7. Science (including biology) is the discipline which should receive the primary emphasis when integrating energy education/conservation into the curriculum.
8. New energy education/conservation programs should be directed first at elementary schools and then at secondary schools, colleges and adults, in that order.

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# GEOGRAPHIC VARIATION IN CUBAN AND MESOAMERICAN POPULATIONS OF *ANOLIS SAGREI* DUMERIL AND BIBRON (REPTILIA: IGUANIDAE)

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## Abstract

Seventeen meristic, mensurable and other characters are analyzed in 22 Cuban and Mesoamerican populations of *Anolis sagrei* Duméril and Bibron (Reptilia: Iguanidae). Geographic variation and sexual dimorphism are determined for each character in each population to ascertain the perimeter of character variation and its subsequent taxonomic implication.

The Cuban and Mesoamerican populations are consubspecific, allocable to *A. s. sagrei*. The Mesoamerican population are derivatives of the Cuban population, having arrived on the Mesoamerican coast at different times and from diverse Cuban populations.

## Introduction

*Anolis sagrei* Duméril and Bibron inhabits numerous islands of the Bahamas, Jamaica, the Swan Islands, the Cayman Islands, the Florida Keys, and mainland Florida. Populations also occur on the littoral of eastern Mesoamerica and on the immediate off-shore islands and cays from southern México south to Honduras. These populations and perhaps others yet unreported are probable derivatives of the ancestral Cuban populations.

The taxonomic status of the insular and mainland populations, currently allocated to *A. sagrei*, is unresolved. The populations of Cayman Brac (*luteosignifer* Garman), the Swan Islands (*nelsoni* Barbour), the Bahamas (*ordinatus* Cope), Mesoamerica (*mayensis* Smith & Burger), and Jamaica and Cuba (*sagrei* Duméril & Bibron) alternatively have been considered species, subspecies, or conspecific with one or more populations.

The taxonomic allocations of the widely distributed populations are complicated by the variability of the purportedly diagnostic characters, the facility of *A. sagrei* to establish extra-territorial colonies, and the preponderant insularity of the species. Stuart (1955) succinctly summarized the difficulties inherent in the systematics of *sagrei*, stating that it would be futile to attach names to the extra-territorial populations until variation has been thoroughly analyzed in the ancestral Cuban populations.

The primary intent of this study is the delimitation of the parameters of variation of selected characters within the ancestral Cuban population and its Mesoamerican derivatives. Detailed analyses will permit subsequent comparisons between the ancestral and other extra-territorial populations.

## Nomenclatorial Review

The lengthy synonomies and re-arrangements evidence the taxonomic referrals of the populations of *A. sagrei*. The nomenclatorial history of the Cuban and Mesoamerican populations, of primary interest herein, is inextricably associated with those of other populations.

Duméril and Bibron (1837) described *A. sagrei* on the basis of co-types reputedly of Cuban provenance. Cocteau (1838) described *A. de la sagra* from Cuba. Gray (1840) named *A. nebulosa* and Fitzinger (1843) described *Dactyloa sagrei*, both from Cuba. Hallowell (1856) was the first to associate *sagrei* with a definite locality (Cienfuegos, Provincia de Las Villas).

Cope (1864) proposed the name *A. ordinatus* for two specimens from the "West Indies." Boulenger (1885) synonomyzed *D. sagrei* Fitzinger, *Draconura catenata* Gosse, *A. ordinatus* Cope, and *A. nebulosa* Gray with *A. sagrei*. Cope (1887) referred the Cuban and certain Bahamian populations to *A. ordinatus*. After Cope's allocation (1894) of specimens from New Providence, Eleuthera, and other Bahamian islands to *A. sagrei*, Gunther (1902) and Barbour (1904) synonomyzed *A. ordinatus* with *A. sagrei*. Stejneger (1905) agreed with Garman's conclusions (1887) while Barbour (1910) reiterated the conspecificity of the Cuban and Bahamian populations.

