophores interspersed among the dark red ones. The pigment in the dark red chromatophores will become maximally concentrated in specimens on a white background and maximally dispersed in individuals on a black one (Fingerman, 1957). After the pigment reached the desired stage the portion of the carapace dorsal to the heart was removed with scissors and forceps and placed inner side uppermost on a depression slide with enough Van Harreveld's solution (Van Harreveld, 1936) to cover the piece of carapace completely. The isolated piece was then viewed with a microscope having one ocular that contained a square grid which was calibrated. At the magnification used (125×) the square grid delimited an actual area of 0.56 mm². The number of dark red chromatophores within the area was determined. Then with the aid of a camera lucida the outlines of the pigment in one or more

chromatophores were traced. These chromatophores were staged according to the system of Hogben and Slome. The camera lucida further magnified the chromatophores to 218×. These outlines were then enlarged an additional 6× by means of a photographic enlarger. The areas of the final tracings were then determined by means of a calibrated planimeter. The planimeter readings were finally reduced to the actual areas of the pigment in the chromatophores.

Student's *t* test was utilized in the statistical analysis of the data. A probability value of 0.05 was considered the maximum value for a statistically significant difference.

RESULTS AND DISCUSSION

The areas of the pigment mass in the dark red chromatophores of adult dwarf crayfish, 2.4-2.6 cm rostral length, were determined for each of the five Hogben and Slome stages. These measurements were performed on 20-25 chromatophores of each stage. Figure 1 consists of drawings depicting the five stages of the dark red chromatophores. In stage 1 the pigment is maximally concentrated and no processes are visible. Stage 2 is identified by the rough edges indicating the beginnings of processes as some of the pigment is starting to flow into the branches of the chromatophores. Stage 3 is characterized by the presence of distinct processes and a large central mass of pigment. In stage 4, compared with stage 3, the processes have enlarged and the central mass of pigment has decreased. Stage 5, the most dispersed stage, is readily identified and distinguished from

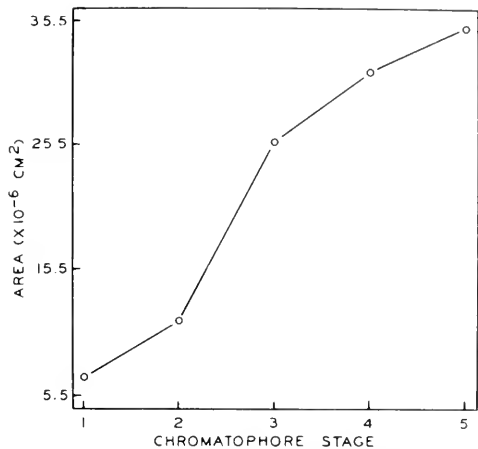


Figure 2. Relationship between the Hogben and Slome stages and the surface area of the pigment in the dark red chromatophores of adult specimens of *Cambarellus shufeldti*.

stage 4 by the branching and thinning of the processes and the minimum size of the central pigment mass as a consequence of the migration of so much pigment from the center into the processes.

The mean surface areas for each of the five stages of the dark red chromatophores from adults are shown in Figure 2. It is quite clear from Figure 2 that the area of the pigment mass undergoes its greatest increase between stages 2 and 3. In order to compare the areas of the pigment in each of the five stages ratios of the areas were calculated. The more dispersed stages increased in size over stage 1 by factors of 1.7 for stage 2, 3.7 for stage 3, 4.5 for stage 4, and 5.0 for stage 5. The surface area thus keeps increasing but only for stages 1 and 5 are the areas proportional to the numerical stages. The measurements were analyzed statistically and it was found that the differences between the areas of stages 1 and 2 and between stages 2 and 3 were highly significant ($p < 0.001$ in both cases) as were the differences between the areas of stages 3 and 4 and between stages 4 and 5 ($p < 0.01$ in the latter two instances).

Measurements were also made of 20 dark red stage I chromatophores in juvenile dwarf crayfish, 1.7-1.9 cm total length. The mean surface area of the maximally concentrated pigment in the juveniles was 5.8×10^{-6} cm² compared with an area of 7.0×10^{-6}

cm² for stage 1 chromatophores of adults. The area of the pigment in adult stage 1 chromatophores is, therefore, 1.21 times larger than in comparable chromatophores of juveniles. The difference was statistically significant, $p < 0.05$.

The means of the numbers of dark red chromatophores within 0.56 mm² of the carapace dorsal to the heart were 40.7 for the adults and 48.2 for the juveniles, the ratio is 0.84:1. The difference was statistically significant, $p < 0.05$. As noted above, the ratio of the areas of the juvenile to adult stage 1 chromatophores was 1.21. The product of these two ratios is 1.02, essentially unity. In other words, the decrease in density of the dark red chromatophores in adults was compensated for by an increase in area with the result that the net coloration due to the chromatophores was unchanged as the crayfish grew.

SUMMARY AND CONCLUSIONS

1. The areas of the pigment in the dark red chromatophores of adult dwarf crayfish, *Cambarellus shufeldti*, were determined for each of the five stages of the Hogben and Slome scale.

2. The differences in area among the five stages of the Hogben and Slome system were statistically significant. The area of the pigment in a stage 5 chromatophore (maximally dispersed pigment) was 5.0 times as large as that in a stage 1 chromatophore (maximally concentrated pigment) but the areas of the pigment in chromatophores of stages 2, 3, and 4 were not simple multiples of stage 1.

3. The areas of the pigment in dark red chromatophores and their numbers in a unit area (0.56 mm²) of the epidermis from the carapace dorsal to the heart of juveniles and adults were compared. The area of the adult chromatophores was 1.21 times larger than that of the juveniles but the density of chromatophores in the adults was 0.84 times that in the juveniles. Because the product of these two ratios (1.02) is for all practical purposes unity, it can be concluded that the decrease in chromatophore density was offset by the increase in area resulting thereby in a constant contribution by the chromatophores to the total coloration of the dwarf crayfish as it grew.

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A NEW PINNIXID COMMENSAL WITH A HOLOTHURIAN
(CRUSTACEA: DECAPODA)¹

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ABSTRACT

A new species of pinnixid crab (*Pinnixa leptosynaptae*) was found associated with a synaptid holothurian (*Leptosynapta crassipatula*) at Bald Point near Panama, Florida.

Pinnixa leptosynaptae sp. n. (Figs. 1-6)

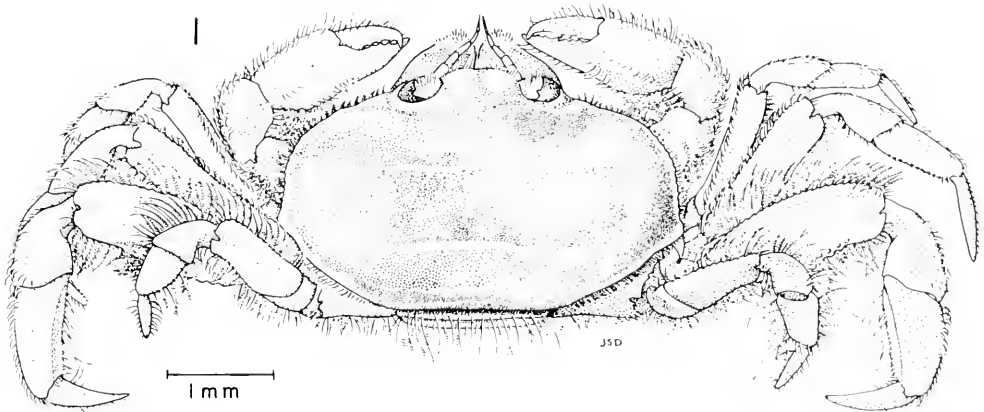
Diagnosis: Dorsal aspect marked by four transverse ridges appearing as dark red lines on a light background.

Types: Male holotype and female allotype (catalog numbers 99389 and 99390) have been deposited in the United States National Museum. Paratypes deposited at the same museum include two adult males and four females, only one of which is mature. All material was collected from Bald Point at the entrance to Ochlockonee Bay, Franklin

County, Florida, in 1955, the types on Dec. 1, the paratypes on Dec. 28.

Description: Carapace less than twice as wide as long, subrectangular, anterolateral angles more broadly rounded than posterolateral. Dorsal surface bearing four prominent transverse ridges, most anterior ridge uniting raised orbital margins posteriorly; second extending across branchial region and ending just short of lateral margins; third ridge crossing cardiac region, beginning at posterolateral furrows and being most prominent medially; fourth ridge lying just inside posterior border and curving forward to level of third ridge at either end. A pair of obscure ridges midway between second and third ridges, nearly reaching lateral margins and separated by a median interspace subequal to their combined lengths. Frontal margin setose and slightly advanced beyond orbits. Carapace otherwise bare except for a few, short, backward-curving bristles near

¹ Contribution No. 259 from the Virginia Institute of Marine Science, Gloucester Point, Virginia.

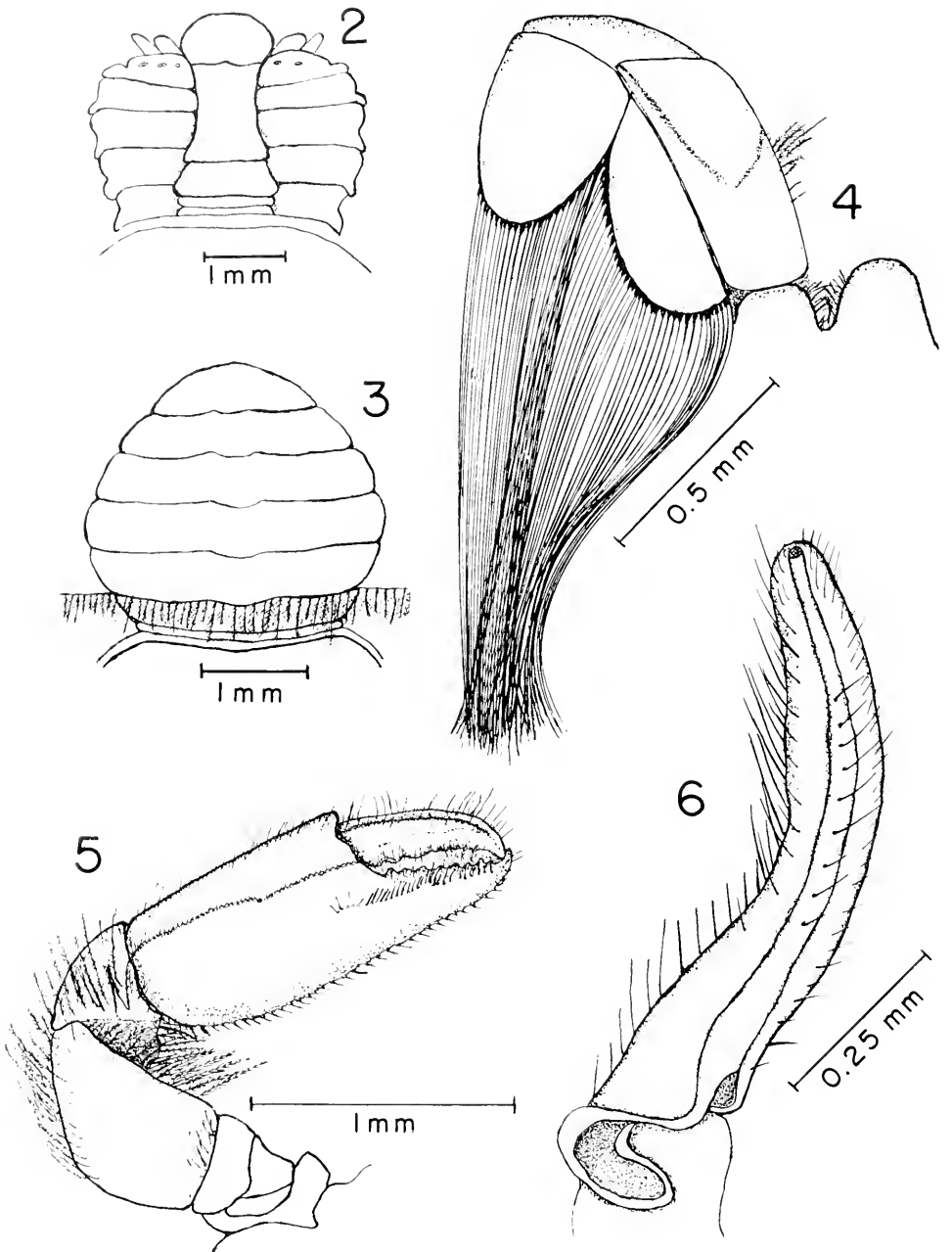


1. Male holotype, dorsal view.

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2. Abdomen and thoracic sternum of male holotype. 3. Abdomen of female paratype. 4. Left third maxilliped. 5. Right cheliped of male in ventral view. 6. Right first pleopod of male.

anterior margin. Orbits ovoid; antennae short, little longer than interorbital space.

Chelipeds stout, equal; chela swollen, with sparse, short bristles and hairs on dorsal third, otherwise bare except for median row of hairs extending from gape posteriorly on outer surface and short row fringing gape ventrally; inner surface with diagonal row of hairs from gape to posteroventral angle, and a row fringing ventral margin. Fingers toothed, strong; movable finger strongly curved, with tip crossing on inside to reach margin of lower finger.

Third walking leg longest; second, first and fourth shorter in order. Legs flattened, first two rather narrow; third leg heavy, merus and propodus triangular in cross section, with tuberculate ventrolateral margins. Margins of meri and propodi of last two pereopods fringed with curved, red hairs. All dactyli fringed on upper margin with minute hairs, fourth fringed on both margins. Dactyli as long as propodi except on fourth pereopod.

Third maxilliped with unusually long plumose hairs originating from: a line on inner surface of merus, a margin on inner side of carpus, a diagonal line on inner side of propodus, and distal margins of propodus and dactylus.

Male abdomen narrow, bare, concave laterally; first two segments narrower than third, which is wide and trapezoid-shaped; fourth, fifth, and sixth fused; seventh wide, with rounded sides and slightly indented anterior margin.

Measurements (mm): Male holotype; carapace length 2.3, width 3.7, fronto-orbital width 1.5, chela length 1.5, dactyl length 0.6, height of manus 0.6, merus of third walking leg length 1.6, width 0.9. Female allotype; carapace length 2.1, width 3.9.

Variations: Female is generally like male, with abdomen fully developed in allotype,

less so in paratypes. Ridges on carapace are variable in prominence, especially the sixth, which also varies in its distance from the posterior border, in some cases being contiguous with the border.

Color: The background color of the carapace varies from light cream to darker shades. The most conspicuous color marks are the bright red lines which mark the transverse ridges. These markings fade in alcohol. Dark red setae occur in some areas.

Habitat: *P. leptosynaptae* was found only on the body of *Leptosynapta crassipatina* Clark (Holothurioidea; Apoda), on which it usually occurred near the anterior end, although never at the mouth region. The ridges and hairs on the carapace may enable the crab to cling to the rough holothurian since it was always found with its dorsal surface appressed to the host. The crabs averaged about one per ten *Leptosynapta*, never more than one occurring on a single host. Large specimens of *Leptosynapta* measuring up to 10 inches in length were preferred by the crabs. The holothurians were dug from the outermost sand bar, which was exposed at very low tide. On May 24, 1956, about 40 *Leptosynapta* were dug from this bar but this species of *Pinnixa* was not found.

Remarks: Although this species is apparently not closely allied to any other members of the genus, it seems to have a slight affinity with *P. transversalis* (H. Milne-Edwards and Lucas) from the Pacific coast of South America and *P. faxoni* Rathbun from Trinidad. This affinity is noted in the general shape of the chelae and the male abdomen. It is readily distinguished by the many transverse ridges on the carapace and the smaller size.

Acknowledgments: I wish to thank Mrs. Jane S. Davis for providing the toto figure under support of National Science Foundation Grant GB-2854.

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THE CUBAN LIZARDS OF THE *ANOLIS HOMOLECHIS* COMPLEX

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ABSTRACT

The *homolechis* complex of Cuban anoline lizards consists of seven species: *A. quadriocellifer*, *A. homolechis*, *A. mestrei*, *A. allogus*, *A. ahli*, *A. rubribarbus*, and *A. imias*. Of these species, *homolechis* and *allogus* are island-wide, *mestrei* is restricted to the western provinces of Pinar del Río and Habana, *ahli* to Las Villas Province, *rubribarbus* and *imias* to Oriente Province, and *quadriocellifer* to the Peninsula de Guanahacabibes in extreme western Pinar del Río Province. Although previously considered as a subspecies of *A. homolechis*, *A. quadriocellifer* clearly is specifically distinct from *A. homolechis* and merits specific status. Analysis of the variation in various scutellar characters of *homolechis*, as well as information on dewlap color, allows for the recognition of five subspecies of *A. homolechis*, of which the nominate subspecies with a white to gray dewlap is widely distributed throughout Cuba and the Isla de Pinos. The remaining subspecies, herein proposed, all with yellow to orange dewlaps, occupy regions more or less peripheral to the main body of *A. h. homolechis*. The status of extreme eastern Oriente populations, as well as those at Banos in Oriente, is left undecided; in both these areas, white and yellow dewlapped lizards occur sympatrically but accurate data for individual specimens is lacking. The apparent sympatry of white and yellow dewlapped *A. homolechis* without intergradation on the northern Camagüey coast is discussed in detail.

Variation in *A. allogus*, as well as the relationships of this species with the nominal species *A. ahli* and *A. rubribarbus*, both of which are apparently allopatric to *A. allogus*, is given in detail. There is evidence for the intergradation of *allogus* and *rubribarbus* in northern Oriente, but this evidence is equivocal and material is lacking from critical areas. The recognition of *ahli* as a species distinct from *allogus* rests principally on philosophical grounds, since these two "species" differ in few meristic characters. Although no subspecies of *A. allogus* have been designated, it seems likely that additional material will ultimately show that this species also has a number of distinctive populations along the length of Cuba.

Anolis imias remains known from only a pair of specimens; the type locality ("Imías") has been changed, since data from the collector indicate that these lizards were not taken on the xeric southern Oriente coast (where further search has not revealed them) but rather from the mountains north of Imías. There is no question that *imias* is a distinctive species, which combines the characteristics of *A. homolechis* and *A. allogus*; *A. imias* appears to be sympatric with *A. allogus* and not with *A. homolechis*.

Anolis mestrei is limited to the province of Pinar del Río (except for an occurrence in Habana Province near the Pinar del Río border). This very distinctive species occurs sympatrically with both *A. homolechis* and *A. allogus*.

The Cuban anoles of the *Anolis homolechis* complex have been discussed in detail by Ruibal and Williams (1961). The complex, as defined by them, is composed of *A. homolechis* Cope, *A. mestrei* Barbour and Ramsden, *A. allogus* Barbour and Ramsden, *A. ahli* Barbour, *A. rubribarbus* Barbour and Ramsden, and *A. imias* Ruibal and Williams. In a later paper, Ruibal (1964) included the above species in a *homolechis-sagrei* group along with *A. ophiolepis* Cope and *A. sagrei* Duméril and Bibron. This group is defined (Ruibal, 1964:478) by having the tail laterally compressed, ventrals not in transverse rows, head scales keeled, supra-orbital semicircles usually not in contact, body scales small, head short-snouted, and no green color phase. Additionally the ventral scales are either keeled or smooth; although most of the species here discussed have these scales smooth, occasional individuals of normally smooth scaled species have the ventrals keeled. Only a single trinomial is now in use, *A. b. quadriocellifer* Barbour and Ramsden, for the population on the Peninsula de Guanahacabibes.

The present paper is based on collections now in the American Museum of Natural

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History (AMNH) made by myself and associates in Cuba and the Isla de Pinos between 1954 and 1960. My work there was under the auspices of two National Science Foundation grants (G-3865 and G-6252) which allowed me to spend a total of slightly more than 15 months on the island, collecting extensively in all provinces. As far as the *homolechis* complex is concerned, it is unfortunate that some of the more significant material was collected during the summer and early fall of 1960, at a time when Ruibal and Williams had more or less completed their own study of the complex. They had access to my material and data taken between 1956 and 1959, but my 1960 specimens were not available to them or to myself for study until I returned from the field in the Antilles in 1962.

Rather than being chauvinistic, I have a valid reason for concentrating on my own material: color is a most important character in members of this complex, as it is in most *Anolis*, and for color my own material is carefully documented. In some areas, color is of extra importance in *A. homolechis*, and usage of non-documented material might cloud the clarity of my own data. Where my material was inadequate or where I knew of specimens from especially pertinent or interesting regions, I have borrowed them. This supplemental material has been drawn especially from the Museum of Comparative Zoology. Many of their lizards, collected by Rodolfo Ruibal and Ernest E. Williams, are equally as well annotated as mine. Dr. Williams, aside from extending me the courtesy of a loan of these lizards, has also acted as my intermediary in borrowing the type material of the Cuban species described by Ahl (1924, 1925) from the Berlin Museum (BM), through Günther Peters. I have borrowed smaller amounts of material from the Instituto de Biología, Academia de Ciencias, La Habana (IB), the Illinois Natural History Survey (INHS), the Museo Felipe Poy (MFP), the Museum of Zoology at the University of Michigan (UMMZ), and the United States National Museum (USNM); for the loan of these lizards I am grateful to Orlando H. Garrido, Philip W. Smith, Miguel L. Jaume, Charles F. Walker, Doris M. Cochran, and James A. Peters. There are also a few specimens in my own collection (AS) as well as some very recent material,

collected by Richard Thomas and Sr. Garrido, in the Albert Schwartz Field Series (ASFS). In the field, I have had the assistance of several students without whose cooperation such numbers of *Anolis* would not have been taken. I wish particularly to thank Edwin B. Erickson, John R. Feick, William H. Gehrmann, Jr., Ronald F. Klinikowski, David C. Leber, James D. Smallwood, Jr., Barton L. Smith, Willard M. Stitzell, Richard Thomas, and George R. Zug for their participation in my work. In addition, a trip to the extreme eastern tip of Cuba by boat was ably organized by Porfirio Azcuy and Armando García, and made in the company of Donald R. Price, Frank C. Sentz, Jr., and Ronald F. Klinikowski. Some of the specimens from the southern coast of the Península de Guanahacabibes were secured by Messrs. Feick and Gehrmann, Dr. Robert S. Howard, and Sr. García. During the latter portion of my Cuban field work, Messrs. Klinikowski and Leber were recipients of National Science Foundation Undergraduate Research Participation grants under my direction.

The color portraits are the work of David C. Leber. All were made from living lizards and the dewlap and body colors are as accurately and painstakingly executed as possible. Unfortunately, when Mr. Leber was in the field with me (1960), we did not collect all the species or subspecies of the *homolechis* complex, so that the gallery of portraits is incomplete. I am very grateful to Mr. Leber for his attention to detail and for his extreme cooperation in making these portraits, and to George C. Gorman for his permission to use living lizards recently collected by him in Cuba. All stylized color designations in the text refer to Maerz and Paul (1950).

Of the eight species included by Ruibal in the *homolechis-sagrei* group, four (*homolechis*, *allogus*, *sagrei*, *ophiolepis*) are island-wide in distribution. Two (*imias*, *rubribarbatus*) are limited to Oriente Province, one to Pinar del Río Province (*mestrei*), and one to Las Villas Province (*abli*). The island-wide species often have great apparent hiatuses in their distribution; for instance, *A. allogus*, which occurs close to Cabo de San Antonio in western Cuba and close to Cabo Maisí in eastern Cuba and is abundant in the forests of Pinar del Río,

Camagüey and Oriente provinces, is unknown from the central intermediate provinces of Matanzas and Las Villas. In the latter province, *A. allogus* is represented by *A. abli* which has a limited distribution in the Sierra de Trinidad. There are also wide areas whence *A. homolechis* is unknown; although some of these gaps are likely due to lack of collecting, others are almost as likely due to absence of suitable habitats for *A. homolechis*. Of the seven species discussed in the present paper, two are island-wide and the others are restricted to local areas in Pinar del Río, Las Villas and Oriente provinces.

I have examined in detail 1424 lizards of the seven species discussed in the present paper. Of these, 994 are specimens with which I had personal experience in the field and they form the main body of the study material. Snout-vent lengths in millimeters were taken on all specimens, and the following counts were made:

1) scales across the snout at the level of the first (counted from the anterior border of the orbit) canthal scale.

2) number of scales between the supra-orbital semicircles at their closest approximation; a count of 0 indicates that the semicircles are in contact and counts of 1 and 2 show that the semicircles are separated by this number of scales.

3) scales between the supraorbital semicircles and the interparietal scale, written as a fraction ($2/2$, $2/3$, $3/3$, etc.) for each specimen, with each half of the fraction the count on the right and left sides in a particular lizard.

4) fourth toe lamellae on phalanges II and III.

5) number of postmental scales

6) number of loreals on one side

I also checked the prenasal scales (whether transversely divided or not), whether the ventral scales were keeled or not, and the presence of brachial and supracarpal keeling. The latter feature, one which distinguishes specimens of *A. homolechis* from *A. allogus* for instance, was verbally quantified into the categories "present," "present but weak" and "absent." In *A. homolechis*, the single supracarpal keel is rarely "present" and is more often "present but weak" but in most specimens is "absent." This categorization is subject to the vagaries of

any such verbalization and observation, and other workers may not reach the same conclusions on this datum as have I, but it does serve a purpose in showing the variation in this character as seen by myself.

Anolis quadriocellifer Barbour and Ramsden

Originally named from three specimens (MCZ 11867, MCZ 11906-07) from the Ensenada de Cajón near the extreme western tip of the Península de Guanahacabibes, *A. quadriocellifer* was later (Barbour, 1937: 127) considered a subspecies of *A. homolechis*. Ruibal and Williams (1961:230 *et seq.*) confirmed the subspecific status of *quadriocellifer*, basing their conclusions primarily on material, collected by myself and parties from localities toward the base of the Península de Guanahacabibes, which appeared to be intergradient between *A. homolechis* and *A. quadriocellifer*. Fresh specimens collected in 1960 and unavailable to Ruibal and Williams suggest reassessment of the status of *quadriocellifer*.

Before proceeding, a brief description of the extreme western portion of Cuba helps in the visualization of the habitats and geography of the area under discussion. Western Cuba is formed by a hook-shaped peninsula, its shaft pointed west, the Península de Guanahacabibes; the terminal portion of the peninsula ends in Cabo de San Antonio. To the east, the peninsula is attached to the Cuban "mainland" by a narrow (12 km) isthmus, on which lies the town of Cayuco. Extending southwestward from the isthmus is an ancillary peninsula about 40 km in length which culminates in Cabo Corrientes and which forms the barb portion of the hook. From Cayuco in the east to Cabo de San Antonio in the west is about 80 km airline, very slightly south of due west (Fig. 1).

The Península de Guanahacabibes is quite varied ecologically. Its northern margin is swampy; its southern edge is typically composed of limestone escarpments and balconies topped by extensive areas of *diente de perro* limestone giving a xeric and bare aspect to the countryside. The central portion of the peninsula supports hardwood forests; there are (as at Vallecito de San Juan) lakes and ponds surrounded by dense hardwood forest. In the Cabo de San Antonio area, the forests are dry and open, with the

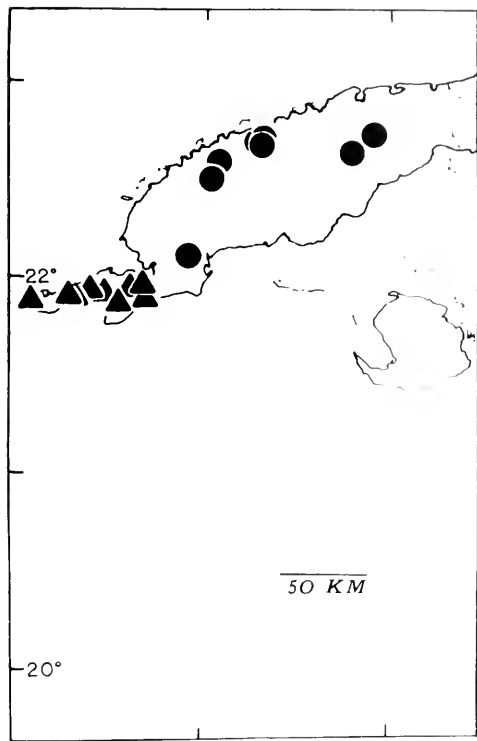


Figure 1. Map of extreme western Cuba (Pinar del Río Province) showing localities whence specimens of two species of anoles (*Anolis quadriocellifer*—solid triangles; *Anolis mestrei*—solid circles) have been examined.

aspect of xeric forests throughout the Antilles. The rainfall varies between 115 and 125 cm annually (Marrero, 1951:442), below the mean annual rainfall for Cuba. Despite the relatively small amount of rain, the red soils in the central portion of the peninsula support, as noted above, fine stands of dense hardwoods. The maximum relief of the Península de Guanahacabibes is about 10 m above sea level, and the country is generally flat. To the east, where the peninsula abuts against the Cuban "mainland," lie the plains of Remates, distinctly different in character from the peninsula itself. These grassy plains are forested in pines and palms (*Acoelorbaphe wrightii*) and are characterized by the occurrence of many small to fairly large lakes in open or lightly forested savannas. The transition between these plains and the hardwood forests of the peninsula west of Cayuco is abrupt. I have not visited the region between

Cayuco and Cabo Corrientes, but Vaurie (1957:301) noted that the Cabo Corrientes section was forested; the status of *A. quadriocellifer* in this latter area has been reported by Garrido and Schwartz (MS).

Access to the peninsula has always been difficult and this accounts for the sparse records of amphibians and reptiles from this area. In 1957, a poor and very rocky road led from Cayuco to a sawmill village (La Majagua) 10 km southwest of Cayuco at the edge of the hardwood forest and proceeded thence to the northwestern coast of Cabo Corrientes and the north shore of the Ensenada de Corrientes (the large and open embayment formed by the Península de Guanahacabibes on the north and the Cabo Corrientes peninsula on the east). In 1957, two visits to the north shore of the Ensenada de Corrientes were made by John R. Feick, William H. Gehrmann, Jr., and Armando García; on one visit they were accompanied by Robert S. Howard. In 1958, George R. Zug and I, along with Sr. García, collected along the southern coast of the peninsula and later made an unsuccessful attempt to reach the Valle de San Juan, a (then) small settlement in the central portion of the peninsula about 10 miles west of Cayuco. Although we did not reach our goal because of the combination of heavy rains and earthen roads, I did have an opportunity to see this heavily forested central portion of the peninsula. In 1960, a new gravel road had been constructed to Valle de San Juan, and David C. Leber and I reached that (now larger) settlement with ease from Cayuco, and we were able to observe and collect in the dense forests of this section. In December 1958, in the company of Ronald F. Klinikowski, Donald R. Price and Frank C. Sentz, Jr., and under the capable guidance of Armando García, I visited the type locality of *A. quadriocellifer* at Ensenada de Cajón near Cabo de San Antonio, travelling by boat from Esperanza on the northern coast of Pinar del Río Province. Orlando Garrido (*in litt.*) advises me that it is possible now to reach Cabo de San Antonio by road, but the trip is long and arduous and cannot be accomplished during the rainy season. There are few settlements of any size on the peninsula proper and the greatest number of people are at the peninsula's base in the Cayuco area; some wood-

cutters, fishermen, and farmers live scattered along roads and coasts in at least the central section and near the cape.

Anolis quadriocellifer (at Ensenada de Cajón) is easily recognized by the presence of a pair of black triangular scapular spots outlined by a more or less continuous white line or series of white spots. There is also a series of three or four vertical white flank bars made up of white dots, and there may also be one or a pair of parallel white longitudinal flank lines. If there are two white flank lines, the upper lies at the level of the bottom of the black scapular triangle, and the lower begins above the axilla and proceeds posteriorly. The black scapular patches occur in males and females; in the latter sex the patches lie lateral to the constriction forming the first of about four pale dorsal rhombs, a pattern typical of females and immatures of several members of the *homolechis* complex. There is some variation in the intensity and expression of the black scapular patches in topotypes. One of the largest males examined (AMNH 83174) lacks black pigment in this region, and other males and females have the spot less well expressed but still indicated. Even in the absence of the black pigment, there is, in topotypes, a conspicuous remnant of the white patch outlines. Occasional males have a white dot in the center of each black patch.

The dewlap color of topotypical *A. quadriocellifer* is a dirty (grayish) yellow with three orange to red horizontal bars. A salient scale character of *A. quadriocellifer* is the presence of keeled supracarpal scales; these scales have usually three fairly distinct keels on their upper surfaces. I have recorded the supracarpal keels as weak in one male topotype with a snout-vent length of 38 mm, and absent in three males with snout-vent lengths of 30 and 32 mm and a female with a snout-vent length of 33 mm. Other young and subadult *quadriocellifer* of similar size have the keels well expressed; apparently this character is not regularly shown in very young individuals. The largest male topotype examined has a snout-vent length of 50 mm and the largest female 33 mm.

In contrast to these characters of *A. quadriocellifer* are those of *A. homolechis*. This species lacks any black scapular patches, vertical white flank barring, or prominent

longitudinal white flank lines. The dewlap (in *homolechis* from the province of Las Villas westward to include Pinar del Río Province—see Pl. 1, upper right) is variably white to grayish and lacks any definite pattern except for some specimens which have obscure indications of grayish bars on a whitish ground. The supracarpal scales are either smooth or have but a single keel; use of the term keeled for the *homolechis* supracarpals is somewhat of an exaggeration, since the scales are more tectiform than truly or strongly carinate. Some western *homolechis* have the supracarpal keel more distinct than others, but the keeling is quite variable in the species and of little significance. The largest male Pinar del Río *homolechis* examined has a snout-vent length of 57 mm and the largest female 46 mm.

Although not particularly pertinent to the present problem, it should be noted that two specimens of *A. quadriocellifer* (AMNH 83189, FN 6679, male, snout-vent length 47 mm; AMNH 83183, FN 2657, male, snout-vent length 49 mm) have keeled ventrals. Both *homolechis* and *quadriocellifer* are normally characterized by having smooth ventral scales.

The presumed intergradient specimens between *homolechis* and *quadriocellifer* are a series of 27 lizards from six localities, as follows (east to west): 1) north shore, Ensenada de Corrientes, 47 km W Cayuco; 2) north shore, Ensenada de Corrientes, 45 km W Cayuco; 3) north shore, Ensenada de Corrientes, ca. 40 km W Cayuco; 4) north shore, Ensenada de Corrientes; 5) western coast, Cabo Corrientes; 6) 7 km SW Cayuco. As a group, these specimens have dewlaps which vary between yellow to yellow-orange; the yellow-orange effect is due to the rather indiscriminate mottling of yellow and red pigments to give an overall orange or yellow-orange color. The specimens from farthest west on this southern coast of the peninsula were recorded as having the dewlap yellow-orange, whereas those from Cabo Corrientes had the dewlaps yellow and those from 7 km SW Cayuco orange. As a series these specimens from various southern coast localities differ from topotypical *quadriocellifer* in dewlap color, since none had the three red dewlap bars which occur on more western *quadriocellifer*.

As far as the black shoulder patch is con-

cerned, none of the Ensenada de Corrientes specimens shows it. However, the position of the black *quadriocellifer* patch is still marked very clearly in most specimens by the remnants of the white outline; additionally, the white dotted flank stripes are a conspicuous feature of the series. At least three males (AMNH 83183—both specimens; AMNH 83189, FN 6651) have the shoulder patch darker brown than the brown ground color; interestingly, AMNH 83183 includes the specimens from 7 km SW Cayuco and thus very close to the region where *homolechis* and *quadriocellifer* were presumed to intergrade.

The supracarpals of the Ensenada de Corrientes specimens were stated (Ruibal and Williams, 1961:231) to be intermediate between the 2 to 3 keeled supracarpals of *quadriocellifer* and the smooth to uncarinate supracarpals of *homolechis*. The keeling is indeed variable in this entire series, but to my eye no more so than in topotypical *quadriocellifer*. I have recorded the supracarpal keeling as weak in seven specimens (snout-vent lengths 46 to 51 mm), absent in one male (snout-vent length 47 mm), and present in all other lizards. There are no small juveniles available from the Ensenada de Corrientes region, so no comment can be made about presence of supracarpal keeling in very small specimens. I do not consider that the number of supracarpal keels is intermediate (1 or 2 keels) between the situation in *quadriocellifer* and that of *homolechis*.

In effect, then, the Ensenada de Corrientes series seems to be very distinctly allied to topotypical *A. quadriocellifer* but to lack the prominent black scapular patches and the distinctly barred dewlap (although both red and yellow pigments occur in the dewlap color).

In the summer of 1960, between Cayuco and Valle de San Juan (16.3 km W Cayuco), specimens of *A. quadriocellifer* and *A. homolechis* were collected synotopically, often on the same trees. Both situations of syntopy (11 km W Cayuco; Valle de San Juan) were in cut-over *monte* (hardwood forest); a third locality (13.2 km W Cayuco) yielded only *A. homolechis* (Fig. 2). A total of 16 *A. quadriocellifer* and seven *A. homolechis* were taken at these two localities; this should not be interpreted

that the former was more abundant than the latter but rather that, once we realized that both species were present, we concentrated on securing *quadriocellifer* in preference to *homolechis*.

The *A. homolechis* from these two localities are fairly easily dismissed. They had white dewlaps, lacked either black or brown scapular patches or white outline remnants thereof, and lacked longitudinal white flank lines or vertical white flank stripes. In color and pattern they are indisputably *A. homolechis* and show no *A. quadriocellifer* traits. They are slightly unusual, however, in that two have the supracarpal keel rather more prominent than usual. The same variation occurs in two of the specimens from the intermediate (8.2 mi. W Cayuco) locality. In all series, however, there are individuals with smooth and weakly keeled supracarpals.

The *A. quadriocellifer* from these two localities are extremely interesting. The dewlaps were recorded as yellowish orange without transverse bars (Pl. 1, upper left). The dorsal pattern is very similar to that of topotypical *quadriocellifer*, with prominent black, white-outlined shoulder patches and vertical flank barring. In one male (AMNH 96522, FN 8668) the patches are much paler and brown but are still visible and outlined with white. The lateral longitudinal lines are seldom present, but may be represented by a longitudinal series of white dashes (AMNH 96522, FN 8671) along the lower sides. Most peculiarly, some specimens show, in addition to the black shoulder patches, a second pair of patches in series along the back; these individuals are thus even more patterned dorsally than are topotypes. Occasional males have a white dot in the center of each shoulder patch.

All specimens from these two localities have the supracarpals keeled (recorded as weakly so in four lizards with snout-vent lengths varying between 47 and 50 mm), and three have the ventrals keeled (AMNH 96522 + FN 8670; AMNH 86523, FN 8698).

In summary, the *A. quadriocellifer* from between Cayuco and Valle de San Juan resemble topotypes in dorsal pattern but are unlike the more southern material from Ensenada de Corrientes in this feature. On the other hand, the Cayuco-Valle de San Juan specimens resemble the southern *A.*

quadriocellifer in dewlap color but are unlike topotypes.

The syntopic occurrence of *A. quadriocellifer* and *A. homolechis* suggests strongly that these two forms are not conspecific. The fact that at the places of syntopy, *A. homolechis* does not demonstrate any characters tending toward *A. quadriocellifer* re-enforces this contention and likewise suggests that the two species are (at least here) genetically isolated.

How, then, may we interpret the supposed intergradient populations from along the northern shore of the Ensenada de Corrientes? I suggest that these lizards lack the definitive dorsal pigmentary pattern of more northern *quadriocellifer* (which occupy arid forests at Cabo de San Antonio and mesic forests at Valle de San Juan) in response to the open and unshaded habitats which they occupy on these southern open and bleak shores. Restriction or obsolescence of dark pattern elements in populations of lizards occupying open and dry areas is a common phenomenon. The lack of a well patterned dewlap in these southern lizards may be a similar or cognate response to more sunny and open situations, resulting in an overall paling of colors. This explanation may not be used to account for the patternless but bright dewlaps of the Valle de San Juan lizards which occur in mesic forest. Were the distribution of these three populations more completely known, it is not unlikely that all or some of them could with complete justification be separated nomenclatorially. Although there is very definite overlap in degree of expression of the scapular patches between all three populations (since some topotypes are indistinguishable on this character from Ensenada de Corrientes lizards, for instance) the three populations are generally quite distinctive as far as both dorsal pattern and dewlap color is concerned.

Attention should be directed to another area of overlap without intergradation between *A. homolechis* and *A. quadriocellifer*. There is a series of 18 *A. homolechis* (AMNH 83182, AMNH 83184) from 3 km W Bartoli sawmill village (= La Majagua), 10 km SW Cayuco; these lizards are typical white dewlapped *homolechis* with smooth to weakly keeled supracarpals. The two *A. quadriocellifer* from 7 km SW

Cayuco overlap the range of *A. homolechis* in this area; in this connection it should be noted that these two *quadriocellifer* (AMNH 83183) are those which have (of all the "southern" lizards) the scapular patches fairly well defined. Geographically they are from a region which is intermediate between the pallid south coast material and the well patterned interior specimens of *A. quadriocellifer*.

Scale counts on 40 *A. quadriocellifer* (topotypes plus Valle de San Juan-Cayuco lizards) are: snout scales between first canthals 5-7 (mean 6.0, mode 6), scales between supraorbital semicircles modally 1 (32 of 37 specimens), scales between supraorbital semicircles and interparietal modally 3 3, fourth toe lamellae 16-21 (mean 18.2, mode 18), postmentals 2-6 (mean 4.6, mode 4), loreals 19-42 (mean 27.2). Counts on 25 Ensenada de Corrientes specimens are: snout scales between first canthals 5-8 (mean 6.3, mode 6), scales between supraorbital semicircles modally 1 (15 of 22 specimens), scales between supraorbital semicircles and interparietal modally 3 3, fourth toe lamellae 14-21 (mean 17.6, mode 18), postmentals 2-7 (mean 4.0, mode 4), loreals 16-35 (mean 24.5). The largest male *A. quadriocellifer* has a snout-vent length of 55 mm, the largest female 40 mm. These data are summarized in Table 3.

Thirty one *A. homolechis* from the areas of overlap of this species with *A. quadriocellifer* have the following counts: snout scales between first canthals 5-9 (mean 7.1, mode 7), scales between supraorbital semicircles modally 1 (27 of 29 specimens), scales between supraorbital semicircles and interparietal modally 3 3, fourth toe lamellae 12-21 (mean 18.0, mode 17), postmentals 2-5 (mean 3.2, mode 4), loreals 18-28 (mean 22.5). The largest male from this series has a snout-vent length of 58 mm, the largest female 41 mm. Meristic scale differences between these *A. homolechis* and *A. quadriocellifer* are slight; most striking are the mean and modal number of snout scales, lower mean of postmentals, and lower mean of loreals in *homolechis*.

Additional scale data on 122 *A. homolechis* from Pinar del Río Province are: snout scales between first canthals 5-8 (mean 6.0, mode 6); scales between supra-



Figure 2. Map of Cuba, showing localities whence specimens of *Anolis homolechis* have been examined. Solid triangles represent localities for white dewlapped *A. homolechis*, semi-solid triangles for non-white dewlapped (yellow to orange) *A. homolechis*. The population at Banes is here regarded as being primarily white dewlapped (solid triangle) and those of extreme eastern Oriente as non-white dewlapped (semi-solid triangles). Figure 3 shows the provinces of Camagüey and Oriente in greater detail.

orbital semicircles modally 1 (103 of 116 specimens), scales between supraorbital semicircles and interparietal modally 3/3, fourth toe lamellae 16-22 (mean 18.7, mode 18), postmentals 2-5 (mean 3.1, mode 4), loreals 15-34 (mean 23.3). Comparison of the data for the two lots of *A. homolechis* shows that the specimens from the area of overlap with *A. quadriocellifer* differ somewhat from their more eastern relatives, namely in having a higher mean and mode of snout scales, and higher mean and mode of fourth toe lamellae. In at least the snout scales, more eastern *homolechis* are more like *quadriocellifer* than *homolechis* from the area of sympatry between the two species. The high mean number of postmentals in the two samples of *A. quadriocellifer* (4.6 and 4.0) is equalled or exceeded only by series of *A. homolechis* from various Camagüey localities (Sierra de Cubitas, Playa Santa Lucía, Los Ballenatos, Cayo Sabinal, with means from 4.0 to 5.2) far to the east in east-central Cuba.

Although I am convinced that *A. quadriocellifer* and *A. homolechis* are two distinct species, moreover I am not at all sure that they are closely related. The presence of multiply keeled supracarpal scales in *quadriocellifer*, for example, would tend to ally that species with *A. allogus*. The latter never has the dorsal pattern of *quadriocellifer* and modally has the prenasal scale transversely divided, a condition not observed in any *quadriocellifer*. There are additional and

trenchant scale and ecological differences which separate the two. Militating against regarding *A. quadriocellifer* and *A. allogus* as conspecific is the fact that a specimen of *A. allogus* was collected 11 km west of Cayuco, within the known range of *A. quadriocellifer*: this *allogus* was typical of its species in all meristic data and shows neither pattern nor scale tendencies toward *quadriocellifer*. The Península de Guana-hacabibes has been a small center of endemism in western Cuba; *Leiocephalus carinatus zayasi* Schwartz, *L. macropus koopmani* Zug, *L. stictigaster stictigaster* Schwartz and *Dromicus andreae peninsulae* Schwartz and Thomas plus two as yet unnamed forms of *Ameiva auberi* Cocteau are endemic subspecies known only from the Península. *A. quadriocellifer* has differentiated further than any of these and has reached specific rank.

Presumably *A. homolechis* occurs only on the eastern portion of the peninsula near its base. As far as my material is concerned, the westernmost records for this species are Valle de San Juan (16.5 km W Cayuco) and 3 km W La Majagua, 10 km SW Cayuco. The eastern limits of *A. quadriocellifer* are 6.9 mi. (11 km) W Cayuco and 7 km SW Cayuco, overlaps of 3.3 miles (5.3 km) in the former case and about 6 km in the latter (Figs. 1 and 2). *A. homolechis* seems to be the more recent invader into the territory of *A. quadriocellifer*, since the former is widespread throughout Cuba and succeeds

in penetrating the Guanahacabibes forest only along its eastern margin whereas *A. quadriocellifer* is widespread and common throughout both xeric and mesic situations on the peninsula but seems not to occur far beyond (if at all) the eastern forest margin. Comments on the habits of *A. quadriocellifer* have been made by Garrido and Schwartz (MS).

Specimens of *A. quadriocellifer* examined (all from Pinar del Río Province, Cuba): Ensenada de Cajón, 24 (AMNH 83174); north shore, Ensenada de Corrientes, 47 km W Cayuco, 1 (AMNH 83190); north shore, Ensenada de Corrientes, 45 km W Cayuco, 10 (AMNH 83189); north shore, Ensenada de Corrientes, ca. 40 km W Cayuco, 5 (AMNH 83188); north shore, Ensenada de Corrientes, 6 (AMNH 83186—2 specimens; AMNH 83187); western coast, Cabo Corrientes, 3 (AMNH 83185); 7 km SW Cayuco, 2 (AMNH 83183); Valle de San Juan, 10.2 mi. W Cayuco, 5 (AMNH 96523); 6.9 mi. (11 km) W Cayuco, 11 (AMNH 96522). Specimens of *A. homolechis* examined from the area of sympatry: 3 km W Bartoli sawmill village (= La Majagua), 10 km SW Cayuco, 18 (AMNH 83182—9 specimens; AMNH 83184—9 specimens); Valle de San Juan, 10.2 mi. (16.3 km) W Cayuco, 4 (AMNH 96528); 8.2 mi. (13.1 km) W Cayuco, 6 (AMNH 96525); 6.9 mi. (11 km) W Cayuco, 3 (AMNH 96524).

Anolis homolechis Cope

Anolis homolechis is one of the most widespread Cuban anoles, since it occurs from one end of the island to the other, on the Isla de Pinos, and on some (and probably many) of the off-shore islands and cays. Ruibal (1961:99) characterized this species as an inhabitant of forest margins, small clearings or along paths in forest in areas of moderate sunlight rather than deep shade. Ruibal (1964:497) later stated that *A. homolechis* occurs to high elevations (almost 6000 feet—1830 meters) in the Sierra Maestra as well as in the lowlands, and that in some areas it has adapted to man-made plant associations in gardens, farms, and pastures. Although *homolechis* is indeed generally associated with forests, these forests are not necessarily dense. Favored areas are open or cut-over woods or

arid coastal forests wherein the trees are widely spaced and there is limited shade; since *homolechis* is a lizard of filtered sunlight (Ruibal, 1961), such open woods offer an ideal habitat for it. In my experience, *A. homolechis* may be encountered in almost any situation where there are trees; isolated trees in pastures, for instance, may have a few *A. homolechis* upon their trunks. Wooded situations of any sort are utilized; although *A. homolechis* generally shuns deep shade, in some areas it and the shade dwelling *A. allogus* occur precisely syntopically within the same dense woods. Such situations are optimal for *allogus* but presumably less so for *homolechis*.

The body color of *A. homolechis* is generally some shade of brown with about four chevrons on the dorsum; the shade of brown varies from tan to rich chocolate brown or velvety black. There are occasional longitudinal lines indicated on the flanks. Females have a dorsal pattern of pale tan median rhombs which extend from the neck onto the tail. Maximal size of males is 62 mm snout-vent length, of females 46 mm.