Rosen (1911) stated that *sagrei* and *ordinatus* represented ontogenetic stages of one species. Barbour (1914), however, referred Cuban populations to *sagrei* and Bahamian populations to *ordinatus*. He later (1930) reaffirmed the arrangement.

With reservations, Cochran (1934) allocated numerous Bahamian populations to *A. ordinatus*, commenting that the status of the populations would remain uncertain until specimens from other parts of the range were minutely compared.

Oliver (1948) agreed with Barbour's earlier (1937) use of the trinomial to designate the relationship of the Cuban, Bahamian, and Key West populations. Smith (1946) tacitly acknowledged the subspecific status of *sagrei* and *stejnegeri*, observing that they were separable only on the color of the interstitial skin of the dewlap. Barbour and Loveridge (1946) retained the specific status of *stejnegeri*, although they had previously suggested that *sagrei* and *stejnegeri* were subspecifically distinct.

Duellman and Schwartz (1958) concluded that the Bahamian, Cuban, and Floridian populations merited trinomial designation, yet Goin and Goin (1960) applied the trinomial to the Key West population.

Ruibal (1964) maintained the subspecific status of the Cuban and Bahamian populations.

Smith and Burger (1947) distinguished the Central American populations under the trinomial *mayensis;* Smith and Taylor (1950) recognized the distinction. Stuart (1955) rejected the aforementioned conclusion, noting that the Central American population does not differ from the parental Cuban stock. Neil and Allen (1959) recognized *mayensis*, and remarked that the population from Belize was morphologically distinct. Stuart (1963) synonomyzed *mayensis* with *sagrei*, and Duellman (1965) concurred.

## CHARACTERS SELECTED FOR ANALYSIS

The characters chosen for analysis are referred arbitrarily to three categories: meristic, mensurable and ratios, and non-mensurable.

Population samples from 22 Cuban and Mesoamerican localities, comprising 1,577 specimens, were examined (Fig. 1, Table 1), each sample containing a minimum of ten specimens. Data were obtained from an additional 196 Cuban and 241 Mesoamerican specimens representing 38 Cuban and eight Mesoamerican localities.

Of the 25 characters analyzed, the following—of taxonomic importance—are discussed hereinafter: number of rows of vertebrals (middorsals), ventrals, loreals, postrostrals, digital lamellae, scales forming the *canthus rostralis*, included in the interparietal-rostral distance, included in the frontal ridges, defining the free edge of the dewlap; nature of the supraorbital semicircles; ratios of snout-vent length (sv) to head length (hl), s-v to tibia length (tl), vertebral scale rows (vs) to ventral scale rows (ves); carination, or the absence thereof, of the vertebral and ventral scales; extent of mottling of the scales of the free edge of the dewlap, and the color of the interstitial skin of the dewlap.

The meristic and mensurable characters are treated by standard statistical procedure (Cazier and Bacon, 1949). Non-meristic and non-mensurable characters are evaluated subjectively.

## ANALYSIS OF CHARACTERS

The vertebral scales are counted from a point on a line tangent to the posterior insertion of the humerus to a point on a line tangent to the anterior insertion of the femur. The vertebral and three or four rows of paravertebrals are distinctly enlarged and abruptly differentiated from the dorsolateral scales.

Modifications were utilized by Smith and Burger (1947) and Stuart (1955). Zweifel (1959) noted that the method favored by workers in anoline taxonomy is to count the scales contained in a standardized body segment. He rejected the procedure because ontogenetic changes in relative size of the member may introduce errors.

The mean number of vertebrals is not geographically variable. Neither clines nor sexual dimorphism is indicated. Although populations 10-12 diverge from other populations, the magnitude of divergence is not significant (Table 2).

The number of rows of ventrals are counted on a line tangent to the posterior insertion of the humerus to a line tangent to the anterior insertion of the femur (*fide* Stuart, 1963). The method varies slightly from that employed by Smith and Burger (1947).

The mean values of populations 12 and 14, exceeding those of other populations, are closely approximated, however, by other populations (Table 2). Neither clines nor sexual dimorphism is indicated.

The loreals are normally aligned in three to six antero-posteriorly-oriented rows. The alignment and number of rows have been accorded diagnostic significance (Smith and Burger, 1947).

Neither significant geographic variation nor clines are indicated among the populations, although populations 12 and 21 have means exceeding other populations (Table 2). The means, however, approximate those of other populations. Sexual dimorphism is not indicated.

The postrostrals (terminology *fide* Smith, 1946) lie immediately posterior to the rostral; dorsolaterally they are delimited by the nasals.

No significant geographic variation nor clinal tendencies are noted among the populations (Table 2). Sexual dimorphism is not present. Although populations 14, 15, and 22 possess greater means than other populations, they are approximated by those of certain populations and fall within the range of variation of others.

The number of digital lamellae on the inferior surface of the right hind foot is of frequent diagnostic use. Collette (1961) noted an increase in number correlated with an increase in body size. Arboreal species, larger and heavier than terrestrial forms, have a larger number of digital lamellae.

TABLE 1. *Cuban and Mesoamerican population samples of* Anolis sagrei.

| Locality | Populations Number | Specimens Examined |
|---|---|---|
| **CUBA** | | |
| *Provincia de Pinar del Río* | | |
| Cabaña, 8.5 mi. SE; Cabañas; Ingeniería Varilas | 1 | 36 |
| Guanajay | 2 | 51 |
| San Vicente, 4.4 mi. NW; San Vicente, 1 mi. S; Cueva de los Indios | 3 | 49 |
| San Diego de los Baños | 4 | 39 |
| *Provincia de la Habana* | | |
| Habana | 5 | 15 |
| Santiago de las Vegas | 6 | 13 |
| *Provincia de Las Villas* | | |
| Cienfuegos; Soledad | 7 | 62 |
| Trinidad | 8 | 211 |
| *Provincia de Camaguey* | | |
| Martí | 9 | 17 |
| *Provincia de Oriente* | | |
| Yara | 10 | 11 |
| Yara, 27 kms. S | 11 | 38 |
| **MESOAMERICA** | | |
| **MÉXICO** | | |
| *State of Campeche* | | |
| Cd. del Carmen | 12 | 355 |
| *Territory of Quintana Roo* | | |
| Isla Contoy | 13 | 47 |
| Isla Mujeres | 14 | 306 |
| San Miguel de Cozumel | 15 | 64 |
| **BRITISH HONDURAS** | | |
| Manatee | 16 | 14 |
| Tom Owen's Camp | 17 | 11 |
| Glover's Reef | | |
| SW Cays | 18 | 30 |
| Middle Cay | 19 | 32 |
| Belize; Belize, 1 mi. NW | 20 | 157 |
| Turneffe Id., Grant Point | 21 | 18 |
| **HONDURAS** | | |
| Puerto Cortés | 22 | 10 |