Ruibal (1961:99) first pointed out that there were some populations wherein the usual white or gray dewlap of *A. homolechis* was yellow in color. This statement was later (Ruibal and Williams, 1961:228-235) amplified in detail. Areas where *A. homolechis* males have non-white or non-gray dewlaps are all in western Cuba (Fig. 2). These regions include (in Camagüey Province) the Sierra de Cubitas and areas between that range and the north coast, Playa Santa Lucía near the Camagüey-Oriente border, Los Ballenatos (islets in the Bahía de Nuevitas) and (in Oriente Province) the southern coast between Cabo Cruz to just east of the Bahía de Santiago, the region about Cabo Maisí, and Banes. In addition to these localities, I have taken yellow dewlapped *homolechis* on Cayo Sabinal on the northern Camagüey coast. I have collected specimens from all these areas of *homolechis* with yellow dewlaps with the exception of Banes. Two other facts are pertinent. Ruibal and Williams (1961:245) stated that *A. homolechis* from Loma de Cunagua in Camagüey Province have yellow dewlaps; this is an observational error since all of my material from that locality has the typical white dewlap of the species. Secondly, apparently the Banes pop-

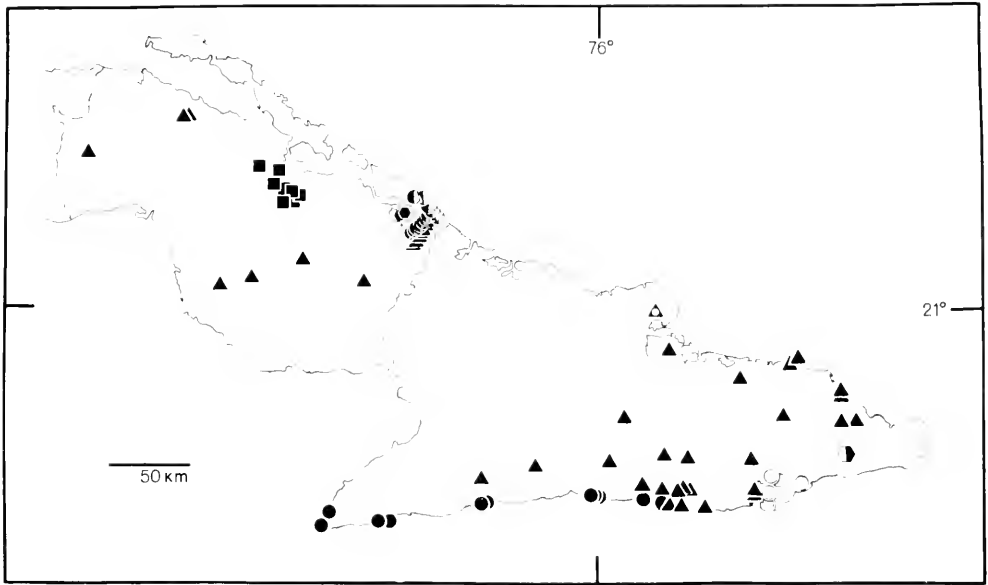


Figure 3. Map of Camagüey and Oriente provinces, Cuba, showing details of distribution of subspecies of *A. homolechis* and *A. imias* (semi-solid hexagon). Solid triangles = *A. h. homolechis*; solid squares = *A. h. jubar*; solid hexagons = *A. h. balaenarum*; semi-solid circles = *A. h. cuneus*; solid circles = *A. h. oriens*; open circles = populations of uncertain status from Bahía de Guantánamo to Río Yumuri. Population at Banes (triangle with included circle) uncertain, but apparently consists of both white and yellow dewlapped individuals. Adjacent symbols (semi-solid circles and solid triangles) south of Playa Santa Lucía in northeastern Camagüey Province represent area of apparent intergradation between *A. h. homolechis* and *A. h. cuneus*.

ulation is not exclusively yellow dewlapped. Dr. Williams (*in litt.*, 31 January 1967) advised me that only one of seven *A. homolechis* in the Museum of Comparative Zoology was recorded (by Chapman Grant) as having a yellow dewlap; the balance of the series reportedly had white dewlaps. There is no fresh material from the Banes area, so the situation there remains anomalous.

The status of these yellow dewlapped populations has been left undecided. Ruibal and Williams (1961:234) suggested that they might represent distinct subspecies, distinct species, or *homolechis* ecotypes adapted to the more stringent conditions of coastal areas, since all but the Sierra de Cubitas population are coastal or nearly so in distribution. Their detailed study of the white and yellow dewlapped lizards in the Playa Santa Lucía area revealed no specimens which were intermediate in dewlap color in a transect by road from the beach to a distance of 21 km inland. They collected only yellow dewlapped *homolechis* from the beach

to a distance 12 km inland; from 13 to 17 km inland they collected primarily white dewlapped specimens, but at two stations within this distance they took two yellow dewlapped specimens. Between 18 and 21 km they secured only white dewlapped lizards (Fig. 3). There is thus a sharp zone of demarcation between the yellow and white dewlapped forms in this particular region and no evidence of orthodox intergradation of dewlap color. My own more limited experiences in the Playa Santa Lucía area precisely parallel theirs, both as to distances involved and dewlap color. In this region, lizards with white or yellow dewlaps act, in their zone of contact, as good species.

A second area of yellow dewlapped *homolechis* is on the southern Oriente coast (Fig. 3). Between Cabo Cruz and the Bahía de Santiago—a distance of 190 km—all *homolechis* collected by myself and others (if dewlap color in life was noted in the field) have yellow dewlaps. At Aguadores, just east of the Bahía de Santiago, the same

situation prevails, so that the physical embayment at present is not a convenient eastern limit to the distribution of these yellow dewlapped lizards as it is for subspecies of some southern Oriente reptiles. At Playa Juraguá, 3.7 miles east of Siboney, white dewlapped specimens occur exclusively, yet only 1.5 kilometers to the west of Playa Juraguá at Arroyo de la Costa we secured solely yellow dewlapped lizards. The transition here is extremely sharp and, as reported for Playa Santa Lucía by Ruibal and Williams, there is no evidence of intermediates. At Playa Juraguá also, there was no discernible area of overlap of the two forms, nor any obvious break in the xeric coastal forest habitat; the yellow dewlapped form occurred to the west and the white dewlapped form to the east in this immediate region without any gradual zone of transition. To the east of Playa Juraguá only white dewlapped specimens have been collected (at 9.1 mi. E Siboney, Laguna de Baconao, Caimanera).

I have had less experience with *A. homolechis* in a third area of yellow dewlapped males—that between the Bahía de Guantánamo east to Cabo Maisí and thence west to the mouth of the Río Yumurí on the north coast (Figs. 2 and 3). Specimens collected by Richard Thomas on the United States Naval Base to the east of the Bahía de Guantánamo had dewlaps which varied from white or pale gray to pale yellow; often the white dewlapped specimens also had yellowish suffusions. At the mouth of the Río Yumurí on the north coast, males had the dewlap white with a yellowish tinge or pale yellow. A similar situation occurs at a locality 14.5 mi. W Baitiquirí in this section of southern coast, where both white and very pale yellow dewlapped specimens were taken from dry woods.

The final mainland area where I have collected yellow dewlapped *homolechis* is the Sierra de Cubitas (Fig. 2). Here the population is completely yellow dewlapped and no white dewlapped specimens occur. That yellow dewlapped specimens are not restricted to the Cubitas massif alone is attested to by Ruibal and Williams, who reported (1961:245) yellow dewlapped males from between Esmeralda and Jaronú to the north of the Sierra de Cubitas and from "near Banao" to the south of the range. I can confirm these findings, since yellow dew-

lapped specimens were collected on the north side of the Cubitas in rich lowland forest 11.9 mi. (19 km) northwest of Banao and on the south side of the mountains at a locality 2 km southeast of Banao.

Specimens of *A. homolechis* from the environs of the Bahía de Nuevitas on the northern Camagüey coast near the Oriente border also are yellow dewlapped; localities include the two of the three islands known collectively as Los Ballenatos, Cayo Sabinal (a large island which forms the northern or seaward margin of the bay), the Playa Santa Lucía area noted previously, and San Jacinto (Ruibal and Williams, 1961:245). One yellow dewlapped specimen has been reported from Banes, some 130 km to the southeast in northern Oriente Province, and many from the Sierra de Cubitas area to the northeast at a distance of about 45 km. Whether these three areas of yellow dewlapped *homolechis* are in actuality continuous is presently unknown. There are no annotated specimens known to me from any areas between them nor were any known to Ruibal and Williams; they suggested (1961:232) that the Bahía de Nuevitas and Sierra de Cubitas populations might be separated by the savanna extending north to the coast near the Río Máximo. However, this savanna is not known to be inhabited by any *homolechis*. Therefore, I do not know if there is an interposed white dewlapped population separating the yellow dewlapped populations in the Sierra de Cubitas and about the Bahía de Nuevitas. There may be physical barriers between the Nuevitas and Banes populations, but there is at present no evidence that white dewlapped *homolechis* occur in the intermediate area, and the situation at Banes itself requires clarification. In summary, one can with some justification presume that there is a continuous yellow dewlapped population of *A. homolechis* from the Sierra de Cubitas to the Bahía de Nuevitas and Playa Santa Lucía (and thence to Banes?) without interruption by white dewlapped *homolechis*. If this is the case, then in some areas (i.e., Playa Santa Lucía) the distribution of the yellow dewlapped populations is fairly narrow (17 km wide).

In areas other than those discussed above, the dewlap of *A. homolechis* is variable in color but this variation appears not to be correlated with geography in any reason-

able manner. Ruibal and Williams (1961: 232) pointed out that "the dewlap may be pure white or there may be two or three grey stripes on a white background . . . Both these types show no systematic geographical distribution and may actually be found in the same population." Thus, specimens of *A. homolechis* from extreme western Cuba in the area of sympatry with *A. quadriocellifer* and extreme eastern Cuba on the southern Oriente coast at Laguna de Baconao, as well as material from the Isla de Pinos, all appear to be identical in having the dewlaps white or gray, and not yellow.

As Ruibal and Williams (1961:232) pointed out, those populations which both they and I refer to as having yellow dewlaps are not identical insofar as pigmentation and or pattern of the dewlap is concerned. They stated that the Sierra de Cubitas lizards have a yellow dewlap with a broad white margin, whereas the Playa Santa Lucía males have the dewlap a deeper yellow or orange color with a narrow white margin and one or two stripes of white or light yellow. My notes on lizards from these two localities agree quite well with their comments. Specimens from 2 km SE Banao (AMNH 83181) were recorded as having the dewlap yellow (PL. 9 L 7) with a white margin and a fairly extensive white basal area anteriorly. Males from Los Ballenatos (AMNH 83176) were recorded as having the same yellow or pale orange shade. Verbal descriptions of dewlaps of *homolechis* from the Sierra de Cubitas area include yellow and dull orange, whereas specimens from Playa Santa Lucía were yellow to orange, with occasional specimens rather yellowish tan (= mustard). On Los Ballenatos the dewlaps were yellow and orange, and on Cayo Sabinal yellow.

The southern Oriente coastal population in general has the dewlap deeper or brighter orange, with colors near Pl. 10 F 1. Even in this lot of specimens there is some variation since some individuals were reported to have the dewlap yellow. The distinctly pale yellow dewlaps of lizards from east of the Bahía de Guantánamo to the mouth of the Río Yumurí has been previously noted.

Complete complements of scale counts were taken on 844 *A. homolechis* from throughout the range of the species, in-

cluding both white and yellow dewlapped populations. The samples and their sizes are as follows: 1) Península de Guanahacabibes (area of sympatry between *A. homolechis* and *A. quadriocellifer*)—31; 2) Pinar del Río Province—122; 3) Isla de Pinos—61; 4) Habana-Matanzas-Las Villas provinces—34; 5) Camagüey—96; 6) Sierra de Cubitas and associated lowlands (yellow dewlap)—68; 7) Playa Santa Lucía (yellow dewlap)—84; 8) Los Ballenatos (yellow dewlap)—15; 9) Cayo Sabinal (yellow dewlap)—9; 10) Oriente (white dewlap) except specimens from coast between Playa Juraguá and Bahía de Guantánamo—122; 11) Oriente coast (white dewlap) between Playa Juraguá and Caimanera—16; 12) Oriente coast (yellow dewlap) between Cabo Cruz and Playa Juraguá—65; 13) Oriente coast (white to pale yellow dewlap) between Bahía de Guantánamo and Río Yumurí—121.

Without discriminating between locality or region, the total variation in *A. homolechis* in the scale data I have taken from throughout its range may be summarized as follows: snout scales between first canthals 4-9, supraorbital semicircles separated by one scale or in contact (depending on population), scales between supraorbital semicircles and interparietal usually 2-2 or 3-3, fourth toe lamellae 14-22, postmentals 1-7, loreals 12-41. The supracarpal scales are either smooth or with a single median, rather inconspicuous, keel. The largest male has a snout-vent length of 62 mm and is from Los Ballenatos, whereas the largest females have snout-vent lengths of 46 mm and are from Pinar del Río and Oriente provinces. In many samples there are very few to no females, and in others (from areas where both white and yellow dewlapped populations occur together or in close juxtaposition) I have not utilized data from females since they are not assignable to either population with certainty. Considering the robust size of males from Los Ballenatos I suspect that females (at present unrepresented) from these islets will be found to exceed even the largest females noted above. Variation in the listed scale characters and size can be seen in Table 1, but further limited discussion is offered below.

1) *Size*. The largest male *A. homolechis*

from Los Ballenatos is no unusually large giant. Eight of 15 males from Los Ballenatos have snout-vent lengths in excess of 58 mm, for instance, and six males have snout-vent lengths of 60 mm or greater; 60 mm is the largest size (specimen from the Guantánamo-Yumurí sample) recorded for any non-Ballenatos male. Males with snout-vent lengths of 58 mm (the next largest maximum) are included in the samples from Guanahacabibes, Habana-Matanzas-Las Villas, and Playa Santa Lucía. These localities include both white and yellow dewlapped populations. The smallest maximally sized males (snout-vent lengths 52 mm) are from Cayo Sabinal (yellow dewlaps). Camagüey (white dewlaps) and Sierra de Cubitas (yellow dewlaps) have maximally sized males with snout-vent lengths of 53 and 54 mm respectively.

The largest females are from Pinar del Río and Oriente provinces. Smallest maximally sized females (40 and 41 mm) occur in the samples from Guanahacabibes, Sierra de Cubitas, and Playa Santa Lucía.

Isla de Pinos material of both sexes is comparable in size to that of western Cuba, although Isla de Pinos females are not known to reach quite the large size of Pinar del Río females.

2) *Snout scales between first canthals.* The highest mean for snout scales (7.1) is that already mentioned for the series of *A. homolechis* from the area of sympatry with *A. quadriocellifer*. The lowest mean (5.3) is for the Guantánamo-Yumurí sample (white to pale yellow dewlaps). Most samples have ranges of 5 to 8 scales, but counts of 4 occur in two samples and 9 in four. The mode of snout scales is usually 6 (eight samples), but modes of 7 (two samples: Guanahacabibes, Cayo Sabinal with a weak mode) and 5 (one sample: Guantánamo-Yumurí, with a very strong mode of 5) also occur. The series from Los Ballenatos has no mode, with equal frequencies (four specimens) for counts of 5, 6, and 7; the Camagüey (white dewlaps) sample is bimodal, with 30 specimens each having counts of 5 and 6.

3) *Scales between supraorbital semicircles.* Of the 13 samples, nine modally have 1 scale between the semicircles and four have modes of 0 (semicircles in contact) scales between the semicircles. The four series with

the semicircles in contact are Playa Santa Lucía (yellow dewlap), Los Ballenatos (yellow dewlap), Cayo Sabinal (yellow dewlap), and southern Oriente coast (yellow dewlap). Of the yellow dewlapped samples, only that from the Sierra de Cubitas modally has 1 row of scales between the semicircles. The white to pale yellow dewlapped sample from extreme eastern Oriente (Guantánamo-Yumurí) also modally has 1 row of scales between the semicircles.

When the modal condition is 1 scale between the semicircles, very few or no specimens have the semicircles in contact; thus, no Isla de Pinos *homolechis* (61 specimens) has the semicircles in contact, only two of 105 Pinar del Río lizards have them in contact, and eight of 116 Oriente (white dewlapped) have these elements in contact. The only serious contradiction to this statement is the series of white to pale yellow dewlapped lizards from the eastern Oriente coast, where 43 of 119 specimens have the semicircles in contact (the series modally has 1 scale between the semicircles).

The reverse of the above statement is also true; if the series modally has the semicircles in contact, few specimens have the semicircles separated by 1 row of scales. This is most obvious in the Cabo Cruz-Playa Juraguá (yellow dewlap) sample where of 42 lizards whose dewlap color was definitely noted in life, only 12 have the semicircles not in contact. The weakest contact modes are those from Los Ballenatos and Cayo Sabinal, but the samples in both cases are small (15 and nine specimens). Additionally, when the Ballenatos sample is broken down by islands, all specimens (3) from Ballenato del Medio have the semicircles separated whereas all but two from the small Ballenato have the semicircles in contact.

Occasional specimens have the semicircles separated by 2 scales: 41 lizards of all examined have this condition. Two scales occur in nine samples, with the highest frequency (13.3 percent) in the Habana-Matanzas-Las Villas specimens and the lowest (1.5 percent) in the Sierra de Cubitas sample. Interestingly, 2 scales as a minor variant are not known from the yellow dewlapped populations associated with the Bahía de Nuevitas (Playa Santa Lucía, Cayo Sabinal, Los Ballenatos—a total of 108 lizards).

4) *Scales between supraorbital semicircles and interparietal*. The modal condition of 3/3 scales between the semicircles and the interparietal occurs in eight of the 13 samples. Samples with 2/2 scales as the mode are Playa Santa Lucía (yellow dewlap), Los Ballenatos (yellow dewlap), south Oriente coast between Cabo Cruz and Santiago (yellow dewlap), extreme eastern Oriente (white to pale yellow dewlap), and southern Oriente coast between Playa Juraguá and Caímanera (white dewlap). Noteworthy are the 3/3 mode on Cayo Sabinal (in contrast to 2/2 on Los Ballenatos), the weak 2/2 mode at Playa Santa Lucía (28 specimens with 2/2, 23 with 3/3), the 3/3 mode in the Sierra de Cubitas, and the strong mode of 2/2 in the Cabo Cruz-Playa Juraguá sample (when annotated specimens alone are considered).

Total variation for the entire lot of *A. homolechis* in scales between the semicircles and the interparietal varies from 1/1 (three specimens from three samples) to 6/6 (one specimen from Oriente). Combinations other than 2/2 or 3/3 are minor variants in most large samples, with most lots having six combinations. Least variation is shown in the material from Los Ballenatos and Cayo Sabinal, but in both cases the samples are small; at Los Ballenatos, only two categories (2/2, the mode, and 2/3) were encountered whereas on Cayo Sabinal there are three categories (2/2, 2/3, and 3/3, the mode).

5) *Fourth toe lamellae*. Means of fourth toe lamellae vary from 16.9 (Oriente coast, white to pale yellow dewlap) to 19.4 (Habana-Matanzas-Las Villas). There is no clear-cut trend from west to east but high means (19.1) occur on Los Ballenatos and Cayo Sabinal, whereas adjacent Playa Santa Lucía has a lower mean of 18.2. The modal number of fourth toe lamellae varies from 16 (Oriente coast, yellow dewlap) to 19 (Isla de Pinos, Camagüey white dewlap, Los Ballenatos).

6) *Postmental scales*. Means vary from 3.0 (Camagüey) to 5.2 (Los Ballenatos), with Playa Santa Lucía and Cayo Sabinal having means of 4.9 and 5.0. The three samples from the Bahía de Nuevitas area (Los Ballenatos, Playa Santa Lucía, Cayo Sabinal) stand out strongly as a group with their high mean number of postmentals; the next highest mean is 4.0 in the Sierra

de Cubitas. Modal numbers of postmentals vary between 3 (Habana-Matanzas-Las Villas, Camagüey) to 6 (Los Ballenatos and one of two bimodes on Cayo Sabinal).

7) *Loreals*. Mean number of loreals varies from 20.9 (Los Ballenatos) to 27.9 (Playa Santa Lucía). The next lowest mean (27.1) is for Cayo Sabinal lizards, adjacent to Playa Santa Lucía.

8) *Supracarpal keeling*. The modal condition in 11 samples is absence of keeling, and the supracarpal scales are smooth. Occurrence of a fairly prominent keel has already been pointed out for some Guanahacabibes and Pinar del Río lizards; two lizards from Camagüey, five from Oriente, two from Oriente south coast yellow dewlapped, and one from extreme eastern Oriente were recorded as having fairly prominent keels. The general Oriente sample has the highest incidence of weak keels (39 of 119 lizards).

9) *Keeling of female head scales*. Head scales of female *A. homolechis* are multicarinate in contrast to the much smoother and unicarinate scales of males. A major exception to this statement are Isla de Pinos females. In these specimens the head keels are much lower and much more like the male condition. In most cases, confirmation of sex of specimens can be easily had by checking the carination of the head scales; in the Isla de Pinos series this is not true and reliance must be placed on the presence or absence of enlarged postanal scales and the well developed dewlap in males, rather than on the lack of head carination in males and its presence in females.

Nomenclatural Arrangement

From the above discussion it is evident that there are several populations of *A. homolechis* which characteristically have colored (in contrast to white or gray) dewlaps and which additionally are distinguishable from the basic *A. homolechis* stock in certain head scale numbers and arrangements, as well as size. These populations occupy compact and meaningful ranges. There is no doubt that these populations are definable and that their nomenclatural recognition adds to our knowledge of the variation, evolution, and zoogeography of the Cuban anoles.

On the other hand, the situation outlined

by Ruibal and Williams at Playa Santa Lucía still seems to pertain for two of these populations: (1) white and yellow dewlapped specimens occur together or very close to one another in some localities, (2) generally no orthodox intergradation is known between lizards with white or yellow dewlaps, and (3) under more ordinary circumstances one might with justification regard the white and yellow dewlapped populations as comprising two species which are virtually allopatric but which on occasion are sympatric. I cannot of course completely refute this latter possibility: white and yellow dewlapped individuals may well represent two full species—there is no evidence to contradict this suggestion. On the other hand, in habits, habitat, physiology (Ruibal, 1961, compared the temperature reactions of both white and yellow specimens without finding striking differences), gross aspect, size, and all such attributes, the white and yellow dewlapped lizards seem either identical or very close to one another. Another possibility is that there are two species involved, and that dewlap color is geographically variable (white, grey or yellow) in one (*A. bomolechis*) and regularly yellow to orange in the other. Either of these two postulates is extremely difficult to affirm or deny on the basis of the material or data presently at hand. It seems far better, given what information is available, to regard both white and yellow dewlaps as part of the variation of *A. bomolechis* and to search elsewhere for explanations of the peculiarity of sympatric occurrence of lizards having both sorts of dewlaps in certain areas.

In the following discussion I have deliberately left unassigned lizards from Banes, since fresh and annotated material from there is not available. Specimens from Banes will be discussed below.

Ahl (1924, 1925) named five species of *Anolis* from "Cuba," based on material collected by Gundlach. The names proposed are: *muelleri*, *abatus*, *calliurus*, *mertensi*, and *cubanus*. Through the courtesy of Dr. Günther Peters and the cooperation of Dr. Ernest Williams, I have been able to examine the type material of four of these five species; the Ahl names deserve special consideration in the present context, since Ruibal and Williams (1961:228) assigned *calliurus*,

muelleri and *cubanus* to the synonymy of *A. bomolechis*, and *abatus* to *A. allogus*. (The holotype of *A. mertensi*—BM 27811—is a specimen of *A. lucius* Duméril and Bibron and need not concern us further.) Data on the holotypes of the three Ahl species are: *cubanus* (BM 27810), male, snout-vent length 55 mm, 6 scales between first canthals, one scale between semicircles, 3 3 scales between semicircles and interparietal, 4 postmentals, loreals 25, 17 fourth toe lamellae, 1 1 prenasals, ventrals smooth, brachials keeled, supracarpals weakly keeled; *calliurus* (BM 9074), male, snout-vent length 53 mm, 6 scales between first canthals, one scale between semicircles, 3 3 scales between semicircles and interparietal, 4 postmentals, 28 loreals, 18 fourth toe lamellae, 1 1 prenasals, ventrals smooth, brachials keeled, supracarpals weakly keeled; *muelleri* (BM 4179), female, snout-vent length 44 mm, 6 scales between first canthals, 1 scale between semicircles, 3 3 scales between semicircles and interparietal, 2 postmentals, 23 loreals, 15 fourth toe lamellae, 1 1 prenasals, ventrals smooth, brachials keeled, supracarpals smooth.

I agree that *cubanus*, *calliurus*, and *muelleri* are all junior synonyms of *A. bomolechis*, and as far as I can ascertain (there are of course no data on these specimens in life so that dewlap colors remain unknown) none of the three names is applicable to any of the yellow dewlapped populations described below. The single scale between the supraorbital semicircles suggests strongly that *cubanus*, *calliurus*, and *muelleri* are synonyms of *A. b. bomolechis* (the subspecies which regularly has 1 scale between the semicircles).

A fourth name, *patricius* Barbour, was based on material from Mina Piloto, municipio of Sagua de Tánamo, Oriente Province. Ruibal and Williams (1961:230) have disposed of this name (the precise type locality cannot now be found on any current map of Cuba¹) as a synonym of *A.*

¹In an effort to locate Mina Piloto, I have corresponded with Dr. Gerardo Canet. The following information is pertinent. Marie-Victorin and Léon (1956:13) presented a detailed sketch map of the topographic features of the Sierra de Nipe and adjacent regions in northern Oriente Province. They showed a Río Piloto, draining the eastern slope of the Sierra de Nipe and emptying into the Río Mayari. The

homolechis, since specimens of the species from the towns of Sagua de Tánamo and Cananova are white dewlapped. I have examined the holotype and paratypes of *A. patricius* and agree with Ruibal and Williams that *patricius* Barbour is a synonym of *A. homolechis*; the paratypes of *patricius* include a single presumed *A. rubribarbus*.

Anolis homolechis homolechis Cope

Xiphosurus homolechis Cope, 1864, Proc. Acad. Nat. Sci. Philadelphia, p. 169 (type locality—unknown; restricted to La Habana, Habana Province, Cuba—Ruibal and Williams, 1961:228).

Anolis calliurus Ahl, 1924, Zool. Anz., 62: 249 (type locality—Cuba).

Anolis muelleri Ahl, 1924, Zool. Anz., 62: 247 (type locality—Cuba).

Anolis cubanus Ahl, 1925, Zool. Archiv. f. Naturgesch., 90:87 (type locality—Cuba).

Anolis patricius Barbour, 1929, Proc. New England Zool. Club, 11:37 (type locality—Mina Piloto, district of Sagua de Tánamo, Oriente Province, Cuba).

Definition: A subspecies of *A. homolechis* characterized by a combination of moderate size (males to 58 mm snout-vent length, females to 46 mm), dewlap white to gray (Pl. 1, upper right) or combining these two colors, supraorbital semicircles usually separated by 1 row of scales, 3 3 scales between the supraorbital semicircles

Sierra de Nipe has long been a center for mining activities (iron and nickel; Marrero, 1951: 634); the first iron mine in this region was begun in 1909. At the time of the visit of Marie-Victorin and Léon in 1940, mining was active in this region; nickel mining ceased about 1947 (Marrero, *loc. cit.*). The concordance of the names Mina Piloto and Río Piloto seems too much to be attributed to chance, and it seems very likely that the Mina Piloto was situated on or near the Río Piloto on the eastern flank of the Sierra de Nipe. However, the Sierra de Nipe region is presently in the municipio of Mayari, not of Sagua de Tánamo; Mina Piloto was said to be in the latter municipio. Dr. Canet advised me (*in litt.*, 19 May 1967) that the municipios of Mayari and Sagua de Tánamo were separated from one another at about the turn of the century, and that it seemed correct to assume that there has been some error in municipio designation on Ramsden's part at the time the specimens were sent to Thomas Barbour at Harvard University. Although the evidence is not incontrovertible, it seems highly probable that Mina Piloto, municipio of Mayari, is the proper designation of the type locality of *Anolis patricius*.

and the interparietal scale, postmentals averaging few (means by populations 3.0-3.3) and modally 4 in number, and locals moderate in number (means 22.5-26.4).

Distribution: Throughout much of Cuba and the Isla de Pinos, with the exception of the distribution of the following subspecies.

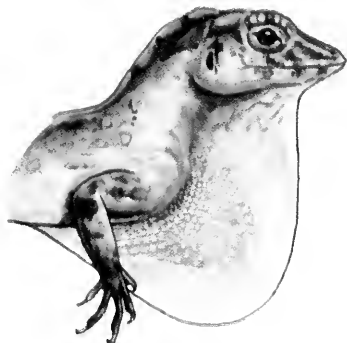
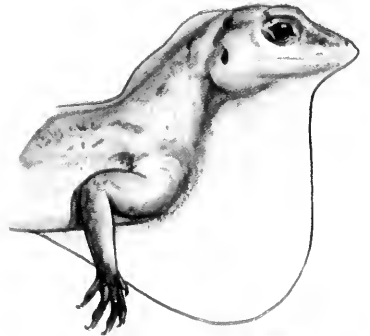
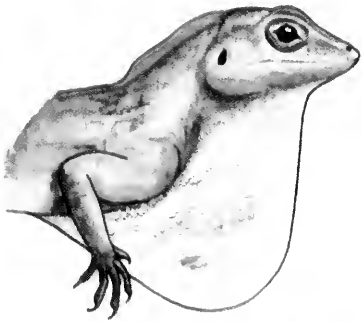
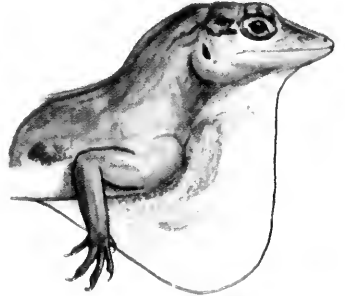
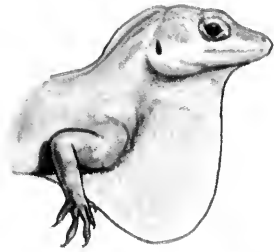
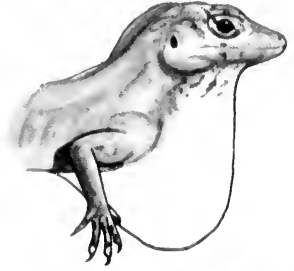
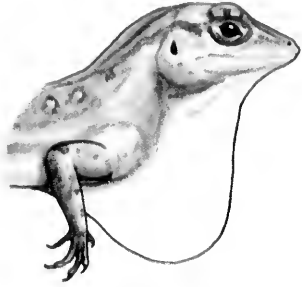
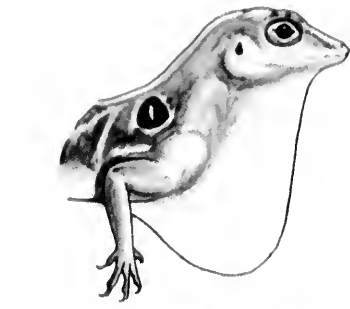
Comments: I have grouped together as *A. h. homolechis* all samples which have white, gray, or white and gray dewlaps. Considering the widespread distribution of this subspecies, there is remarkable agreement in scutellation between specimens from western Pinar del Río Province and lizards from Oriente. The only scale character which does not seem to vary is the number of scales across the snout at the level of the first canthal; consequently it has not been employed in the subspecies definitions. Differences in the carination of the head scales of Isla de Pinos females from Cuban females have been noted above; there is a possibility that the Isla de Pinos *A. homolechis* should be nomenclaturally recognized as distinct from their Cuban relatives, but aside from the peculiarity of the female head scales I can detect no other differences. Specimens of *A. homolechis* with white to gray dewlaps from areas of sympatry or near-sympatry with the yellow dewlapped subspecies will be discussed in detail in the cases where this phenomenon occurs.

Specimens examined: Cuba, Pinar del Río Province, 3 km W Bartoli sawmill village (= La Majagua), 10 km SW Cayuco, 18 (AMNH 83182—9 specimens; AMNH 83184—9 specimens); Valle de San Juan, 4 (AMNH 96528); 8.2 mi. (13.1 km) W Cayuco, 6 (AMNH 96525); 6.9 mi. (11 km) W Cayuco, 3 (AMNH 96524); 2.9 mi. (4.6 km) E Isabel Rubio, 8 (AMNH 79674-81); 7.6 mi. (12.2 km) E Isabel Rubio, 5 (AMNH 79669-73); Cueva de Santo Tomás, 10 km N Cabezas, 1 (AMNH 79661); 0.4 mi. (0.6 km) NE Cabezas, 1 (AMNH 79666); San Vicente, 62 (AMNH 76496, AMNH 79498-502, AMNH 76505, AMNH 79651, AMNH 79658-60, AMNH 79682-722, AMNH 83164, AMNH 83059—4 specimens, AMNH 83060—2 specimens, AMNH 83063—3 specimens); mountains NW San Vicente, 5 (AMNH 76497, AMNH 76506-09); mountains near San Vicente (not mapped), 2 (AMNH 76503-04); mountains N San Vicente, 1

(AMNH 79655); 1 mi. (1.6 km) S San Vicente (not mapped), 1 (AMNH 79656); San Vicente, Cueva de los Indios (not mapped), 3 (AMNH 79652-54); San Vicente, cliffs at Cueva del Río (not mapped), 1 (AMNH 79657); 8.4 mi. (13.4 km) W San Vicente, 1 (AMNH 83061); 1 km NW La Coloma, 1 (AMNH 76662); 1 km N La Coloma, 2 (AMNH 96541); south base, Pan de Guajaibón, 3 km W, 13.5 km S Las Pozas, 7 (AMNH 83064); Rancho Mundito, 3 (AMNH 83062); Rangel, 6 (AMNH 83065); Soroa, 2 (AMNH 79667-68); 8.5 mi. (13.6 km) SE Cabañas, 8 (AMNH 79643-50); 10 km NE Cabañas, finca de la viuda Casanova, 2 (AMNH 79723-24); *Habana Prov.*, 2 mi. (3.2 km) E Playa de Guanabo, Cueva de Rincón de Guanabo, 6 (AMNH 79663-65, AMNH 79725-27); 9 km SW San José de las Lajas, 1 (AMNH 79642); *Matanzas Prov.*, Alacranes, 3 (INHS 2625); 5.5 mi. (8.8 km) NE Canasí, 8 (AMNH 83049); Pan de Matanzas, 2.5 mi. (4.1 km) S Corral Nuevo, 5 (AMNH 83051); 6 km NE Matanzas, 1 (AMNH 83050); 8.9 mi. (14.2 km) NE Varadero, 3 (AMNH 96542); *Las Villas Prov.*, Salto de Hanabanilla, 3 (AMNH 79585-87); 8 mi. (12.8 km) S Manicaragua, 1 (AMNH 79589); 5 mi. (8 km) S Topes de Collantes, 1 (AMNH 79894); 4 km W, 8 km N Trinidad, 1 (AMNH 79588); San José del Lago, 2 (AMNH 79590-91); Cayo Bahía de Cádiz, 1 (AMNH 83053); *Camagüey Prov.*, 0.6 mi. (0.9 km) W Majagua, Río Majagua, 7 (AMNH 79619-25); Loma de Cunagua, 12 mi. (19.2 km) E Morón, 27 (AMNH 79592-618); Loma de Cunagua, 14 mi. (22.4 km) E Morón, 5 (AMNH 79626-30); Loma de Cunagua, 2 (MCZ 50162-63); ca. 15 km SW Vertientes, 4 (MCZ 63872-75); 24 km SW Camagüey, Finca El Porvenir, Loma de la Yagua, 2 (AMNH 79631-32); Cuatro Caminos, 1 (UMMZ 70993); Martí, 2 (UMMZ 70995-96); *Oriente Prov.*, Finca Búcares, 22 km S Bucycito, 1 (AS 450); 14.6 mi. (23.4 km) SW Maffo, 4 (AMNH 96544); La Cantera, Miranda, 6 (AMNH 83728—4 specimens, AMNH 83729, AMNH 83731); Cayo del Rey, Miranda, 2 (AMNH 83730); Florida Blanca, near Alto Songo, 1 (INHS 9254); 6.5 km S Palma Soriano, 3 (AMNH 83716); Santiago de Cuba, 1 (MCZ 6923); 6 mi. (9.6 km) E La Maya, 14 (AMNH 83718); 1.9 mi. (3.0 km) SE, 3 mi. (4.8 km) NE Sevilla, 1 (AMNH 96543); Gran Piedra, La Isabelica, 3500 feet (1068 meters), 1.9 mi. (3 km) SE, 10 mi. (16 km) NE Sevilla, 8 (AMNH 83724—7 specimens, AMNH 83727); La Favorita, 3 km E Gran Piedra, 3 (AMNH 96545); Playa Juraguá, 3.7 mi. (5.9 km) E Siboney, 4 (AMNH 83720); 9.1 mi. (14.6 km) E Siboney, 5 (AMNH 83725); Laguna de Baconao, 21.8 mi. (34.9 km) E Siboney, 4 (AMNH 83733); 2 mi. (3.2 km) N Caimanera, 1 (AMNH 83741); Caimanera, 1 (MCZ 59247); Guantánamo, 32 (MCZ 63954-59, MCZ 63961-80, MCZ 63982-85, MCZ 63987-88); 8 mi. (12.8 km) NE Felicidad, 1 (AMNH 83742); west slope, El Yunque de Baracoa, 9 (AMNH 83734); 9 km W, 1 km S Baracoa, 1 (AMNH 83735); Bahía de Taco, 20 (AMNH 83743—14 specimens, AMNH 83744—6 specimens); 3 mi. (4.8 km) S Bahía de Taco, 3 (AMNH 83745); Cayo Grande de Moa, 2 (USNM 80413-14); Puerto Moa, 2 mi. (3.2 km) up Río Moa, 1 (USNM 80408); Mina Piloro, Sagua de Tánamo, 10 (MCZ 28759, MCZ 28768-75, UMMZ 71409— one of two specimens with this number; holotype and paratypes of "*A. patricius*"); Preston, 1 (UMMZ 98015); *Isla de Pinos (Habana Prov.)*, Sierra de Casas, just W Nueva Gerona, 23 (AMNH 79561-83); east base, Sierra de Casas, just W Nueva Gerona, 8 (AMNH 83055); Bibijagua, 1 (AMNH 83057); 2 km N Santa Fé, 11

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Pl. 1. Color portraits from life of males of five species of the *homolechis* complex of *Anolis* in Cuba. Upper left, *A. quadriocellifer*, AMNH 96522, 6.9 mi. W Cayuco, Pinar del Río Province; upper right, *Anolis homolechis homolechis*, San Vicente, Pinar del Río Province; second row, left, *Anolis homolechis jubar*, Paso de la Trinchera, Camagüey Province; second row, right, *Anolis homolechis oriens*, Cabo Cruz, Oriente Province; third row, left, *Anolis homolechis* subsp., Baitiquiri, Oriente Province; third row, right, *Anolis mestrei*, AMNH 95977, San Vicente, Pinar del Río Province; fourth row, left, *Anolis allogus*, San Vicente, Pinar del Río Province; fourth row, right, *Anolis allogus*, Los Paredones, Camagüey Province; lower left, *Anolis allogus*, AMNH 96563, La Favorita, 3 km E Gran Piedra, Oriente Province; lower right, *Anolis ahli*, AMNH 96568, 1.1 mi. NE San Blas, Las Villas Province.



(AMNH 79543-53); Paso de Piedras, ca. 20 km SSW Santa Fé, 8 (AMNH 79554-60, AMNH 83054); Puerto Francés, 1 (AMNH 79584); Jacksonville, 5 (AMNH 83056); Punta del Este, 1 (AMNH 83058).

Anolis homolechis jubar, new subspecies

Holotype: AMNH 96529, an adult male, from Paso de la Trinchera, Sierra de Cubitas, Camagüey Province, Cuba, one of a series taken 16 July 1960 by Ronald F. Klinikowski and David C. Leber. Original number 9357.

Paratypes (all from Camagüey Province, Cuba): AMNH 96530 (17 specimens), same data as holotype; AMNH 83708, Los Paredones, Sierra de Cubitas, 27 June 1959, R. F. Klinikowski, A. Schwartz, B. L. Smith; AMNH 83178, 5.5 mi. (8.8 km) NE Banao, 15 August 1957, J. R. Feick, W. H. Gehrmann, Jr.; AMNH 83179, 5.5 mi. NE Banao, 14 August 1957, native collector; AMNH 83180 (2 specimens), 5.5 mi. NE Banao, 17 August 1957, native collector; AMNH 83181 (5 specimens), 2 km SE Banao, 18 August 1957, J. R. Feick; AMNH 96531 (5 specimens), 11.9 mi. (19 km) NW Banao, 4 August 1960, D. C. Leber; MCZ 21049, Sierra de Cubitas, no date, C. de la Torre; MCZ 63991, Sierra de Cubitas, nr. Banao, July 1957, R. Molina, R. Ruibal; MCZ 63994-98, Sierra de Cubitas, nr. Banao, 1 August 1957, R. Molina, R. Ruibal; MCZ 64000-01, Sierra de Cubitas, south of Jaronú, 22 August 1958, R. Molina, R. Ruibal; MCZ 64005-10, Sierra de Cubitas, south of Jaronú, no date, R. Molina, R. Ruibal; MCZ 64011-12, Paso de Lesca, Sierra de Cubitas, no date, R. Molina, R. Ruibal; MCZ 64013-16, Los Paredones, 21 August 1959, R. Ruibal; MCZ 64088, Río Jigüey, between Esmeralda and Jaronú, R. Molina, R. Ruibal, 1 August 1957; MCZ 67986-91, Sierra de Cubitas, nr. Banao, no date, R. Ruibal; MCZ 74028-32, near Cueva del Indio, Paso de Lesca, 3 November 1959, R. Molina, R. Ruibal, E. E. Williams.

Definition: A subspecies of *A. homolechis* characterized by a combination of small size (males to 54 mm snout-vent length, females to 40 mm), dewlap yellow to very pale orange with a broad white to very pale yellow margin (Pl. 1, second row, left), supra-orbital semicircles usually separated by one row of scales, 3-3 scales between the supra-

orbital semicircles and the interparietal scale, postmental mean moderate (4.0) and modally 4, and loreal mean moderate (24.6).

Distribution: The Sierra de Cubitas and associated lowlands to the north, as well as marginal forested lowlands to the south, Camagüey Province, Cuba (Fig. 3).

Description of holotype: An adult male with snout-vent length of 51 mm; snout scales between first canthals 5, supraorbital semicircles separated by one scale, 3-4 scales between semicircles and interparietal, 16 fourth toe lamellae, 5 postmentals, 23 loreals.

Comments: Of the yellow dewlapped subspecies, *A. b. jubar* is closest in scutellation to *A. b. homolechis*. It differs from that race in the dewlap color (which varies from yellow with a broad white margin to pale orange with a broad yellow margin), colors which are not known to occur in *A. b. homolechis*. The difference in size between *homolechis* and *jubar* is not particularly striking, but male *jubar* are noticeably smaller and less bulky than male *homolechis*. The postmental mean (4.0) is higher than that of any of the populations with white dewlaps which I assign to the nominate form.

The Sierra de Cubitas is a limestone massif, about 50 km in length, near the northern coast of Camagüey Province. To the south it abuts directly on the serpentine savannas (part of the Camagüey-Tunas-Holguín Peneplane) which extend thence for a distance of about 35 km southward to the city of Camagüey. The Sierra de Cubitas is presently covered with moderately dense hardwood forest. Three major passes cross the range—the Paso de la Trinchera, Los Paredones, and Paso de Lesca. To the north of the Sierra de Cubitas lies a low plain, presumably primitively well forested but now primarily denuded and cultivated except for some excellent and extensive stands of hardwoods (such as at the locality 11.9 mi. NW of Banao). These northern non-montane forests are inhabited by *A. b. jubar*. Some suitable forested situations to the south of the sierra are peripheral to the range itself and separated from it by savanna; specimens from 2 km SE Banao are from such a marginal situation—a local shaded stand of coffee and shade trees along a stream margin. The serpentine sa-

vannas themselves offer little haven for a shade-requiring anole as *A. homolechis*. The serpentine savannas are generally bare or support low herbaceous and shrubby growth; on the low gravelly hills occur open stands of small palms and moderately sized shrubs which supply little shade.

Although one tends to think of some widely distributed anoles (such as *A. sagrei* and *A. homolechis*) as occurring from one end of Cuba to the other (and in a gross sense this is true), it seems probable that there are areas whence these species are absent. *A. sagrei*, for instance, has not been collected on much of the Peninsula de Guanahacabibes nor did I observe or collect this species along the northern coast of Oriente Province between the Río Yumurí and Bahía de Taco. It seems probable that *A. b. jubar* is effectively cut off from *A. b. homolechis* to the south by the open serpentine savannas. Possibly the same situation exists to the west of the Sierra de Cubitas, but I am not familiar with the details of geography in that region. To the east, *A. b. jubar* presumably approaches the mainland yellow dewlapped subspecies about the Bahía de Nuevitas, as Ruibal and Williams (1961:232) suggested.

The subspecific name *jubar* is derived from the Latin for "light of the sun," a reference to the dewlap color of the Sierra de Cubitas subspecies.

Anolis homolechis cuneus, new subspecies

Holotype: AMNH 96536, an adult male, from 1 mi. (1.6 km) E Playa Santa Lucía, Camagüey Province, Cuba, one of a series taken 26 July 1960 by David C. Leber and Albert Schwartz. Original number 9503.

Paratypes (all from Camagüey Province, Cuba): AMNH 96535 (11 specimens), same data as holotype; AMNH 96538 (23 specimens), 2 mi. (3.2 km) W Playa Santa Lucía, 27 July 1960, R. F. Klinikowski, J. D. Smallwood, Jr.; AMNH 96533 (9 specimens), 3 mi. (4.8 km) W Playa Santa Lucía, 27 July 1960, R. F. Klinikowski, J. D. Smallwood, Jr.; AMNH 96534 (4 specimens), 0.5 mi. (0.8 km) S Punta Prácticos, 29 July 1960, D. C. Leber, A. Schwartz; AMNH 83709 (2 specimens), Playa Santa Lucía, 29 June 1959, R. F. Klinikowski; AMNH 83710 (6 specimens), Playa Santa Lucía, 30 June 1959, R. F. Klinikowski, B.

L. Smith; MCZ 64017-20, Playa Santa Lucía, 21 August 1957, R. Molina, E. E. Williams, R. Ruibal; MCZ 64021-26, Playa Santa Lucía, 24 August 1957, R. Molina, E. E. Williams, R. Ruibal.

Definition: A subspecies of *A. homolechis* characterized by a combination of moderate size (males to 58 mm snout-vent length, females to 41 mm), dewlap yellow with three whitish transverse bars, supra-orbital semicircles usually in contact, 2/2 scales (3/3 modal on Cayo Sabinal) between the supraorbital semicircles and the interparietal scale, postmental mean high (4.9) and modally 5 scales, and loreals numerous (means 27.9 on the mainland, 27.1 on Cayo Sabinal).

Distribution: Known only from the vicinity of Playa Santa Lucía on the north coast of Camagüey Province and adjacent Cayo Sabinal, near the Camagüey-Oriente border, Cuba (Fig. 3).

Description of holotype: An adult male with snout-vent length of 56 mm; snout scales between first canthals 5, supraorbital semicircles in contact, 3/3 scales between semicircles and interparietal, 19 fourth toe lamellae, 6 postmentals, 23 loreals.

Comments: *A. b. cuneus* differs from *A. b. homolechis* in having a basically yellow rather than basically white dewlap. The mean number of postmental scales is 4.9 (mode 5) in *cuneus*, 3.0 to 3.8 in various samples of *homolechis* (mode 4), and *cuneus* has a slightly higher mean number of loreals (27.9) than any population of *homolechis* (22.5-26.4), the highest mean number of loreals in *homolechis* (26.4) being from the Habana-Matanzas-Las Villas sample. *A. b. homolechis* and *A. b. cuneus* are comparable in size of males.

A. b. cuneus differs from *A. b. jubar* to the west in having the dewlap yellow with three white bars rather than a wholly yellow dewlap with an extensive white edge. The major scale difference between the two subspecies is the modal presence of semicircle contact in *cuneus* and its absence in *jubar*. *A. b. cuneus* males reach a larger size than male *A. b. jubar*, and the former subspecies has both a high mean and mode of number of postmental scales and a higher number of loreals.

The Cayo Sabinal series (AMNH 96532—9 specimens; Playa Bonita, west end,

Cayo Sabinal) agrees extremely well with specimens of *A. b. cuneus*. Cayo Sabinal is separated from Punta Prácticos (where *cuneus* occurs) by a narrow channel, 15 fathoms deep, which forms the channel into the pocket harbor of the Bahía de Nuevitas. Although narrow, this channel effectively isolates two subspecies of *Leiocephalus stictigaster* (Schwartz, 1964) but apparently the mainland and cay populations of *A. homolechis* do not differ greatly from one another. The only striking difference is the modality of 2 2 scales between the semicircles and the interparietal on the mainland (28 lizards, but 23 have 3 3 scales); the modality is 3 3 (six of eight lizards) on Cayo Sabinal. If *A. b. cuneus* has but recently invaded Cayo Sabinal, the preponderance of 3 3 scales on the latter island may well be due to the condition of these scales in the founders of the insular population. Since Cayo Sabinal is the easternmost of an 190 km line of large cays off the northern coast of Camagüey Province, it would be most interesting to learn what subspecies (*homolechis*, *jubar*, or *cuneus*) occur on the other cays. Considering that the largest of these cays (Cayo Romano) is more or less attached to the mainland by a narrow isthmus in the region which on the mainland probably supports *A. b. jubar*, one would expect that that subspecies occurs at least on Cayo Romano.