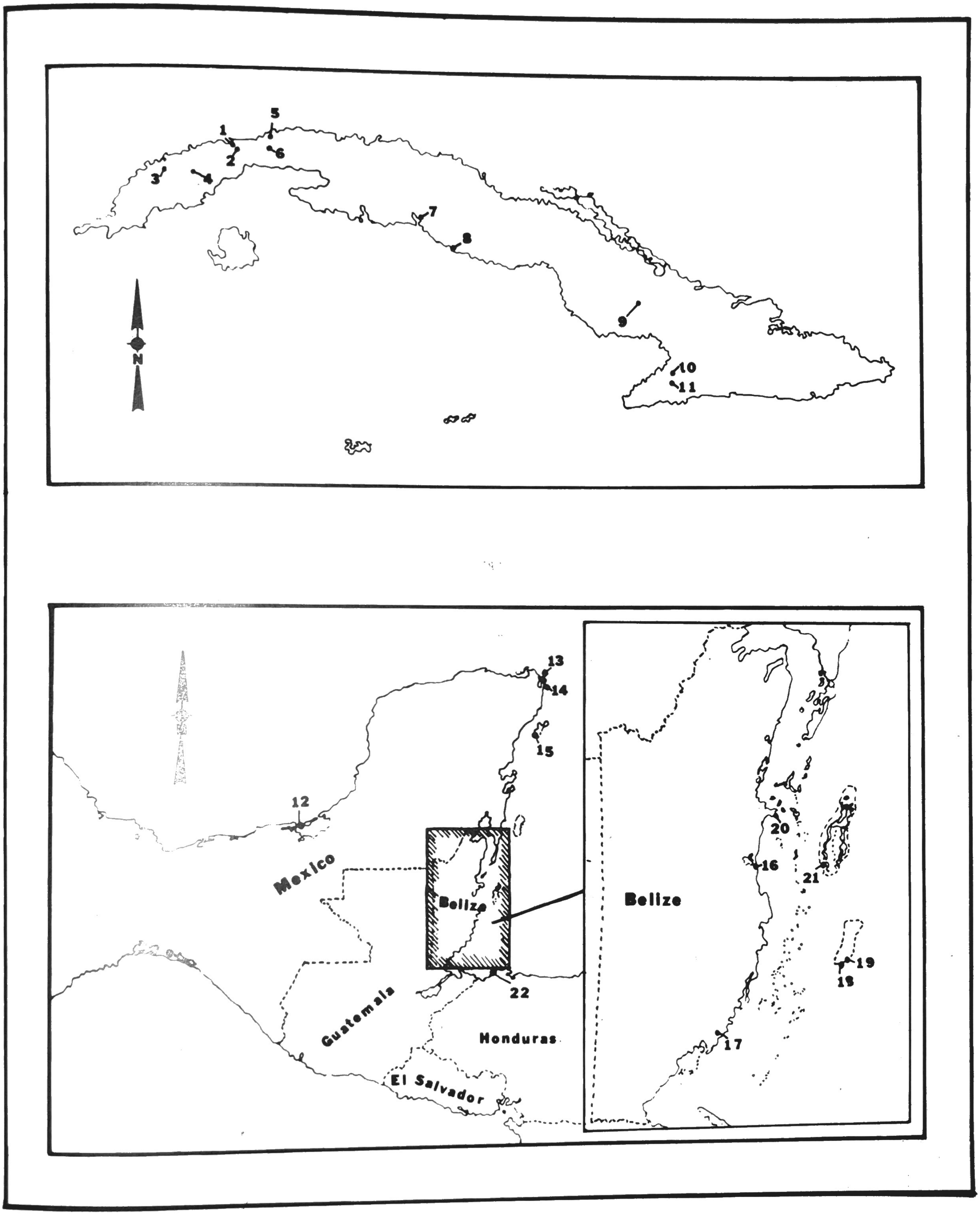


FIG. 1: *Cuban and Mesoamerican localities of populations of* Anolis sagrei *Duméril and Bibron.*

TABLE 2: *Georgraphic variation in mean number of vertebral, ventral, loreal, and postrostral scales among selected population samples of Cuban and Mesoamerican populations of* Anolis sagrei.