South of Playa Santa Lucía *A. b. cuneus* and *A. b. homolechis* occur together without intergradation, at least in dewlap pigmentation (see previous discussion for details). It is instructive to construct a north-south series in this region, and compare the scutellation of *A. b. cuneus*, *A. homolechis* from the vicinity of overlap between *A. b. cuneus* and white to gray dewlapped specimens, and *A. b. homolechis* from the balance of Camagüey Province. There are 48 specimens of *A. homolechis* with white dewlaps from the Playa Santa Lucía region (localities between 13 and 21 km south of Playa Santa Lucía; see following list of specimens examined), and 47 specimens from elsewhere in Camagüey Province (see list of localities for *A. b. homolechis*).

Two scale characters of the white dewlapped *A. homolechis* from the region of overlap between these lizards and *A. b. cuneus* are extremely interesting. The num-

ber of scales between the semicircles and the interparietal is modally 2 2 in *cuneus* and strongly 3 3 in Camagüeyan *A. b. homolechis* (as is typical for that subspecies). The white dewlapped specimens from the area of overlap resemble *A. b. cuneus* in having 2 2 scales in this position; the mode is very strong (27 lizards have 2 2, only nine have 3 3). In number of postmentals, *A. b. cuneus* varies between 2 and 7, with a mean of 4.9 and a mode of 5; Camagüeyan *A. b. homolechis* have between 2 and 5 postmental scales, with a mean of 3.0 and a mode of 3. The white dewlapped *A. homolechis* from the region of overlap have from 2 to 5 postmentals, with a mean of 3.4 and a mode of 4. The mean of 3.4 postmentals in the overlapping white dewlapped specimens is the highest for any white dewlapped *A. homolechis* with the exception of specimens from the southern Oriente coast (mean 3.6).

As far as semicircle contact is concerned, no white dewlapped specimens from the region of overlap with *cuneus* have these scales in contact; the six Camagüeyan lizards with semicircle contact are from areas removed from the region of overlap (Loma de Cunagua; near Majagua; southwest of Camagüey city). Other scale counts taken show no significant differences between the three samples involved.

In summary, in the Playa Santa Lucía region there are two populations of *A. homolechis*: *A. b. cuneus* with a yellow dewlap with three whitish transverse bars, semicircles in contact, 2 2 scales between the semicircles and the interparietal, and a high mean and mode of postmental scales; and *A. homolechis* with a white dewlap, semicircles separated by one scale, 2 2 scales between the semicircles and the interparietal, and a moderate mean and mode of postmental scales. Of these characters, dewlap color and semicircle contact do not appear to be intermediate between *A. b. cuneus* and *A. b. homolechis* in the balance of Camagüey Province, whereas scales between the semicircles and the interparietal and number of postmentals are variously intermediate between (show characteristics of both) *A. b. cuneus* and *A. b. homolechis* from the rest of Camagüey.

Such a situation suggests that *A. b. cuneus* and *A. b. homolechis* are actually intergradi-

ent in the region of overlap (between 13 km and 17 km S Playa Santa Lucía) despite the apparent dichotomy of dewlap color and semicircle contact. Perhaps there is even intergradation in these two latter characters. Material collected in the area of overlap was assigned to "yellow dewlap" or "white dewlap"; it seems conceivable that within the "yellow dewlap" category were grouped various shades of yellow, some of which may well have been intermediate between the yellow to very pale orange of typical *A. b. cuneus* and the white to gray of *A. b. homolechis*. Consequently, once this basic separation was made, some intergradient specimens may have been grouped with the "yellow dewlapped" population (*cuneus*) since original segregation placed emphasis upon a character which varied almost imperceptibly. A second source of possible error involves the categorizations "semicircles in contact" and "semicircles separated by 1 row of scales." Although these two categories are perfectly valid and easily determinable, it should be noted that "semicircles in contact" embraces a variable amount of contact—from specimens which may have the semicircles barely in contact to those wherein there may be broad contact between the semicircle scales. I have not been able to quantify this feature satisfactorily, but such variability does exist. Consequently, it is possible that some yellow dewlapped specimens from the area of overlap have the semicircles less broadly in contact than material from the immediate environs of Playa Santa Lucía and are thus intermediate in this character between *A. b. cuneus* and *A. b. homolechis*. This much can be stated: of 74 yellow dewlapped specimens from the Playa Santa Lucía region, 36 lizards with semicircle contact are from the beach area itself and 12 are from areas 4.8 to 17 km south of the beach. Of this same lot of 74 lizards, 22 specimens with the semicircles separated by one row of scales are from the beach proper, and four are from the localities south of the beach. These data do not indicate intergradation in this character; of the total beach sample (58 lizards), 36 specimens (66 percent) have the semicircles in contact, whereas of 16 specimens from the area of overlap, 12 (75 percent) have the semicircles in contact. Such higher incidence in the area of

overlap may mean that the semicircle contact is firmly linked with any shade of yellow dewlap; it should be recalled that no white dewlapped lizard from the area of overlap has the semicircles in contact. The situation, at least on the basis of characters I have used, remains anomalous; I have no doubt whatsoever that two forms are involved here, and the evidence indicates that these forms are to be regarded as subspecies. More adequate yellow dewlapped material from the area of intergradation may well clarify the status of the lizards in that zone.

The boundary between *cuneus* and *jubar* to the west remains to be determined. Ruibal and Williams (1961:232) suggested that the two forms might be separated by the savanna extending north to the coast near the Río Máximo. I do not know this region in detail, but the presence of an extensive savanna might well be an effective barrier between *cuneus* and *jubar* just as the plains south of the Sierra de Cubitas isolate *jubar* from *homolechis*.

The subspecific name *cuneus* is Latin for "wedge," an allusion to the interposed position of *A. b. cuneus* between *A. b. jubar* to the west and *A. b. homolechis* to the east.

Specimens examined (other than paratypes of *A. b. cuneus*): *A. b. cuneus* × *A. b. homolechis* (yellow dewlaps): Camagüey Province, 3 mi. (4.8 km) S Playa Santa Lucía, 1 (AMNH 83713); 5 km S Playa Santa Lucía, 1 (MCZ 64027); 7 km S Playa Santa Lucía, 4 (MCZ 64028-31); 6 mi. (9.6 km) S Playa Santa Lucía, 2 (AMNH 96537); 10 km S Playa Santa Lucía, 2 (MCZ 64032-33); 11 km S Playa Santa Lucía, 2 (MCZ 64034-35); 12 km S Playa Santa Lucía, 3 (MCZ 64036-38); 15.2 km S Playa Santa Lucía, 1 (MCZ 64039); 17 km S Playa Santa Lucía, 2 (MCZ 64040-41). *A. b. homolechis* × *A. b. cuneus* (white dewlaps): Camagüey Province, 13 km S Playa Santa Lucía, 2 (MCZ 64042-43); 9 mi. (14.4 km) S Playa Santa Lucía, 1 (AMNH 83711); 15 km S Playa Santa Lucía, 14 (MCZ 64044-57, MCZ 64067); 15.2 km S Playa Santa Lucía, 2 (MCZ 64068-69); 14-20 km S Playa Santa Lucía, 9 (MCZ 64070-78); 17 km S Playa Santa Lucía, 9 (MCZ 64058-66); 20 km S Playa Santa Lucía, 4 (MCZ 64079-82); 13.4 mi. (20.6 km) S Playa

Santa Lucía, 1 (AMNH 83712); 21 km S Playa Santa Lucía, 5 (MCZ 64083-87).

Anolis homolechis balaenarum,
new subspecies

Holotype: AMNH 95975, an adult male, from smallest cay of Los Ballenatos in the Bahía de Nuevitas, Camagüey Province, Cuba, one of a series taken 26 August 1957 by Albert Schwartz and Richard Thomas. Original number 4271.

Paratypes: AMNH 83176 (9 specimens), AMNH 83177, same data as holotype; AMNH 83175 (4 specimens), Ballenato del Medio, Bahía de Nuevitas, Camagüey Province, Cuba, 26 August 1957, R. Thomas.

Definition: A subspecies of *A. homolechis* characterized by a combination of large size (males to 62 mm snout-vent length, females unknown), dewlap yellow to orange without an extensive white border or white transverse bars, supraorbital semicircles usually in contact, 2 2 scales between the supraorbital semicircles and the interparietal scale, postmental mean high (5.2) and modally 6 scales, and loreals few in number (mean 20.9).

Distribution: Known only from two of the three cays known as Los Ballenatos in the Bahía de Nuevitas, Camagüey Province, Cuba (Fig. 3).

Description of holotype: An adult male with snout-vent length of 61 mm; snout scales between first canthals 5, supraorbital semicircles in contact, 2 2 scales between semicircles and interparietal, 19 fourth toe lamellae, 5 postmentals, 16 loreals.

Comments: The three islets known as Los Ballenatos lie in the Bahía de Nuevitas, closest to (2.3 km) Punta Pastelillo. The islands are aligned in a northeast to southwest direction, with the largest (Ballenato Grande) in the northeast, intermediately sized Ballenato del Medio in the center of the line, and a smaller (apparently unnamed) island in the southwest. The two larger islands have elevations of somewhat less than 200 feet (61 meters), whereas the smallest is generally much lower. Richard Thomas and I visited only Ballenato del Medio and the smaller island. The two visited islands were well wooded but *A. homolechis* was not especially abundant. When the first yellow dewlapped male was collected, an effort was made to secure as

many specimens (males) as possible; the resulting series of 15 lizards attests to the scarcity of the form at the time of our visit. Whether *A. b. balaenarum* occurs also on Ballenato Grande remains to be determined.

A. b. balaenarum is the largest subspecies of *A. homolechis*. The bulk and length of the males, and especially their very high tail fins, are strikingly in contrast to the condition in the other subspecies. The dewlap color, varying from bright yellow to orange, without an extensive white border or transverse white bars, likewise differentiates *balaenarum* from the other races. *A. b. balaenarum* resembles *A. b. cuneus* in high mean number of postmentals (5.2 and 4.9), but the former has a higher mode (6) than the latter (5). Of the described subspecies, *balaenarum* has the lowest mean (20.9) of loreal scales (*homolechis* 22.5-26.4; *jubar* 24.6; *cuneus* 27.9). Only *A. b. cuneus* has the semicircles modally in contact as does *A. b. balaenarum*. The two Ballenatos subsamples (11 topotypes; four from Ballenato del Medio) apparently differ in the presence or absence of semicircle contact; this feature is determinable on only three of the Ballenato del Medio lizards (all of which have the semicircles separated by a single row of scales), whereas of the topotypes, only two of 11 lizards have the semicircles separated. The number of scales between the semicircles and the interparietal is determinable on only two of the Ballenato del Medio specimens, one of which has a typical 2 2 count and the other 2 3. Since one of the topotypes also has a count of 2 3, this variant occurs in both populations. Note that no *A. b. balaenarum* has a count of 3 3, the mode in *A. b. jubar* and of fairly high incidence in *A. b. cuneus*, the two adjacent subspecies.

Presumably *A. b. balaenarum* (the name is derived from the Latin *balaena* for "whale") is a derivative of *A. b. cuneus*. The two resemble each other in basic dewlap color (but not in details of dewlap pattern), in high mean number of postmentals, and in having the semicircles usually in contact. They differ in the larger size and higher tail fin of *balaenarum* and in *cuneus* having a higher mean number of loreals. Judging from the small sample available from Ballenato del Medio some differentiation has taken place within these islets but, on the basis of avail-

able material, this differentiation has not progressed to a level which should be recognized nomenclaturally.

Anolis homolechis oriens, new subspecies

Holotype: AMNH 95976, an adult male, from Cabo Cruz, Oriente Province, Cuba, one of a series taken 5 July 1959 by Ronald F. Klinikowski and Albert Schwartz. Original number 7366.

Paratypes (all from Oriente Province, Cuba): AMNH 83715 (4 specimens), same data as holotype; AMNH 83714 (4 specimens), 5 km SW Belie, 5 July 1959, R. F. Klinikowski, B. L. Smith; AMNH 83723 (3 specimens), 20.4 mi. (32.8 km) W Santiago de Cuba, 17 July 1959, R. F. Klinikowski; AMNH 83722, 18.6 mi. (26.4 km) E Santiago de Cuba, 17 July 1959, B. L. Smith; AMNH 83726, 5 km W Aserradero, 24 July 1959, R. F. Klinikowski; AMNH 83717 (3 specimens), Aguadores, 11 July 1959, R. F. Klinikowski, A. Schwartz; AMNH 83719 (3 specimens), Aguadores, 15 July 1959, R. F. Klinikowski, B. L. Smith; AMNH 83732, Aguadores, 1 August 1959, R. F. Klinikowski; AMNH 83721 (2 specimens), Playa Juraguá (Arroyo de la Costa), 3.7 mi. (5.9 km) E Siboney, 16 July 1959, R. F. Klinikowski; AMNH 96539 (2 specimens), Playa Juraguá (Arroyo de la Costa), 22 August 1960, R. F. Klinikowski; AMNH 96540 (3 specimens), Playa Juraguá (Arroyo de la Costa), 24 August 1960, D. C. Leber; USNM 138112-13, Cabo Cruz, 6 September 1956, J. D. Hardy; USNM 81675-77, Río Puercos, 29 August 1930, P. Bartsch, USNM 81685, Punta Hicacos, 30 August 1930, P. Bartsch; USNM 81686, Cabo Cruz, 31 August 1930, P. Bartsch; USNM 138084, Ocuja, 28 August 1956, J. D. Hardy; USNM 138100-109, USNM 138111, Ocuja, 28-31 August 1956, J. D. Hardy; MCZ 42476-79, UMMZ 80771 (4 specimens), coast south of Pico Turquino, June 1936, P. J. Darlington; ASFS V12068-71, IB 1240-42, MFP—3 specimens, between Verreón and Cabo Cruz (not mapped), 14 March 1967, O. H. Garrido, M. L. Jaume.

Definition: A subspecies of *A. homolechis* characterized by a combination of moderate size (males to 56 mm snout-vent length, females to 42 mm), dewlap varying from yellow-orange to deep orange without an

extensive white margin or white transverse bars (Pl. 1, second row, right), supraorbital semicircles usually in contact, 2 2 scales between the supraorbital semicircles and the interparietal scale, postmental mean (3.5) and modally 4 scales, and loreals few in number (mean 22.7).

Distribution: The southern coast of Oriente Province, from the vicinity of Belie and Cabo Cruz east to the Bahía de Santiago (but unknown by specimens from the city of Santiago de Cuba itself) and to the east of the Bahía as far as Arroyo de la Costa (west of Playa Juraguá) (Fig. 3).

Description of holotype: An adult male with snout-vent length of 53 mm; snout scales between first canthals 7, supraorbital semicircles in contact, 2 2 scales between semicircles and interparietal, 16 fourth toe lamellae, 5 postmentals, 21 loreals.

Comments: *A. b. oriens* occupies the southern Oriente coast, primarily in the rain shadow of the high Sierra Maestra, from Cabo Cruz east to the vicinity of the Bahía de Santiago. The subspecies is known also from two localities further east on the coast to the south of the Sierra de la Gran Piedra. These coastal areas are arid; wooded areas are common and forests are open and dry in aspect.

A. b. oriens differs from *A. b. homolechis* in having a yellow-orange to orange dewlap rather than a white or gray dewlap. Likewise, the southern Oriente subspecies differs from the northern Camagüey forms *jubar* and *cuneus* in details of dewlap pattern. Most close to *oriens* in dewlap color is *balaenarum*, which, like *oriens*, has a dewlap variably colored (yellow to orange), but the dewlap colors of *oriens* are brighter (tending more toward shades of orange) than those of *balaenarum*. Of these two subspecies, *balaenarum* is larger (snout-vent length of males to 62 mm) than *oriens* (to 56 mm), and *balaenarum* has a much higher mean (5.2) and mode (6) of postmentals than does *oriens* (mean 3.5, mode 4).

Aside from differences in dewlap color and pattern between *oriens* and *jubar* and *cuneus*, *oriens* differs from these two subspecies in having a lower loreal mean (22.7 versus 24.6 and 27.9), lower mean number of postmentals (3.5 versus 4.0 and 4.9), and from *jubar* in having the supraorbital semicircles in contact, and 2 2 (rather than

3 3) scales between the semicircles and the interparietal.

Since *A. b. oriens* occurs very close (within 1.5 kilometers) to Playa Juraguá, it is pertinent to compare *oriens* specifically with specimens of *A. b. homolechis* from Playa Juraguá east to the Bahía de Guantánamo. In this region, male *homolechis* are slightly larger (snout-vent lengths to 57 mm) than *oriens*, modally have the semicircles separated by one scale, modally have 2 2 scales between the semicircles and the interparietal (although there is a greater incidence of 3 3 scales in the south Oriente *homolechis* sample—25 percent—than in the *oriens* sample—14 percent), the postmental mean is 3.6 and the loreal mean is 26.4. The contact of the semicircles in *oriens* is the opposite of the condition in *homolechis* (separated by one scale) in this region, and the loreals are more numerous in local *homolechis* than in *oriens*. Although the scales between the semicircles and the interparietal are modally 2 2 in these *homolechis* (six individuals), the more usual count of 3 3 occurs in five individuals, a much higher incidence of 3 3 than in *oriens*, where 27 specimens have 2 2 and only seven have 3 3. The postmental mean of 3.6 in the southern *A. b. homolechis* is the highest mean of any sample of that subspecies; it is slightly higher than that of *oriens* (3.5).

These data, which include specimens from the locality of close approximation between *homolechis* and *oriens*, may indicate a degree of intergradation between the two forms along this coast, at least in scale counts. The situation is further complicated by the lizards from between the Bahía de Guantánamo to the Río Yumurí which are discussed below. However, despite certain trends in the *homolechis* populations in this region, there is still a distinct dichotomy in some counts which indicates that *oriens* and *homolechis* maintain their distinctness both at the locality of their approximation and along the coast between Playa Juraguá and the Bahía de Guantánamo.

Although I have included AMNH 83715 (5 km SW Belie) as paratypes of *A. b. oriens*, there is a possibility that this series of three males and one female actually represents a western terminal to an intergradient population between *homolechis* and *oriens*. The dewlaps were recorded in life as being

pale yellow (Pl. 10 F 1), a lighter shade than that recorded for *oriens* elsewhere in its range. For instance, at the type locality (just 13 km from the Belie series) the dewlaps were recorded as orange (Pl. 9 D 12 for the holotype of *oriens*). Specimens from between Verreón and Cabo Cruz, taken in March 1967 and received by me in April, still had the dewlaps distinctly orange; Srs. Garrido and Jaume, who collected these lizards, were impressed by the orange dewlap color in life. I have not collected *A. homolechis* along this western coast of Oriente north of Belie, nor did Ruibal and Williams have color noted specimens from between Belie and Birama, some 130 kilometers airline to the northeast. The Birama material had white dewlaps and is *A. b. homolechis*. Considering the linear coastal range of *A. b. oriens*, the Belie area seems appropriate as a point of more orthodox intergradation (in contrast to the situation at the eastern extreme of the *oriens* range at Arroyo de la Costa—Playa Juraguá) of *oriens* with *homolechis*.

Ruibal and Williams (1961:245) noted the occurrence of yellow dewlapped specimens (within the range presently ascribed to *A. b. oriens*) from the coast south of Pico Turquino, and white dewlapped *A. b. homolechis* from the mountains to the north of the range of *A. b. oriens* at Pico Turquino, "near Santiago," Los Negros, and the Sierra del Cobre. A few additional *A. b. homolechis* localities from this same region and from the area to the north of the Sierra de la Gran Piedra are included in my list of specimens examined of *A. b. homolechis*. Accurately documented material from the lower southern slopes of the Sierra Maestra is lacking. I suspect that some of the specimens labeled as "OcujaI" were native-collected and are from lower elevations on this southern Sierra Maestran slope; dewlap color data were not taken by the collector. Reason for this suspicion is that, of 12 specimens from "OcujaI," eight have the semicircles separated by 1 scale, a much higher incidence of this character than in all other specimens of *A. b. oriens* combined. I have included these OcujaI lizards as paratypes, although I cannot be certain that all of them had yellow dewlaps in life or that all of them are from the coastal lowlands in this region. Were these specimens not included

in the calculations of *A. b. oriens*, differences between that subspecies and *A. b. homolechis* would be even more striking than the present data show. The precise altitudinal relationships of *A. b. oriens* and *A. b. homolechis* along these southern slopes will be most interesting to determine.

The name *oriens* is from the Latin for "the rising sun," an allusion to the bright dewlap color of this subspecies.

A. homolechis at Banés

As pointed out in the introduction, the population of *A. homolechis* at Banés on the north-central Oriente coast consists of lizards which have both yellow and white dewlaps (Fig. 3). There are eight specimens (MCZ 55975-81, USNM 137649) from Banés, all collected by Chapman Grant. One of these (MCZ 55977) was recorded as having a yellow dewlap and the balance were noted as having the dewlaps white. The largest males have snout-vent lengths of 52 mm (one of these is the yellow dewlapped specimen). Snout scales vary from 5 to 9 (mode strongly 5; mean 6.0). Three specimens have 0 scales between the semicircles and five have the semicircles separated by one scale; the yellow dewlapped specimen has the semicircles in contact. Scales between the semicircles and the interparietal vary between 2/2 (two specimens), 2/3 (3) and 3/3 (3, one of which is the yellow dewlapped male). Fourth toe lamellae vary between 15 and 21. Postmentals range from 2 to 6 (mean 3.1, mode 2) and loreals vary between 17 and 34 (mean 23.8).

Were it not for the fact that one of these lizards was recorded as having a yellow dewlap, I would have no hesitation in regarding the lot as *A. b. homolechis*. In scale counts, the series agrees very well with Oriente *A. b. homolechis* except that there is an unusually high incidence of semicircle contact (four of eight lizards at Banés, eight of 116 in all white dewlapped Oriente specimens with the exception of those from the southern coast between Playa Juraguá and the Bahía de Santiago). There is no material available from localities close to Banés either to the east or west, and thus there is no further evidence that *A. homolechis* from this immediate region have yellow dewlaps. The status of the Banés populations is insoluble at present; there is a possibility that

these lizards represent extreme intergrades between *A. b. cuneus* and *A. b. homolechis*. Material from the entire northern coast between Banés and Playa Santa Lucía is lacking, and it is possible that *A. b. cuneus* extends as far east as the Banés region. Further collecting in this northern Oriente region should clarify the situation.

A. homolechis between the Bahía de Guantánamo and the Río Yumurí

There remain for discussion the *A. homolechis* populations between the east side of the Bahía de Guantánamo on the south Oriente coast and the Río Yumurí on the north coast of the same province (Fig. 3). Adequate assessment of these lizards is hampered by lack of extensive material with color data from living individuals, but the rather limited material which Richard Thomas and I have collected is of interest for several reasons, and discussion of it has bearing on the balance of the *A. homolechis* problem. Ruibal and Williams (1961: 245) listed, in addition to my material which they examined, yellow dewlapped specimens from Cabo Maisí and the lower Río Ovando within the area of present discussion, but material from Guantánamo, Imías, and north of Imías was recorded as having white dewlaps (and thus presumably assignable to *A. b. homolechis*).

The eastern tip of Cuba is a region of extreme ecological contrasts. The southern coast is arid, in the rain shadow of the interior montane massifs from the Bahía de Guantánamo east to Cabo Maisí. On the other hand, the northern coast is heavily forested and extremely mesic; at the mouth of the Río Yumurí there are luxuriant hardwood forests descending to the coast. These two coasts, both apparently inhabited by yellow dewlapped *A. homolechis*, present two very distinct ecologies.

Specimens which Richard Thomas and I have collected (and on which there are some color data in life) are limited; the material includes nine specimens from the United States Naval Base, six from 14.5 miles west of Baitiquirí, one from 4 miles west of Baitiquirí, and two from the mouth of the Río Yumurí. On the other hand there are large but undocumented series available from the United States Naval Base and scattered specimens from elsewhere in this

section, so that I have studied a total of 121 *A. homolechis* from this region.

At least my recently collected material can be divided into specimens having white, and others having pale yellow, dewlaps. The active word in the latter dewlap color is *pale*. In no case have I seen *A. homolechis* from this area with dewlaps approaching bright yellow, yellow-orange, or orange (see Pl. 1, third row, left; the dewlap of this particular lizard is almost pale tan rather than pale yellow). Despite this dichotomy, full data for individual lizards are lacking in several instances; however, AMNH 83739 is white dewlapped and AMNH 83738 is yellow dewlapped, and both are from the same precise locality. Thomas' recent series from the Naval Base includes individuals which were either white or yellow dewlapped, but these colors were not associated in the field notes with particular individuals.

Inspection of Table 1 (wherein all material from this area, regardless of dewlap color, has been grouped) and comparison of the data for this sample with those of other *A. homolechis* samples, as well as with *A. b. oriens* to the west of the Bahía de Guantánamo, are instructive. Like *oriens* (and also like southern coastal *A. b. homolechis*) this eastern lot modally has 2/2 scales between the semicircles and the interparietal. The semicircles are modally separated by 1 scale, but the mode is rather weak (73 of 119 specimens have 1 scale, 43 have 0 scales). This condition is different from both south coastal *homolechis* and *oriens*, each of which has a strong mode (1 scale in the former, in contact in the latter). In number of postmentals, the mean of 3.6 is moderate and comparable to that in most samples of *homolechis* (3.0 to 3.8) and equal to that of *oriens* (3.6). The mean number of loreals (22.2) is close to that of *oriens* (22.7) but lower than that of south coastal white dewlapped *homolechis* (26.0). The most striking difference between these extreme eastern lizards and other *A. homolechis* is the high mode of 5 scales between the first canthal scales (83 of 121 specimens) and a consequent very low snout scale mean (5.3), lower than that of any other sample of *A. homolechis* (most closely approached by the Isla de Pinos with a mean of 5.9).

Separating the material from this region

by dewlap color (specimen by specimen) is not practical, since such data are not available for many individual lizards. At those localities whence both colors have been associated with precise specimens, there seem to be no differences in such crucial scale associations as scales between the semicircles or scales between the semicircles and the interparietal, although a positive correlation between these counts and dewlap color may well exist. At least the only two males available from the north coast at the mouth of the Río Yumurí had pale yellow dewlaps; specimens from the vicinity of Baracoa, 20 kilometers to the west, are regularly white dewlapped and show no tendencies, either in scutellation or dewlap color, to the Yumurí and southern coastal lizards.

The lizards from this region are open to three interpretations: 1) as at Playa Santa Lucía and Playa Juraguá, there are two forms which in some places occur sympatrically, one of which is *A. b. homolechis* and the other an undescribed subspecies with a pale yellow dewlap, modally 5 scales between the first canthals, semicircles in contact, and 2 2 scales between the semicircles and interparietal; 2) the lizards comprise one rather variable population of *A. b. homolechis* wherein the dewlap varies from white to pale yellow; or 3) these lizards, at least along the southern coast, are somehow "intergradient" between *A. b. homolechis* and *A. b. oriens*, despite the fact that, as far as known, the populations from east of the Bahía de Guantánamo are completely separated by an intervening population of white dewlapped *A. b. homolechis* from *A. b. oriens*.

Dewlap color data taken by Richard Thomas on the series from the Naval Base suggest, by the fact that the dewlap may be white with yellow suffusions or blotches, that at least in the area immediately to the east of the Bahía de Guantánamo *A. homolechis* is intermediate in dewlap color. Irregularly pigmented or blotched dewlaps in some anoles (as for instance, intergrades between *A. s. sagrei* and *A. s. bremeri*) occur in areas which are intermediate geographically between the ranges of subspecies whose dewlaps are solidly pigmented. In contrast to the apparent intermediacy of the dewlap coloration at the Naval Base are the two series (one white dewlapped, the other with the dewlap pale yellow) from west of

TABLE 1. Measurements and meristic data for 13 populations of *Anolis homolechis*, as discussed in detail in text. Snout-vent length in millimeters. Ranges of counts are given for snout scales at level of first canthal, fourth toe lamellae, postmentals, and loreals; in these categories, $M =$ mean, $M_n =$ mode. In counts of scales between supraorbital semicircles and scales between semicircles and interparietal, incidence for each category is given in parentheses and modal condition is in italics. Superscript numbers for scales between semicircles and interparietal and postmentals for Camaguey (white dewlap specimens) indicate: (1) data for Camaguey A. N. *homolechis* outside the region of overlap between white and yellow dewlapped specimens at Playa Santa Lucia, and (2) data only for white dewlapped *A. homolechis* from the region of overlap with yellow dewlapped anoles at Playa Santa Lucia. All other data shown for Camaguey (white dewlap) specimens includes specimens both from within and outside of the area of overlap with yellow dewlapped specimens.

Locality	N	Largest ♂ ♀	Snout Scales	Scales bet. semicircles	Scales bet. semicircles and interparietal	Fourth toe lamellae	Postmentals	Loreals	Supracarpal keeling
Península de Guanahacabibes	31	♂—58 ♀—41	5-9 $M = 7.1$ $M_n = 7$	1 (27) 2 (2)	2 3 (2) 3 3 (14) 3 4 (6) 1 4 (4) 4 5 (1) 5 5 (1)	16-21 $M = 18.0$ $M_n = 17$	2-5 $M = 3.2$ $M_n = 4$	18-28 $M = 22.5$	+ (= 4) + (weak) = 10 — = 18
Pinar del Río	122	♂—57 ♀—46	5-8 $M = 6.0$ $M_n = 6$	0 (2) 1 (103) 2 (11)	1 2 (1) 2 2 (19) 2 3 (29) 3 3 (47) 3 4 (13)	16-22 $M = 18.7$ $M_n = 18$	2-5 $M = 3.1$ $M_n = 1$	15-34 $M = 23.3$	+ = 2 + (weak) = 21 — = 99
Isla de Pinos	61	♂—57 ♀—43	5-8 $M = 5.9$ $M_n = 6$	1 (53) 2 (5)	2 2 (4) 2 3 (7) 3 3 (33) 3 4 (6) 1 4 (8) 1 5 (1)	15-22 $M = 18.5$ $M_n = 19$	2-6 $M = 3.3$ $M_n = 3$	16-31 $M = 24.9$	+ = 0 + (weak) = 1 — = 10
Halabana-Matanzas- Las Villas	31	♂—58 ♀—43	5-8 $M = 6.5$ $M_n = 6$	0 (2) 1 (24) 2 (4)	2 2 (6) 2 3 (4) 3 3 (13) 3 4 (2) 1 4 (2) 4 5 (1)	16-22 $M = 19.4$ $M_n = 18$	2-6 $M = 3.3$ $M_n = 3$	18-34 $M = 26.4$	+ = 0 + (weak) = 4 — = 27
Camaguey (white dewlap)	95	♂—53 ♀—43	5-9 $M = 6.2$ $M_n = 5, 6$	0 (6) 1 (76) 2 (6)	1 1 (1) ¹ 2 2 (9) 2 3 (5) 3 3 (16) 3 4 (4) 4 4 (3) 4 4 (1)	15-21 $M = 18.5$ $M_n = 19$	2-5 ¹ $M = 3.0$ $M_n = 3$ 2-5 ² $M = 3.1$ $M_n = 4$	16-35 $M = 25.4$	+ = 2 + (weak) = 7 — = 86
Oriente (white dewlap except)	119	♂—57 ♀—46	5-8 $M = 6.2$	0 (8) 1 (106)	2 2 (17) 2 2 (17)	16-21 $M = 18.5$	1-6 $M = 3.2$	15-38 $M = 26.0$	+ = 5 + (weak) = 39

TABLE 1 (Continued)

Locality	N	Largest ♂ ♀	Snout Scales	Scales bet. semicircles	Scales bet. semicircles and interparietal	Fourth toe lamellae	Postmentals	Locals	Supracarpal keeling
south coast bet. Juraguá and Cáimanera			M _n = 6	2 (8)	2-3 (32) 3-3 (46) 3-1 (40) 4-1 (7) 4-5 (11) 6-6 (1)	M _n = 18	M _n = 4		— = 75
Oriente (white dewlap) between Juraguá and Cáimanera	16	♂-57 ♀-?	5-8 M = 6.3 M _n = 6	0 (4) 1 (12)	1-2 (1) 2-2 (6) 2-3 (3) 3-3 (5) 3-4 (2) 2-2 (11) 2-3 (10) 3-3 (30)	16-20 M = 17.2 M _n = 17	2-6 M = 3.6 M _n = 4	17-35 M = 26.1	+ = 0 + (weak) = 2 — = 14
Sierra de Cubitas (<i>A. h. ruber</i>)	68	♂-51 ♀-40	5-9 M = 6.3 M _n = 6	0 (15) 1 (50) 2 (1)	1-1 (2) 1-2 (5) 2-2 (28) 2-3 (15) 3-3 (23) 3-1 (2) 2-2 (6) 2-3 (3)	15-21 M = 18.1 M _n = 17.48	2-7 M = 4.0 M _n = 1	12-37 M = 21.6	+ = 0 + (weak) = 5 — = 63
Playa Santa Lucía (<i>A. h. cuneus</i>)	84	♂-58 ♀-41	5-8 M = 6.0 M _n = 6	0 (48) 1 (26)	1-1 (2) 1-2 (5) 2-2 (28) 2-3 (15) 3-3 (23) 3-1 (2) 2-2 (6) 2-3 (3)	15-21 M = 18.2 M _n = 18	2-7 M = 4.9 M _n = 5	17-41 M = 27.9	+ = 0 + (weak) = 9 — = 75
Los Ballenatos (<i>A. h. ballenatum</i>)	15	♂-62 ♀-?	4-8 M = 6.1 M _n = 5, 6, 7	0 (9) 1 (4)	2-2 (6) 2-3 (3)	17-21 M = 19.1 M _n = 19	3-7 M = 5.2 M _n = 6	16-32 M = 20.9	+ = 0 + (weak) = 15 — = 15
Cayo Sabinal (<i>A. h. cuneus</i>)	9	♂-52 ♀-?	5-7 M = 6.2 M _n = 7	0 (4) 1 (3)	2-2 (1) 2-3 (1) 3-3 (6)	18-21 M = 19.1 M _n = 18	3-6 M = 5.0 M _n = 5.6	19-31 M = 27.1	+ = 0 + (weak) = 0 — = 9
Oriente (yellow dewlap), Cabo Cruz to Juraguá <i>A. h. orientis</i>	65	♂-56 ♀-42	5-9 M = 6.2 M _n = 6	0 (38) 1 (21) 2 (1)	1-1 (1) 1-2 (2) 2-2 (32) 2-3 (6) 3-3 (10) 1-1 (4) 1-1 (1) 1-1 (1) 1-2 (3) 2-2 (41) 2-3 (30) 3-3 (27) 3-3 (11) 1-4 (2) 5 (1)	15-21 M = 17.8 M _n = 16	2-6 M = 3.5 M _n = 1	13-37 M = 22.1	+ = 2 + (weak) = 6 — = 59
Oriente (white to pale-yellow dewlap); Bahía de Guantánamo to Yumuri	121	♂-60 ♀-43	4-8 M = 5.3 M _n = 5	0 (43) 1 (73) 2 (3)	1-1 (1) 1-2 (3) 2-2 (41) 2-3 (30) 3-3 (27) 3-3 (11) 1-4 (2) 5 (1)	11-21 M = 16.9 M _n = 17	2-6 M = 3.6 M _n = 4	13-31 M = 22.2	+ = 1 + (weak) = 21 — = 96

Baitiquirí (the precise locality, 14.5 mi. W Baitiquirí, is in actuality quite close to the Naval Base near the Río Yateras); at this locality there is a clear dichotomy between white and yellow dewlapped lizards. The differences were so distinctive in the field that my notes state "dewlaps pale yellow; in dry woods with white dewlapped *homolechis*."

The situation seems unresolvable at the present time. I suspect that the lizards from between the Bahía de Guantánamo along the southern coast and around Cabo Maisí to the Río Yumurí represent an unnamed, white to pale yellow dewlapped subspecies of *A. homolechis*, but further material is needed before definitive action can be taken.

Specimens examined: Cuba, Oriente Province, Bahía de Guantánamo, north side, 1 (USNM 81655); Boquerón, 4 (USNM 81817-20); United States Naval Base (not mapped), 88 (UMMZ 110189, UMMZ 110190—4 specimens, UMMZ 110191—2 specimens, UMMZ 110188—2 specimens, UMMZ 115711—2 specimens, UMMZ 115712—8 specimens, UMMZ 115713—6 specimens, UMMZ 115714, UMMZ 115715—4 specimens, UMMZ 115716, UMMZ 115717—3 specimens, UMMZ 115729—5 specimens, UMMZ 115720-28, UMMZ 110207—30 specimens, MCZ 67383-85, MCZ 85144, MCZ 69423-28); east side, Bahía de Guantánamo, United States Naval Base, 3 (ASFS V6229-31); east of the Bahía de Guantánamo west of Kittery Beach, United States Naval Base, 6 (ASFS V6236, ASFS V6249, ASFS V6267-70); United States Naval Base, Cusco Valley (not mapped), 5 (USNM 81660-64); 14.5 mi. (23.2 km) W Baitiquirí, 6 (AMNH 83739—2 specimens, yellow dewlaps, AMNH 83738—1 specimens, white dewlaps); 4 mi. (6.4 km) W Baitiquirí, 1 (AMNH 83740); Imías, 2 (UMMZ 80770); lower Río Ovando, 2 (MCZ 42565-66); Cabo Maisí, 1 (MCZ 42549); mouth of Río Yumurí, east side, 2 (AMNH 83736-37).

Aside from the equivocal material from east of the Bahía de Guantánamo to the Río Yumurí just discussed, evidence for intergradation between white and yellow dewlapped populations of *A. homolechis* is limited. There is no evidence of intergradation between *homolechis* and *jubar* in the Sierra

de Cubitas, possibly because there is at least presently no material from localities which might be presumed to harbor intergradient populations, and possibly because the savannas surrounding this isolated massif are virtually devoid of suitable habitat for the species itself. Thus *jubar* seems to be isolated from the balance of the species. Details of presumed intergradation between *homolechis* and *cuneus* have been given in the discussion of the latter form, and, although I am convinced that these two taxa behave in the area of overlap as two good subspecies, the evidence itself is inferential. Intergradation between *homolechis* and *oriens* devolves upon the small lot of specimens from the Belie area and from the peculiarities of the (presumably) non-homogeneous series from Ocuja. The easternmost coastal contact between *homolechis* and *oriens* in the Playa Juraguá area demonstrates a sharp dichotomy between white and yellow dewlapped populations, at least insofar as dewlap color itself is concerned and in most scale features as well (exception: scales between semicircles and interparietal). The lizards from the extreme eastern tip of the island, with their white to pale yellow dewlaps, may represent a somehow intermediate or intergradient population also, but I cannot resolve their status without further detailed information on specimens from this region.

Along with non-white dewlap, there are fairly regularly associated two scale characters—semicircles in contact and 2 2 scales between the semicircles and the interparietal. These three characters are associated in the subspecies *cuneus*, *balaenarum* and *oriens*, but not in *jubar* where the modal condition is 3 3 scales between the semicircles and the interparietal. White dewlap is usually associated with 1 scale between the semicircles and 3 3 scales between the semicircles and the interparietal. A case could thus be made for the presence of two species, one with a white dewlap, 1 scale between the semicircles and 3 3 scales between the semicircles and the interparietal, and the other with a non-white dewlap, semicircles in contact, and 2 2 scales between the semicircles and the interparietal. The major problem in such an arrangement is *jubar* which has the semicircles separated by one scale and 3 3 scales between the semicircles (both

white dewlap characters) but has a yellow dewlap (although the dewlap has relatively extensive white areas). Further comparison of other scale features is unnecessary; such a system of two species would result in combining, for instance, yellow dewlapped forms which have both the highest and lowest numbers of loreals (20.9 in *balaenarum*, 27.9 in *cuneus*) in contrast to white dewlapped specimens having means between 22.5 and 26.4. Finally, the status of the extreme eastern specimens would be unresolvable, since this population (apparently) has a variably colored dewlap, semicircles separated by 1 scale (although the mode is not strong) and 2-2 scales between the semicircles and the interparietal. As noted above, this population is perhaps actually composed of two taxa, and with carefully taken data it can be shown that the presumed excessive variability in both dewlap color and scalation is due to the pooling of data from two kinds of lizards.

Rather than multiply the number of species unnecessarily, I have adhered to a systematic arrangement in *A. homolechis* which does not violate the data presented by the specimens and which is cogent geographically. Further collecting conceivably will show that we are indeed dealing here with two species, but it seems incautious to state definitely that this is the case. The amount of variation and overlap between the various populations, whether white or yellow dewlapped, would make it most difficult to segregate two specific entities at present, at least based upon the characteristics which I have used.

It would be satisfying to propose a history of *A. homolechis* at this point in order to explain the differentiation of the subspecies involved. A tentative history of *jubar* has been presented previously, but none of the other subspecies lends itself to any sort of equally definite treatment. The association of two yellow dewlapped races with the Bahía de Nuevitas area (*balaenarum*, *cuneus*) and the occurrence of *cuneus* on Cayo Sabinal, suggests that the lizards from this region have been somehow isolated from the balance of *A. b. homolechis*. Possibly *A. b. cuneus* should be regarded as a form which evolved on the Camagüeyan *cayeria* and thence invaded the mainland where it it came into contact with the more inland *A. b. homolechis*. My interpretation, based

on the differences between the Sabinal and Playa Santa Lucía *cuneus*, is the reverse of this, however: i.e., that the peculiarities of the Cayo Sabinal *cuneus* are the result of limited invasion from the adjacent mainland.

The southern Oriente coast, from Cabo Cruz to Cabo Maisí, is becoming noteworthy for the distinct forms which it supports. Not only does the coastal fauna include endemic subspecies which differ from those of transmontane Oriente (for example, Schwartz, 1965, *Arrbyton*), but this coast also has several species, limited more or less to the coast itself, which have distinctive subspecies along it (for example, Schwartz and Garrido, 1967, *Leiocephalus macropus*; Thomas and Schwartz, 1966, *Sphaerodactylus torrei*; Schwartz, 1960, *Leiocephalus raviceps*). It is not then surprising to discover that a widely ranging species, both geographically and altitudinally, like *A. homolechis* has likewise differentiated on this southern arid coast. The presence of high and mesic mountains descending abruptly to a xeric coastal strip in this region appears to favor the development of endemic subspecies of widely ranging forms in the latter situation. The longitudinally narrow but latitudinally long xeric coastal area, coupled with other physiographic features such as rivers whose headwaters are in the uplands and which descend torrentially to the coast, and deep embayments such as the Bahía de Santiago and the Bahía de Guantánamo, favor serially arranged subspecies along this coast. *A. homolechis* appears to be no exception; the situation with this species may prove to be even more complex than herein proposed, once the status of the populations at the extreme eastern end of Cuba is known as well as those elsewhere along this coast.

One other fact regarding these southern Oriente *A. homolechis* is pertinent. Despite the fact that the Bahía de Santiago acts as a barrier for several southern coastal reptilian species and subspecies, it does not separate *A. b. oriens* from *A. b. homolechis*: the break between these two populations—and it will be recalled that the break is sharp—is to the east of the Bahía de Santiago near Playa Juraguá. A somewhat comparable situation has been reported (Thomas and Schwartz, 1966:19) for the subspecies *Sphaerodactylus torrei ocnjal* and *S. t. torrei*: in this species, a specimen of *S. t. ocnjal*

(the subspecies to the west of the Bahía de Santiago) was reported from a locality to the east of the mouth of that bay, suggesting that, with changing topography along this stretch of coast, isolated populations of western subspecies have been trapped on the eastern side of the bay. The same may well have been the case with the eastern populations of *A. b. oriens*.

Anolis mestrei Barbour and Ramsden

Anolis mestrei is restricted to the western Cuban province of Pinar del Río and adjacent Habana Province in the Sierra de Anafe (Buide, 1967:33). Although most Pinar del Río locality records for this species involve the Sierra de los Organos and the Sierra del Rosario (Fig. 1), *A. mestrei* occurs in at least one area removed from these massifs. One adult male (AMNH 83109) was collected near Isabel Rubio on a low isolated rocky outcropping in a small patch of woods, otherwise surrounded by flat fields and pastureland. This same outcropping was also occupied by *Anolis bartschi* Cochran, another confirmedly montane Pinar del Río species. Such isolated anoline outliers may well occur where suitable situations occur in Pinar del Río, even remotely peripheral to the main limestone masses of the ranges themselves.

Ruíbal (1964:497) stated that the scalation of *A. mestrei* is very similar to that of *A. homolechis*, except that the posterior supraciliaries of *mestrei* are small and granular whereas those of *homolechis* are larger, elongate, and keeled. This difference is a tenuous one at best, and I am unable to confirm it on a great many specimens of *mestrei*. There is, of course, no question whatsoever that the two are very distinct species, since they differ in ear size (round in *mestrei*, higher than wide in *homolechis*, as pointed out by Ruibal), dewlap color and pattern, and habitat; the two species are generally sympatric in Pinar del Río, but less commonly syntopic, since *mestrei* usually occupies the shaded portions of woods and forests and often perches on rocky outcroppings, whereas *homolechis* prefers semi-shaded situations and seldom utilizes rocks as perching stations.

I have examined 62 specimens of *A. mestrei*. The largest male has a snout-vent length of 56 mm, the largest female 46 mm.

Scale counts on this series are: snout scales between first canthals 5-10 (mean 6.8, mode 6), scales between supraorbital semicircles modally 1 (31 specimens) but 27 lizards have the semicircles in contact and one has two rows of scales between the semicircles, scales between supraorbital semicircles and interparietal modally 3-4 (16 specimens) with 13 specimens having 3-3 and 11 specimens having 4-4, fourth toe lamellae 13-20 (mean 17.2, mode 17), postmentals 2-7 (mean 4.0, mode 4), loreals 19-36 (mean 28.1). All specimens have the supracarpal scales smooth (see Table 2). None of these scale characteristics will separate *mestrei* from *homolechis*; however, *mestrei* has generally higher numbers of scales between the semicircles and the interparietal (32 of 57 lizards have counts ranging between 3-3 and 6/6 scales, whereas *homolechis* has counts above 3-3 only rarely as variants in all populations), lower mean number of fourth toe lamellae (17.2, in contrast to 17.2 to 19.4 in all *homolechis* samples with the exception of 16.9 in extreme southeastern Oriente coastal material), and higher mean number of loreals (28.1 in *mestrei*, 20.9 to 27.9 in all *homolechis* samples with the highest mean in *A. b. cuneus*). The virtually bimodal contact or lack of contact of the semicircles in *mestrei* does not occur in any population of *homolechis*.

In dewlap color, *A. mestrei* is quite distinct from *A. homolechis* and resembles in a general way the color and pattern of dewlaps of toptypical *A. quadriocellifer*. In its simplest pattern, the dewlap (which is quite large) is white-edged with a central or basal extensive reddish (brick) blotch crossed by one or two yellow bars or semicircles. The basal blotch shade is variable in intensity; Maerz and Paul designations for individual males are Pls. 4 F 11, 5 K 12, 5 H 11, 6 I 11, and verbal designations include orange, reddish-brown, maroon, brick-red, and brownish. The transverse included bars or semicircles were considered yellow to pale orange. The expression of these bars or semicircles varies from two well defined bars to no included pattern, with the dewlap having only an unpatterned dark basal blotch or spot (Pl. 1, third row, right). These variants in dewlap color and pattern are not correlated with geography

(since all have been recorded from specimens at San Vicente) but may be somewhat correlated with age, the larger males having two included yellow bars and smaller males lacking them. Such correlation is not absolute however, since dewlap data on particular specimens of comparable snout-vent lengths show that even fully adult males (snout-vent lengths in excess of 50 mm) have the dewlap variously colored and patterned. The dewlap color and pattern of *A. mestrei* resemble that in a very general fashion of *A. quadriocellifer* topotypes in that the former combines two pigments (brick and yellow) just as the latter combines two (yellow and orange) in a pattern of transverse lines, bars or stripes. Details of dewlap pattern in *quadriocellifer* and *mestrei* are not close, however, and the resemblance is rather superficial.

The body color of *A. mestrei* varies from pale (grayish to grayish tan) to darker colors (dark gray to brownish) and a greenish cast or wash is often apparent. There may be some yellowish to orange spots scattered over the body. Sleeping *A. mestrei* are at once distinguishable from any other anoles which occur with them. At night, specimens of both sexes and all ages of *mestrei* have the head a vivid pea-green, in striking contrast to the gray body color; the pea-green head is more prominent in females and juveniles than it is in adult males, but even the latter show the color quite distinctly (but less brightly than do females). Where *A. mestrei* occurs syntopically with its relatives *A. homolechis* and *A. allogus* (such as the forests at Soroa in the Sierra del Rosario), nocturnally collected specimens of *A. mestrei* are quite simply separable from the other species by their very distinctive head color.

Ruibal (1964:497) considered *A. mestrei* to be "more terrestrial than either *homolechis* or *allogus*," and "usually found on the limestone rocks rather than on tree trunks" in shady portions of the forest. My observations agree very well with this concise statement, although *A. mestrei* does not shun tree trunks as perches. In the rich moist woods at the bases of the *mogotes* in Pinar del Río, *A. mestrei* occurs on trees and saplings, as well as upon limestone rocks and boulders, and even occasionally on the limestone walls and faces of the *mogotes* themselves which are typically the habitat of *A.*

bartschi. Moderate to heavy shade is a requirement for *A. mestrei*, and in this the species is intermediate in tolerance between *A. homolechis* and *A. allogus* which occur with it.

Specimens examined: Cuba, Pinar del Río Province, 2.9 mi. (4.6 km) E Isabel Rubio, 1 (AMNH 83109); Cueva de Santo Tomás, 10 km N Cabezas, 4 (AMNH 83105-06, AMNH 83126—2 specimens); San Vicente, 21 (AMNH 83110-13, AMNH 83118—3 specimens, AMNH 83120-21, AMNH 83122—3 specimens, AMNH 83123—3 specimens, AMNH 83124—5 specimens, AMNH 83125, AMNH 95977); Cueva del Cable, San Vicente, 21 (AMNH 83108); cliffs at Cueva del Río, San Vicente, 2 (AMNH 83107, AMNH 83117); north base, Pan de Azúcar, 8 km E Matahambre, 1 (AMNH 83119); Rangel, 1 (AMNH 83127); Soroa, 11 (AMNH 83113—2 specimens, AMNH 83114—5 specimens, AMNH 83115, AMNH 83116—3 specimens).

Anolis imias Ruibal and Williams

Anolis imias was described (Ruibal and Williams, 1961:237) from two lizards collected by P. J. Darlington in 1936. The type locality was given as the village of Imías, Oriente Province; Imías lies on the southern xeric Oriente coast in the rain shadow of the Sierra de Purial. Despite many weeks of collecting along this coast, including visits to Imías, I was never able to collect this species. Orlando H. Garrido and Miguel L. Jaime had the same lack of success in 1967; their search for *A. imias* at and about the type locality failed. Mr. George C. Gorman, upon his return from Cuba, determined by conversation with Dr. Darlington that the two specimens of *A. imias* had not been taken in the environs of the village of Imías, but rather in the mountains (Sierra de Purial) north of that town (Fig. 3). Accordingly, the type locality of *A. imias* should be amended to "mountains north of Imías, Oriente Province, Cuba." I have little doubt that the species, which is large and presumably conspicuous, does not occur at Imías itself. Within the village there is the usual assortment of fruit trees, but elsewhere the region is arid with low shrubs and scattered xerophytic trees on a substrate of sand and limestone rock. The entire aspect of the

Imías region is bleak and is relieved principally by the cultured greenery in the town.

My data on the holotype and paratype (listed in that sequence in each case) are: snout-vent lengths, 64, 46; snout scales between first canthals 6, 7; scales between semicircles 1, 1; scales between semicircles and interparietal 3 3, 4 4; fourth toe lamellae 15, 15; postmentals 1, 2; loreals 25, 27; ventral, brachial and supracarpal scales smooth (see Table 2). Ruibal and Williams (1961:239) described the color of the dewlap as brown and the male pattern as now consisting primarily of 12 broad dark vertical bands on the high-crested tail, six dark bands on the hindlimbs and four dark bands on the forelimbs. The dorsum has five indistinct dark crossbands and the chin is weakly reticulate. The chin of the female paratype is strongly reticulate, and there is a pair of dark lineate scallops on the nape of the otherwise unpatterned dorsum.

I have no doubt that *A. imias* is a very distinctive species. Although it is apparently most closely related to *A. homolechis*, the two species can be easily distinguished on the basis of the smooth brachial scales, chin pattern in both sexes, and smooth head scales of *imias*. It should be pointed out, however, that there is a tendency for *A. homolechis* on this southern Oriente coast (and even elsewhere) to have the brachial scales very weakly keeled or smooth. I had at first assumed that weak or absent brachial keeling in *A. homolechis* was due to the vicissitudes of long preservation and epidermal softening with subsequent loss of scutellar detail, but even freshly collected and well preserved *A. homolechis* show reduction or absence of brachial keeling in some specimens, and I infer that this character is not so constant in *A. homolechis* as has been presupposed. Nevertheless, the absence of brachial keeling on *A. imias* almost surely is natural and not a preservation or age artifact.

In all meristic data, *A. imias* resembles *A. homolechis* from the same general region (much as *A. mestrei* resembles Pinar del Río *A. homolechis*), and no counts on the two *A. imias* will separate them from local *A. homolechis*. The male *A. imias*, however, is larger than any male *A. homolechis* from this area (maximum snout-vent length 60

mm) and the female *A. imias* likewise exceeds local female *A. homolechis* (43 mm), although female *A. homolechis* from other areas (Pinar del Río; Oriente white dewlap) equal the female *A. imias* in size. The male *A. imias* is unusual in having the prenasal transversely divided unilaterally, a feature which does not occur in any *A. homolechis* I have examined but does occur in some populations of *A. allogus* (see below). The reticulate chin markings of *A. imias* also are reminiscent of those of *A. allogus*; the latter species is however characterized by having the brachials and supracarpals heavily keeled in contrast to the smooth scales in *A. imias*.

The relationships of *A. imias* would seem to be partially with *A. homolechis* and partially with *A. allogus*. *A. imias* resembles the former species in having smooth supracarpals and in having the semicircles separated by 1 scale (usually, but by no means always, 2 scales in *A. allogus*). Resemblances to *A. allogus* include the reticulated throat pattern and the postmentals meeting the mental along a straight suture (although this arrangement occurs in those *A. homolechis* which have few postmentals also). In gross aspect, *A. imias* seems much more like *A. allogus* in general build and proportion, but comparison of the characters of these two species (not the least of which is the very different vertically barred tail of the male *A. imias*) shows that they are quite distinct. Judging only from the locality records, *A. imias* is sympatric with *A. allogus* but not with *A. homolechis*; the latter species is known from Imías but not from the mountains to the north. I am at a loss to explain either the origin or the apparent distribution of *A. imias*; surely more material will be most revealing both as to its affinities and range.

Specimens examined: Cuba, Oriente Province, mountains north of Imías, 2 (MCZ 42555-56, holotype and paratype).

Anolis allogus Barbour and Ramsden

Anolis abli Barbour

Anolis rubribarbus Barbour and Ramsden

As Ruibal and Williams (1961:241) very correctly pointed out, three species of Cuban anoles of the *homolechis* group are quite closely related and are not readily distinguishable except by color. These three species are

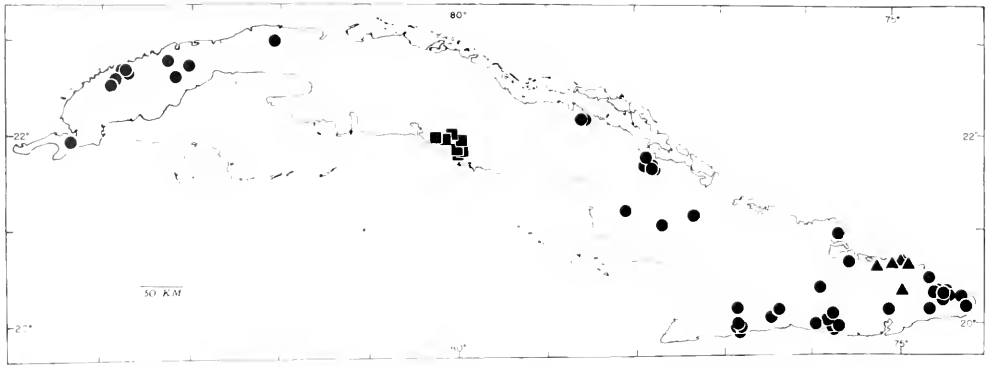


Figure 4. Map of Cuba, showing localities whence specimens of three species of anoles have been examined: solid circles—*A. allogus*; solid squares—*A. abli*; solid triangles—*A. rubribarbus*.

A. allogus Barbour and Ramsden 1919, *A. rubribarbus* Barbour and Ramsden 1919, and *A. abli* Barbour 1925. Of them, *A. allogus* is islandwide in distribution (Fig. 4), *A. abli* is limited to the Sierra de Trinidad in Las Villas Province (Fig. 4), and *A. rubribarbus* to portions of the northern coast and interior (Cuchillas del Toa) of Oriente Province (Fig. 4). Although *allogus* is islandwide in a broad sense, it has been collected only in the provinces of Pinar del Río, Habana (one locality), Camagüey, and Oriente; the species is most widespread in the latter province and is known from all the major montane massifs, as well as from lowland areas along the mesic northern Oriente coast. As far as is presently known, *allogus*, *rubribarbus* and *abli* are allopatric to one another. All three species resemble one another structurally in having multicarinate supracarpal scales (in contrast to the sympatric *A. homolechis*, but like the narrowly sympatric *A. quadricellifer*), blue to blue-gray irides (*vide* Ruibal and Williams, 1961:243), and mean body femoral ratio (*ibid.*). Dewlaps of the three species are similar but not identical and involve the same general pigments: in *allogus* the dewlap varies from unicolor peach without any transverse bars to a tan to yellow ground with three or four transverse orange to red bars, in *abli* the dewlap is basally red with an anterior yellow edge. I have not collected *A. rubribarbus*, and so my comments on that form are necessarily limited; Ruibal and Williams (1961:223) described the *rubribarbus* dewlap as having

4 or 5 thin red transverse bars on a deep yellow ground. Of the three taxa, *rubribarbus* has a very distinctive body pattern, consisting of about six vertical dark (blackish) bands or bars separated by light (yellowish or gray) vertical bands; the tail is likewise vertically barred and the limbs are banded. Neither *allogus* nor *abli* has so striking and contrasting a body pattern.

Since these three species are allopatric and since they are also obviously closely related *intra se*, it seemed possible that they compose a single species with several distinctive subspecies. According to Ruibal and Williams (1961:221) *allogus* and *abli* cannot be distinguished on the basis of scalation nor body femoral ratio. Barbour (1937:221) used the combination *A. allogus abli* (thereby suggesting the proximity of these two taxa); he also (p. 127) used the combination *A. homolechis rubribarbus*, but there is no justification for this suggested relationship. Of the two Barbour and Ramsden names published in 1919 (*allogus* and *rubribarbus*), *A. rubribarbus* has page priority over *A. allogus*, and both these names antedate *A. abli* Barbour; thus, if the three species are combined, *A. rubribarbus* is the name for the entire assemblage.

Anolis abatus Ahl, 1924, has been placed in the synonymy of *A. allogus* (Ruibal and Williams, 1961:215). I have not examined the syntypes of this Ahl species; one character of the type material given by Ahl (1924:248)—that the supraorbital semicircles are separated by three rows of scales—occurs in some samples of *Anolis allogus* (in

contrast to, for instance, *A. homolechis*). Although Ahl did not mention the supracarpal keeling, despite the carefully detailed description of the head and body scalation, it is possible that the two *abatus* were drawn from a population of *allogus* in which the supracarpal keeling is weak (see discussion beyond). Since Ruibal and Williams examined the syntypes of *abatus*, I agree with their assessment of the status of this name. It should be pointed out that, if in the future *A. allogus* is separated into subspecies, *abatus* Ahl is a name which will have to be considered before any nomenclatorial changes are proposed within the species. It is even possible (although I consider it unlikely) that *abatus* Ahl will be found to be the prior name for *abli* Barbour. Barbour's (1925:167) comments on the two syntypes effectively select the male *abatus* as the lectotype: Barbour's further statement, that the female syntype of *abatus* belongs to his new species (*abli*), suggests that perhaps both syntypes might in actuality represent *abli*. However, no *abli* examined by me has three scales between the semicircles. The color description of the male syntype (Ahl, 1924:249) in some ways suggests *A. rubribarbus* ("grünlichgrau oben und an den Seiten, mit unbestimmten dunkleren Rückstreifen und 3-4 undeutlich dunkleren Querbinden an den Seiten") by emphasizing the vertical crossbands which are such a distinctive *rubribarbus* feature. In any event, as the nomenclature now stands, no changes would be necessary if *abatus* is found to be either an *allogus* or *rubribarbus*, since *abatus* postdates these two names but antedates *abli*.

Table 3 shows the mensural and meristic data on nine samples of *A. allogus*, one of *A. abli*, and one of *A. rubribarbus*, arranged in more or less geographical sequence from west to east. The samples and their sizes are: 1) *allogus*—Pinar del Río Province (79); 2) *abli* (21); 3) Loma de Cunagua, Camagüey Province (22); 4) Sierra de Cubitas, Camagüey Province (65); 5) Central Miranda at the foothills of the Sierra de Nipe, Oriente Province (25); 6) Mayarí, Oriente Province (21); 7) Sierra Maestra and Sierra del Cobre, Oriente Province (33); 8) Sierra de la Gran Piedra and immediately adjacent northern lowlands, Oriente Province (33); 9) Sierra del Guaso and Sierra de

Purial, Oriente Province (20); 10) northern Oriente from the Río Yumurí to the Bahía de Taco (111); 11) *rubribarbus* (29). Comments on the variation shown in the table follow.

1) *Size*. The smallest maximally sized male *allogus* are from Central Miranda (snout-vent length 50 mm) with the largest males from the Sierra de Cubitas only slightly longer (snout-vent length 53 mm). The largest males are from Mayarí and the Sierra Maestra (62 mm) with Gran Piedra and northern Oriente coast *allogus* only slightly smaller (61 mm). Smallest females are from the Sierra de Cubitas and Central Miranda series (41 mm) with largest females among the specimens from the Gran Piedra lot (49 mm). Compared with *allogus*, *abli* males are small (Ruibal and Williams, 1961:221, gave a maximum snout-vent length for *abli* of 58 mm, but the largest male I have examined measures 55 mm) but are within the known variation in size for all male *allogus*. Male *rubribarbus* are moderately large (Ruibal and Williams, 1961:222, gave a maximum snout-vent length for *rubribarbus* of 62 mm, but the largest male I have examined measures 58 mm) but are also comparable in size with male *allogus*.

2) *Snout scales between first canthals*. In *allogus*, snout scales range from 5 to 13, in *abli* from 6 to 10, and in *rubribarbus* from 7 to 11. Means vary between 7.9 in *abli* to 9.3 in northern Oriente *allogus*. The Pinar del Río *allogus* have a snout scale mean of 8.1, slightly higher than the "adjacent" *abli* (7.9), whereas the snout scale mean of Loma de Cunagua *allogus* (the next "adjacent" population to the east represented by long series) has a mean of 8.2; thus the mean of *abli* is comparable to, and only slightly lower than, those of the closest *allogus* populations. The extreme eastern populations (Guaso-Purial, northern Oriente coast, *rubribarbus*) have the highest means (8.5 to 9.3), in contrast to *allogus* from elsewhere and *abli* (7.9 to 8.4). There seems to be a general tendency for the lowest means to be in the west and the highest in the east, but the trend is neither regular nor smooth.

3) *Scales between supraorbital semicircles*. Ruibal and Williams (1961:242) stated that all three species had the semicircles separated by 2 scales. This is far from a

TABLE 3. Measurements and meristic data for nine populations of *Anolis alltagus*, as well as *A. allti* and *A. rubribarbatus*, arranged from west to east. Categories and symbols as in Table 1. Prenasals are indicated as a fraction: 1 1 = prenasal undivided on both sides, 1 2 = prenasal undivided on one side and divided on the other, 2 2 = prenasal divided on both sides.

Locality	N	Largest		Snout Scales	Scales bet. semicircles	Scales bet. semicircles and interparietal		Fourth toe lamellae	Postmentals	Lorals	Prenasals	Supracarpal keeling
		♂	♀			Scales bet. semicircles	Scales bet. semicircles and interparietal					
Pinar del Río	79	♂—58	♀—45	6-9 M = 8.1 M _n = 8	1 (5) 2 (71) 3 (2)	2 2 (1) 2 3 (1) 3 3 (5) 3 4 (9) 4 4 (23) 4 5 (17) 5 5 (14) 5 6 (3)	13-18 M = 16.0 M _n = 16	0-3 M = 1.8 M _n = 2	20-43 M = 29.3	1 1 (1) 2 2 (78)	+ = 77 + (weak) = 1	
		♂—55	♀—48	6-10 M = 7.9 M _n = 8	1 (4) 2 (17)	2 2 (1) 2 3 (2) 3 3 (1) 3 4 (3) 4 4 (7) 4 5 (1) 5 5 (5) 6 6 (1)	14-20 M = 16.1 M _n = 16	1-4 M = 2.0 M _n = 2	16-34 M = 25.1	1 1 (2) 1 2 (3) 2 2 (15)	+ = 21	
<i>allti</i>	21	♂—55	♀—48	6-10 M = 7.9 M _n = 8	1 (4) 2 (17)	2 2 (1) 2 3 (2) 3 3 (1) 3 4 (3) 4 4 (7) 4 5 (1) 5 5 (5) 6 6 (1)	14-20 M = 16.1 M _n = 16	1-4 M = 2.0 M _n = 2	16-34 M = 25.1	1 1 (2) 1 2 (3) 2 2 (15)	+ = 21	
		♂—55	♀—41	7-9 M = 8.2 M _n = 8	1 (8) 2 (14)	2 2 (3) 2 3 (4) 3 3 (6) 3 4 (4)	14-19 M = 15.5 M _n = 16	0-6 M = 1.4 M _n = 2	23-38 M = 31.5	2 2 (22) + (weak) = 2	+ = 20	
Sierra de Cubitas	65	♂—53	♀—41	6-10 M = 8.1 M _n = 8	1 (15) 2 (46) 3 (3)	3 3 (9) 3 4 (8) 4 4 (24) 4 5 (10) 5 5 (11) 5 6 (1) 6 6 (1)	15-20 M = 16.8 M _n = 17	0-4 M = 2.0 M _n = 2	21-41 M = 29.2	1 1 (1) 1 2 (2) 2 2 (61)	+ = 63 + (weak) = 2	
		♂—50	♀—41	7-11 M = 8.2 M _n = 8	1 (3) 2 (21) 3 (1)	3 3 (1) 3 4 (1) 4 4 (11) 4 5 (5) 5 5 (4) 5 6 (1) 6 6 (1)	14-19 M = 16.8 M _n = 17	0-4 M = 2.1 M _n = 2	24-42 M = 31.4	2 2 (25) + (weak) = 17	+ = 8	
Mayarí	21	♂—62	♀—42	7-10 M = 8.4 M _n = 8	1 (3) 2 (17) 3 (1)	3 3 (2) 3 4 (5) 4 4 (6) 5 5 (2) 6 6 (3)	14-19 M = 15.9 M _n = 17	2-4 M = 2.4 M _n = 2	24-39 M = 30.2	1 1 (1) 2 2 (20) + (weak) = 8	+ = 13 + (weak) = 8	

TABLE 3 (Continued)

Locality	N	Largest ♂ ♀	Snout Scales	Scales bet.		Postmentals	Lorals	Prebasals	Supracarpal keeling
				semicircles semicircles	interparietal and Fourth toe lamellae				
Sierra Maestra + Sierra del Cobre	33	♂-62 ♀-46	5-10 M = 8.1 M _n = 8	5-3 (1)	14-20	1-3	19-52 M = 30.6	1 1 (1) 1 2 (2) 2 2 (25)	+ = 14 + (weak) = 19
				1 (15) 2 (18)	M = 17.1 M _n = 17	M = 1.9 M _n = 2			
Sierra de la Gran Piedra	33	♂-61 ♀-49	6-10 M = 8.0 M _n = 8	1 (19) 2 (12) 3 (1)	14-20 M = 16.6 M _n = 17	1-2 M = 1.9 M _n = 2	17-39 M = 28.1	1 2 (2) 2 2 (29)	+ = 31 + (weak) = 2
				3 (3) 3 (3) 3 (3) 3 (4) 4 (4) 4 (5) 4 (5) 5 (5) 5 (5) 6 (6) 6 (6) 2 (3) 3 (3) 3 (3) 4 (1) 4 (5) 4 (5) 5 (9) 5 (9) 6 (1) 2 (3) 3 (5) 3 (1) 3 (1) 4 (1) 4 (5) 4 (5) 5 (4) 5 (6) 5 (6) 8 (3) 1 (2) 2 (6) 2 (11) 2 (6) 3 (9) 3 (13) 3 (13) 4 (2)	M = 16.6 M _n = 17	M = 2.5 M _n = 2	19-38 M = 29.6	2 2 (20) 2 2 (20)	+ = 14 + (weak) = 6
Sierra del Gusao + Sierra de Purial	20	♂-57 ♀-42	7-11 M = 8.7 M _n = 9	1 (7) 2 (13)	14-18 M = 16.5 M _n = 16, 17, 18	2-4 M = 2.5 M _n = 2			
				0 (4) 1 (29) 2 (60) 3 (13) 4 (2)	M = 17.2 M _n = 17		18-13 M = 31.3	1 1 (6) 1 2 (1) 2 2 (101)	+ = 102 + (weak) = 9
Rio Yumuri to Bahía de Taco	111	♂-61 ♀-43	5-13 M = 9.3 M _n = 9	0 (4) 1 (29) 2 (60) 3 (13) 4 (2)	14-22 M = 17.2 M _n = 17	0-6 M = 2.5 M _n = 2	18-13 M = 31.3	1 1 (6) 1 2 (1) 2 2 (101)	+ = 102 + (weak) = 9
				0 (1) 1 (19) 2 (8)	15-20 M = 17.5 M _n = 17	2-4 M = 2.6 M _n = 2	20-11 M = 29.7	1 1 (16) 1 2 (3) 2 2 (8)	+ = 11 + (weak) = 17
<i>rubribarbatus</i>	28	♂-58 ♀-42	7-11 M = 8.5 M _n = 8	0 (1) 1 (19) 2 (8)	15-20 M = 17.5 M _n = 17	2-4 M = 2.6 M _n = 2	20-11 M = 29.7	1 1 (16) 1 2 (3) 2 2 (8)	+ = 11 + (weak) = 17

regular condition in these species, and the semicircles may be separated by 0 (= semicircles in contact) to 4 scales. Separation by two scales is certainly modal (with 296 of 452 specimens of the three combined species having this condition), but over one-third (34.5 percent) of the three combined species have counts other than 2 in this position, and, if *allogus* is treated singly, 32.7 percent of the specimens of that form have counts other than 2 between the semicircles.

Other than a count of 2 scales between the semicircles, the next most frequent category is 1 (occurring in all samples), followed by 3 scales (in samples from Pinar del Río, Sierra de Cubitas, Central Miranda, Mayarí, Guaso-Purial, northern Oriente coast). Only two samples (northern Oriente coast *allogus*, *rubribarbus*) have specimens with the semicircles in contact, and only one sample (northern Oriente coast) has two specimens with the semicircles separated by 4 scales.

The modal condition, as pointed out above, is usually 2 scales between the semicircles; the mode is usually very strong. There are two exceptions to this statement: *allogus* from the Sierra de la Gran Piedra and *rubribarbus* have the semicircles modally separated by 1 scale. The mode of 2 is very weak in *allogus* from the Sierra Maestra (the region of the type locality of *A. allogus*), where 18 specimens have 2 scales between the semicircles and 15 have 1 scale in this position.

Of the series of *abli*, 17 of 21 specimens have 2 scales between the semicircles and the balance have 1; of the series of 27 *rubribarbus*, 19 have 1 scale between the semicircles, seven have 2 and one has 0. Note that in this character *abli* resembles *allogus*, and that *rubribarbus*, with a strong mode of 1 differs from most *allogus* populations except that from the Sierra de la Gran Piedra.

4) Scales between supraorbital semicircles and interparietal. The mode for most samples of *allogus* is 4 4 but there are several exceptions. A mode of 3 3 occurs in *allogus* from Loma de Cunagua, northeastern Oriente coast, and *rubribarbus*, and 3 3 and 4 4 are bimodes (each with 5 specimens) in the Guaso-Purial sample. The Gran Piedra material has a mode of 5 5. The greatest number of combinations (10) occurs in

northeastern Oriente, with Pinar del Río having nine combinations; the least variability in this character occurs in the Loma de Cunagua sample.

Note that in number of scales between the semicircles and the interparietal, *abli* agrees with *allogus*, whereas *rubribarbus* agrees with adjacent *allogus* from the northern Oriente coast (and with the material from Loma de Cunagua).

5) Fourth toe lamellae. Fourth toe lamellae show a total variation in *allogus* between 13 and 22, in *abli* between 14 and 20 and in *rubribarbus* between 15 and 20. Mean fourth toe lamellae range from 15.5 at Loma de Cunagua to 17.5 in *rubribarbus*; modal number of lamellae is either 16 (including *abli*) or 17 (including *rubribarbus*); only the Guaso-Purial sample has these categories (16, 17, 18) with the same incidence (4 specimens) and no mode.

6) Postmental scales. The modal condition in all populations (including *abli* and *rubribarbus*) is 2 postmentals; the number of postmentals varies between 0 (most frequent at Loma de Cunagua, but occurring also in Pinar del Río, Cubitas, Miranda, northern Oriente coast) to 6 (one specimen, Loma de Cunagua). All samples but one (Guaso-Purial) have at least three categories of number of postmentals. From a mode of 2 postmentals, five samples (Pinar del Río, Loma de Cunagua, Cubitas, Sierra Maestra, Gran Piedra) show a tendency toward a lesser number of postmentals (0 or 1), whereas five samples (Miranda, Mayarí, Guaso-Purial, northern Oriente coast, *rubribarbus*) show a tendency to higher numbers of postmentals (3 or 4). Means range from 1.4 (Loma de Cunagua) to 2.6 (*rubribarbus*), with Guaso-Purial and northern Oriente coast having means of 2.5, in contrast to means elsewhere of 1.4 to 2.4 (the latter at Mayarí in Oriente).

7) Loreals. The total variation in *allogus* loreals is 17 to 52, in *abli* from 16 to 34, and in *rubribarbus* from 20 to 41. Means range from 25.1 (*abli*) to 31.5 (Loma de Cunagua *allogus*), with Central Miranda and northern Oriente coast *allogus* having only slightly lower means (31.4 and 31.3). The *rubribarbus* mean (29.7) is near to that of the northern Oriente coast (31.3) and almost identical to that of Guaso-Purial (29.6).

8) *Supracarpal keeling*. No specimen of this complex of three taxa has the supracarpal scales smooth. In general, the supracarpals are sharply multicarinate, but in several samples there is a high preponderance of specimens with weak keels. Weak keels are strongly modal at Central Miranda and modal but less strongly so in the Sierra Maestra and *rubribarbus*. Only the *abli* sample includes specimens all of whose supracarpals are strongly keeled; all others include at least a very few individuals whose supracarpals scales are weakly keeled.

9) *Prenasal scale*. Ruibal and Williams (1961:222) stated that most specimens of *rubribarbus* had the prenasal scale single, whereas in *abli* and *allogus* this scale is divided by a transverse suture to give two scales before the naris; in fact, they (p. 243) suggested that this was a good scale difference between *rubribarbus* on one hand and *allogus* and *abli* on the other. Of the 27 *rubribarbus* before me, 16 have the prenasal undivided on both sides, three have this scale single on one side and divided on the other, and eight have the scale divided on both sides. Thus, eight of 27 specimens cannot be separated on the basis of this character from specimens of *allogus*.

The occurrence of divided prenasals in *rubribarbus* achieves more than academic interest. Before proceeding, however, comments on the specimens of *rubribarbus* must be made. The taxon was described by Barbour and Ramsden on the basis of a holotype from El Puerto de Cananova, near Sagua de Tánamo, Oriente Province; no paratypes were designated, although these authors stated (1919:158) that there was "a small series" from Cananova. There are at present three specimens (MCZ 11910-12) which are from Cananova and presumably are the short series referred to by Barbour and Ramsden. These specimens may, in the very loosest of interpretations, be considered paratypes (as they were by Barbour and Loveridge, 1929:222, although they list the "paratypes" as being three specimens, "MCZ 11908-12," a presumed *lapsus calami*) but I adhere to paratypic status by declaration of the describer and do not so consider them. In any event, these three specimens and the holotype plus a series of eight lizards (MCZ 28760-67) from Mina Piloto, Sagua de Tánamo, form a group of specimens which

may be termed the old series, since they were collected some time ago; these lizards have a community of localities in that they all are from the western portion of the known range of *rubribarbus*. There is a second or new series of specimens (MCZ 50187, MCZ 63660-61, MCZ 63665-74, MCZ 63662-63, MCZ 93651), more recently collected, from the vicinity of Moa, in the eastern portion of the range of *rubribarbus*.

These two series of *rubribarbus* differ from one another in some interesting ways. As far as prenasals are concerned, the new series has the higher incidence of undivided prenasals (12 specimens undivided on both sides; two specimens undivided on one side, divided on the other; and two specimens with divided prenasals on both sides) whereas the old series has the higher frequency of divided prenasals (six specimens with divided prenasals on both sides; one specimen with the prenasal single on one side, divided on the other; and four specimens with the prenasal single on both sides). (The series differ in other scale characters as well: for instance, the old series has the semicircle separation by 0 scales in one lizard, 1 scale in five lizards, and 2 scales in six lizards, whereas the new series has 14 of 16 specimens with 1 scale between the semicircles and the exceptions have 2 scales in this position.)

Although a transversely divided prenasal is overwhelmingly the modal condition in *A. allogus*, the incidence of undivided prenasals is variable by population. No lizards from Loma de Cunagua, Central Miranda, or Guaso-Purial have undivided prenasals. Other than these, the lowest incidence of undivided prenasals occurs in the Pinar del Río material (1 of 79 specimens; 1.3 percent) and the highest in the Sierra Maestra material (3 of 31 specimens; 9.7 percent). Five of 25 *abli* (25.0 percent) and 20 of 28 *rubribarbus* (71.4 percent) have undivided prenasals. The northern Oriente coast *allogus* rank second (8.2 percent) of all *allogus* populations in this character. Despite the high incidence of undivided prenasals in the northern Oriente *allogus*, in this character these specimens do not begin to approach the very high incidence in *rubribarbus*. It is suggestive, however, that of the nine specimens of *allogus* with undivided

prenasals, three are from an interior montane locality 9 km west and 3 km south of Baracoa and thus toward the geographic western extreme of *allogus* material from this region, and the remaining six are from Cabacú, to the southeast of Baracoa. At least the first series might indicate a tendency at this locality toward the predominantly undivided prenasal condition in *rubribarbus*. There is no material between this locality and the easternmost *rubribarbus* locality except for two lizards from the Bahía de Taco; these have divided prenasals on both sides.

There are no specimens assignable to this complex of forms between the Bahía de Taco (*allogus*) and Punta Gorda (*rubribarbus*), a distance of 25 kilometers airline (Fig. 4). Ruibal and Williams (1961:240) were faced with a similar lack of specimens from intermediate localities (although the gap has been somewhat closed since then by the Bahía de Taco specimens) but suggested that if intermediates between *allogus* and *rubribarbus* were found along this northern Oriente coast, it would be necessary to regard *allogus* and *rubribarbus* as conspecific. Although I suspect that such will eventually prove to be the case (despite the striking pattern of *rubribarbus*), I am likewise unwilling now to consider these two taxa as being conspecific. At a locality 8 km northwest of Bahía de Taco, I observed three boldly vertically barred anoles on deciduous growth along the margins of a small stream coursing through pinewoods; none was secured but I am convinced that they were *rubribarbus*. No *allogus* I have observed had such bold dorsal markings; the habitat is precisely that cited for this species by Ruibal and Williams (1961:228). If *allogus* and *rubribarbus* are subspecies, the transition from one to the other must be extremely abrupt, much as in the case of *A. b. homolechis* and *A. b. oriens* at Playa Juraguá.²

² Garrido (1967, Trabajos de divulgación, Museo "Felipe Poey," 55:1-7) has recently summarized both ecological and observational data on *Anolis rubribarbus* at a locality 20 km SE Moa; he has shown conclusively that *A. rubribarbus* and *A. allogus* are not allotopic at this locality (called Potosí), that *A. rubribarbus* no longer occurs at the type locality due to destruction of forested habitats, and that *A. rubribarbus* does not occur so far east as Cayo Güim (about 11 km NW Baracoa) where he en-

Less information is available for the zone of contact between *allogus* and *rubribarbus* on the west. In this region, there is an excellent series of *allogus* from 16 km E Mayarí (only one of which has the prenasals undivided). A single specimen from Mina Piloto (UMMZ 71409, one of the paratypes of *Anolis patricius* Barbour) has divided prenasals; this lizard is from a known *rubribarbus* locality but presently it is undistinguishable from *A. allogus*. I have considered it *A. rubribarbus* purely on the basis of its provenance. From the meager evidence shown by the Mayarí series, it seems that *allogus* and *rubribarbus* approach one another by about 30 km airline on the west. It should be pointed out once more that the old series of *rubribarbus* from the western portion of the range of that form (Mina Piloto; Cananova) are precisely those specimens which have the high incidence of divided prenasals, an *allogus* character. Such high incidence may reflect tendencies toward (intergradation with) *A. allogus* in this region, whereas specimens from farther east (Moa, south of Moa, east of Moa) with high incidence of undivided prenasals may be more "pure" *rubribarbus* (at least in this character).

The nomenclatural status of *A. abli* is problematical. As Ruibal and Williams (1961:240) pointed out, *allogus* is unknown from Las Villas and Matanzas provinces; *abli* is the only representative of this group of lizards in Las Villas Province and it occurs only in the Sierra de Trinidad. *A. abli* is like *A. allogus* in scalation and size, but as Ruibal (1964:498) noted, male *abli* appear to lack a tail crest, a variably developed feature in male *allogus*. Although *allogus* remains unknown from Las Villas and Matanzas provinces, there is much suitable habitat for it remaining there; such areas as Pan de Matanzas and the mountains in the vicinity of Mayajigua, to mention but two areas, seem suitable for such a shade-dwelling species. Absence of *abli* from the heavily wooded *seboruco* areas in the Soledad region at the foot of the Sierra de Trinidad is strange, but the species is known only from

countered only *A. allogus*. Ethological and ecological data presented by Garrido suggest that *A. allogus* and *A. rubribarbus* inhabit different situations but he admitted (p. 6) that much yet remains to be determined about the distribution and relationships of *A. rubribarbus*.

higher elevations in this range. Ruibal (1964:499) suggested that *abli* is limited to the deeply shaded portions of the Trinidad forests. My experience differs from his, since *abli* was encountered regularly in more open situations (but usually associated with wooded or at least shrubby situations) along roadsides and on the open trail leading to the bottom of the river valley at the Salto de Hanabanilla. In any event, *abli* appears to be a geographical isolate of a basic *allogus* stock, restricted to the Sierra de Trinidad. It differs from *allogus* in absence of a tail fin in males, low mean number of scales between the first canthals, low mean number of loreals, and high incidence of undivided prenasals; dewlap coloration is discussed below.

Dewlap color and pattern of *A. allogus* vary between localities in a rational manner. Pinar del Río specimens regularly have the dewlap yellow to pale yellow with three transverse red bars (Pl. 1, fourth row, left). Males from Loma de Cunagua have the dewlap yellow with three orange bars or an extensive orange central spot. The aspect of the dewlap in Sierra de Cubitas males is faded with a very pale yellow ground and about three transverse orangish bars or an orange spot (Pl. 1, fourth row, right). At Central Miranda, the dewlap is regularly very pale peach (Pl. 11 E 9), slightly deeper centrally, but without definite bars; at most there are indications of two very faintly darker transverse bars. Sierra de la Gran Piedra males either have faintly yellow dewlaps (Pl. 10 F 3) with three reddish (Pl. 5 E 11) bars or they lack bars and have an orange or reddish (Pl. 4 F 11) center or basal blotch (Pl. 1, lower left). Northern Oriente coast specimens have the dewlap yellow to peach with three or four red to brick bars. In general Pinar del Río and northern Oriente males have the most vividly colored dewlaps, whereas those of other samples which I have seen in life are paler and often lack expression of the bars completely; the latter is the rule in males from Central Miranda.

The dewlap in *abli* is yellow to very pale yellow (Pls. 10 I 1 and 10 I 4) anteriorly, with a large basal red spot (Pls. 3 H 12 and 11 F 11); there is often an extensive black area on the neck, extending to the posterior portion of the expanded dewlap

(Pl. 1, lower right). Although the *abli* style dewlap is not known to occur in any *allogus* populations, at least the general two color schema (absence of barring and a darker central area) is shown in some samples of male *allogus*.

Ruibal (1961) has discussed the ecology of *A. allogus*. This species is non-heliophilic and is confined to heavily shaded broadleaf forests, from sea level to elevations of 6000 feet (1830 meters) in the Sierra Maestra. *A. allogus* is absent from the arid southern Oriente coast; there are three specimens recorded from the same region (Ocuja; coast south of Pico Turquino, both coastal localities), but I doubt the precision of the locality data for these lizards. The forests (when present) on this southern coast are open and dry, and far more suitable for *A. homolechis* than *A. allogus*. On the northern Oriente coast, however, where dense broadleaf forests descend to the coast, *A. allogus* accompanies them (such as at the mouth of the Río Yumuri and the Bahía de Miel). One of the Bahía de Taco *allogus* was collected in mangroves; this seemingly unlikely situation for this species may be easily explained since in this region dense forests occur immediately adjacent to the coast in many places, and dense mangrove growth offers an equally shaded situation to a non-heliophilic lizard, provided the mangroves are readily accessible by proximity to broadleaf forest.

The occurrence of *A. allogus* on the extreme western Península de Guanahacabibes has been reported by Garrido and Schwartz (MS). The presence of this lizard on the peninsula, far removed from its more usual haunts in the Sierra de los Organos and Sierra del Rosario, is not surprising, since the central portion of the peninsula is densely forested, providing optimal habitat for the species. The lone record of *A. allogus* from Habana Province likewise is from dense broadleaf forest in the Escaleras de Jaruco; the presence of *A. allogus* at this locality strongly suggests that it occurs in the same range to the east (such as at Pan de Matanzas, where it remains uncollected). In Camagüey Province, *A. allogus* is known from the forested Loma de Cunagua (an isolated steep-sided mountain in the Llanura de la Trocha), the Sierra de Cubitas and

associated forested lowlands between that range and the northern coast, the Sierra de Najasa (a less well-forested massif to the southeast of Camagüey city), Loma de la Yagua (an isolated and wooded hill to the southwest of Camagüey city), and Martí (a locality which presently seems unsuitable; the specimen may have come from some locality near Martí rather than from the environs of the city itself).

A. allogus is widespread in Oriente, occurring in the Banes area, in the Sierra Maestra, Sierra del Cobre, Sierra de la Gran Piedra (including the mesic foothills to the immediate north of that range as at Dos Bocas), Sierra del Guaso, and Sierra de Purial. Along the northern Oriente versant, *A. allogus* occurs from sea level (mouth of Río Yumurí; Bahía de Miel; Bahía de Taco) to higher elevations (El Yunque de Baracoa). The series from 9 km W and 3 km S Baracoa was secured in an unusual situation; here, at a locality known as La Minita, *A. allogus* was inhabiting abandoned houses and shacks which had been in use when the mine was active. The area lacked arborescent vegetation, and the flora consisted of stunted trees and shrubs on red lateritic soils. The elevation is unknown, but to reach La Minita we passed through broadleaf forest. This is the only occasion where I encountered *A. allogus* associated with human habitation, albeit in this case a deserted settlement. Occurrence of *A. allogus* in mangroves at Bahía de Taco has been mentioned. At the mouth of the Río Yumurí, *A. allogus* inhabits coastal *Coccoloba* forests; these seagrape woods are immediately adjacent to dense broadleaf forest, and the lizards have doubtless invaded the somewhat less suitable situation from the latter more suitable one.

Anolis allogus is regularly encountered at night, sleeping on the leaves of shrubs; I have not found it sleeping on stems, twigs, or branches. During the day, males were observed on the trunks of trees in or at the edges of forests or at least well shaded woods. Females are more terrestrial and were at times collected on the ground. Although the occurrence of *A. allogus* about dwellings and in proximity to humans happens rarely, at Gran Piedra this species was common on the walls of the ruins of the French plantation house, La Isabelica, and at the mouth

of the Río Yumurí *A. allogus* was exceptionally abundant, occurring not only on trees but rocks and fence posts along the open but well shaded road. During overcast days, which are frequent in the Sierra de la Gran Piedra, *A. allogus* was encountered under rocks lying on the ground, where presumably they had sought temporary refuge from the cool breezes and blowing mist.

Anolis abli, as noted above, also was found in *monte* and in less well shaded situations along open trails and adjacent to roads. Sleeping perches are primarily leaves of low shrubs, 2 to 4 feet above the ground, but occasional individuals were encountered sleeping on slender twigs. The tail, while the lizard sleeps, may be either tightly curled or may be prehensily twisted about the leaf petiole or some minor surface irregularity. At night the heads of *A. abli* are greenish but not so bright as the pea-green of dormant *A. mestrei*. Female *abli* at night show a prominent broken and irregular middorsal band.

Although I have made no taxonomic changes in the three species of this group (*allogus*, *rubribarbus*, *abli*), primarily for lack of intergradient or intermediate material from crucial areas, I have little doubt that they are subspecifically related. Inspection of Table 2 shows that there are few scale differences between them, and all are allopatric to one another insofar as known. The body pattern of *rubribarbus* and the dewlap pattern of *abli* are certainly distinctive characters, but at least some populations of *allogus* approach the dewlap pattern (although not the intensity of color) of *abli*. Whether *allogus* and *abli* are considered conspecific appears to be primarily a matter of philosophy; the specific status of *allogus* and *rubribarbus*, because of the geographic approximation of these two species, is perhaps more certain and clear evidence of intergradation should be at hand before considering them subspecifically related. So much of the interior of Oriente Province remains still unknown that the relationships of these two species in that area are still not at all clear.

Considering the disjunct nature of the distribution of *A. allogus* outside of Oriente (in which province it has a fairly broad and more or less continuous distribution), it would not be surprising if some popula-

tions (especially Pinar del Río, and possibly also those of the Sierra de Cubitas and Loma de Cunagua) might not appropriately be regarded as nomenclaturally distinct from other samples. Not only is there evidence that such is the case in these outlying populations, but within Oriente itself there is material (most especially that from Central Miranda, which I assume to be drawn from a basically Sierra de Nipe population) which differs quite markedly in dewlap color and pattern and other features of scalation. However, without resolution of the status of *abli* and *rubribarbus*, it seems profitless to name additional forms of *A. allogus*.

Specimens examined: Anolis allogus: Cuba, Pinar del Río Province. Vallecito de San Juan, 11 km W Cayuco, 1 (AMNH 83161); Cueva de Santo Tomás, 10 km N Cabezas, 18 (AMNH 83131—3 specimens, AMNH 83132—6 specimens; AMNH 96557—9 specimens); north base, Pan de Azúcar, 8 km E Matahambre, 1 (AMNH 83158); San Vicente, 27 (AMNH 83134, AMNH 83153-55, AMNH 83156—6 specimens, AMNH 83157, AMNH 83159, AMNH 83162—6 specimens, AMNH 83163—5 specimens, AMNH 83168—3 specimens, AMNH 83169); Cueva de los Indios, 2 (AMNH 83128); 0.5 mi. (0.8 km) S San Vicente (not mapped), 2 (AMNH 83129-30); Valle de Ancón, 1 (AMNH 83133); south base, Pan de Guajaibón, 3 km W, 13.5 km S Las Pozas, 3 (AMNH 83165—2 specimens AMNH 83166); Soroa, 22 (AMNH 79633-41, AMNH 83146-47, AMNH 83148—5 specimens, AMNH 83149, AMNH 83150—3 specimens, AMNH 83152—2 specimens); Rangel, 2 (AMNH 83171); *Habana Province.* 6.8 mi. (8.9 km) W Jaruco, 2 (AMNH 83151); *Camagüey Province.* Loma de Cunagua, 12 mi. (19.2 km) E Morón, 1 (AMNH 83135); Loma de Cunagua, 14 mi. (22.4 km) E Morón, 21 (AMNH 83136—18 specimens, AMNH 83137—2 specimens, AMNH 83138); 24 km SW Camagüey, Finca El Porvenir, Loma de la Yagua, 3 (AMNH 83144—2 specimens, AMNH 83145); Sierra de Najasa, 3.8 mi. (6.1 km) S, 5.1 mi. (3.2 km) W Ecuador, 2 (AMNH 96562); Martí, 1 (UMMZ 70994); Paso de la Trinchera, 6.5 mi. (10.4 km) NW Banao, 14 (AMNH 83143—7 specimens, AMNH 96558—7 specimens);

Los Paredones, 38 (AMNH 83142—5 specimens, AMNH 96559—20 specimens, AMNH 83688—13 specimens); Olla de Bonnet, 6 (AMNH 83141); 5.5 mi. (8.8 km) NE Banao, 1 (AMNH 83139—3 specimens, AMNH 83140); 11.9 mi. (19.0 km) NW Banao, 3 (AMNH 96560, AMNH 96561—2 specimens); *Oriente Province.* La Cantera, Miranda, 25 (AMNH 83692—1 specimens, AMNH 83693, AMNH 83694—20 specimens); Banes, 2 (MCZ 55982-83); 16 km E Mayarí, 21 (MCZ 63764-79, MCZ 63781-85); nr. Buey Arriba, SW of Bayamo, 8 (MCZ 63756-63); 14.6 mi. (23.4 km) WSW Maffo, 2 (AMNH 96566); Los Negros, Jiguani, 5 (MCZ 8568, MCZ 8571, MCZ 8597-99); Pico Turquino, 2 (UMMZ 80775); Cueva del Aura, Pico Turquino (not mapped), 3 (MCZ 42451-53); Loma Cardero, Pico Turquino, 1 (MCZ 39663); Joachimal, Pico Turquino (not mapped), 1 (MCZ 50172); Pico Palma Mocha, 1 (MCZ 50171); Sierra del Cobre, 5 (UMMZ 80774—2 specimens, MCZ 42535-36, MCZ 42538); Florida Blanca, nr. Alto Songo, 2 (INHS 9259-60); Jutinicú, Alto Songo, 1 (MCZ 8595); "coast south of Pico Turquino," 2 (MCZ 42470-71); "Ocuja," 1 (USNM 138110); 1.9 mi. (3.0 km) SE, 5 mi. (8.0 km) NE Sevilla, 4 (AMNH 96564); Gran Piedra, La Isabelica, 3500 feet (1068 meters), 1.9 mi. (3.0 km) SE, 10 mi. (16.0 km) NE Sevilla, 13 (AMNH 83689—7 specimens, AMNH 83690, AMNH 83691—5 specimens); La Favorita, 3 km E Gran Piedra, 3500 feet (1068 meters), 12 (AMNH 96563—11 specimens, AMNH 96567); Dos Bocas, 4 (AMNH 96565); Mal Paso, Guantánamo (not mapped), 2 (MCZ 8688, MCZ 9358); Mt. Libano, Guantánamo, 4 (MCZ 8433, MCZ 8539-41); "Guantanamo Mt., Pinarea Range," 1 (UMMZ 98016); mountains N Imías, 7 (MCZ 41490-92, UMMZ 80772—4 specimens); upper Río Ovando, 6 (MCZ 42521-23, UMMZ 80773—3 specimens); mouth of Río Yumurí, east side, 32 (AMNH 83704—20 specimens, AMNH 83705—12 specimens); 7 km W Río Yumurí, 3 (AMNH 83703); Baracoa, 2 (AMNH 83702, MCZ 11210); Baracoa, east side, Bahía de Miel, 16 (AMNH 83698); 4.5 km W Baracoa, 3 (AMNH 83695); La Pasana, Baracoa, 1 (MCZ 11212); Cabacú,

Baracoa, 23 (UMMZ 94044—5 specimens, MCZ 47108-09 + 11 specimens, UMMZ 94045 — 5 specimens); Joa, Baracoa, 2 (MCZ 47110-11); Yaticito, Baracoa (not mapped), 6 (UMMZ 94046—4 specimens, MCZ 47120-21); Jair, Baracoa (not mapped), 3 (UMMZ 94047); 9 km W, 3 km S Baracoa, 7 (AMNH 83700); El Yunque de Baracoa, 3 (MCZ 42508-10); west slope, El Yunque de Baracoa, 7 (AMNH 83696—4 specimens, AMNH 83697—3 specimens); 3 mi. (.48 km) S Bahía de Taco, 1 (AMNH 83707); Bahía de Taco, 2 (AMNH 83701, AMNH 83706).

Anolis rubribarbatus: Cuba, Oriente Province, El Puerto de Cananova, nr. Sagua de Tánamo, 4 (MCZ 11868—holotype; MCZ 11910-11); Mina Piloto, Sagua de Tánamo, 9 (MCZ 28760-67, UMMZ 71409—one of two paratypes of *A. patricius*); Moa, 1 (MCZ 50187); Moa, Río Cabañas, 2 (MCZ 63660-61); ca. 7 km E Moa, 12 (MCZ 63665-74, MCZ 63662-63); 35 km S Moa, 1 (MCZ 93651).

Anolis abli: Cuba, Las Villas Province, Salto de Hanabaniilla, 2 (AMNH 83173); 8 mi. (12.8 km) S Manicaragua, 1 (AMNH 96569); 1.4 mi. (2.2 km) NE San Blas, 1 (AMNH 96568); Mina Carlota, 1 (UMMZ 63086); Topes de Collantes, 1 (INHS 9264); 1.8 mi. (2.9 km) S Topes de Collantes, 8 (AMNH 96570); 4 km W, 12 km N Trinidad, 7 (AMNH 83172—6 specimens, AMNH 95968).

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