| Population Number | Vertebral Scales | Ventral Scales | Loreal Scales | Postrostral Scales |
|---|---|---|---|---|
| 1 | 52.7±5.0±0.8(39-60)36 | 41.0±4.7±0.7(35-52)37 | 17.1±2.0±0.0(10-21)92 | 5.9±0.0±0.0(5-7)38 |
| 2 | 53.8±5.4±0.7(42-67)51 | 44.4±3.6±0.5(37-53)50 | 19.4±3.9±0.3(14-24)101 | 5.9±0.0±0.0(5-7)50 |
| 3 | 58.8±6.8±0.9(46-75)49 | 42.9±4.1±0.7(37-54)52 | 19.8±3.1±0.4(13-29)60 | 6.3±0.5±0.0(5-8)48 |
| 4 | 58.4±11.8±2.1(41-86)30 | 43.2±3.9±0.7(37-54)29 | 19.9±3.2±0.4(13-28)59 | 6.4±0.4±0.0(6-7)31 |
| 5 | 53.9±8.8±2.4(40-66)15 | 44.2±3.3±0.8(31-52)16 | 19.0±3.3±0.5(13-26)31 | 5.8±0.0±0.0(5-6)16 |
| 6 | 55.8±4.3±1.2(49-63)13 | 42.3±3.0±0.8(37-47)13 | 20.5±4.2±0.8(12-31)24 | 5.9±0.0±0.0(5-6)13 |
| 7 | 56.8±14.4±1.8(46-84)62 | 44.7±4.3±0.5(37-58)62 | 19.4±3.0±0.2(13-30)120 | 5.8±0.0±0.0(5-7)61 |
| 8 | 63.1±8.8±0.6(43-89)211 | 47.4±4.4±0.3(36-60)191 | 17.2±3.3±0.1(11-29)389 | 5.6±0.0±0.0(5-7)310 |
| 9 | 54.0±4.4±1.0(46-62)17 | 41.2±3.3±0.8(40-51)17 | 18.9±3.3±0.5(14-35)34 | 5.7±0.0±0.0(5-8)16 |
| 10 | 73.5±6.6±1.9(64-83)11 | 47.3±2.0±0.6(39-51)11 | 20.8±3.3±0.7(15-30)22 | 6.0±0.0±0.0(6)10 |
| 11 | 76.9±7.7±1.2(60-92)38 | 47.8±3.3±0.5(37-57)38 | 20.7±3.3±0.3(15-30)78 | 5.9±0.0±0.0(5-7)38 |
| 12 | 70.9±7.5±0.2(50-95)355 | 50.5±3.4±0.3(37-64)367 | 25.2±3.4±0.1(16-41)733 | 6.0±0.1±0.0(5-7)369 |
| 13 | 61.1±6.4±0.9(47-83)47 | 47.2±3.8±0.5(39-55)47 | 23.6±3.9±0.4(15-31)85 | 6.5±0.7±0.1(6-7)48 |
| 14 | 62.0±5.7±0.3(46-81)306 | 50.6±3.3±0.1(41-58)300 | 23.7±3.3±0.1(15-35)591 | 6.7±0.1±0.0(5-8)305 |
| 15 | 64.9±5.8±0.7(54-80)64 | 47.2±3.9±0.4(40-64)67 | 21.6±2.6±0.2(15-28)129 | 6.8±0.4±0.0(5-8)66 |
| 16 | 51.7±5.3±1.4(43-61)14 | 45.6±5.4±1.4(39-55)14 | 23.0±2.6±0.5(16-27)25 | 6.4±0.7±0.1(6-8)15 |
| 17 | 48.9±6.5±1.9(42-59)11 | 45.3±4.0±1.1(39-51)12 | 24.3±4.6±1.0(21-38)21 | 5.9±0.2±0.0(5-6)12 |
| 18 | 50.9±7.2±1.3(37-62)30 | 46.0±5.7±1.1(39-59)12 | 20.3±3.8±0.4(12-26)62 | 6.0±0.3±0.0(6-7)32 |
| 19 | 50.1±6.6±1.1(40-65)32 | 44.3±9.2±1.6(36-53)32 | 23.3±3.4±0.4(15-31)61 | 5.9±0.5±0.0(5-7)34 |
| 20 | 63.7±17.7±1.4(43-71)157 | 47.4±3.5±0.2(37-56)172 | 18.1±8.5±0.4(14-30)408 | 6.3±0.5±0.1(5-8)171 |
| 21 | 57.2±7.7±1.8(47-72)18 | 49.5±3.9±0.8(43-57)19 | 25.3±3.5±0.5(17-33)35 | 5.8±1.4±0.3(6-7)19 |
| 22 | 60.3±2.7±0.8(57-65)10 | 47.5±3.2±1.0(40-51)10 | 20.7±2.2±0.4(18-25)20 | 6.7±0.4±0.1(6-7)10 |

Explanation of Table: Mean ± 1 Standard Deviation ± 1 Standard Error (Range of Character) Number of Specimens, Counts, or Ratios

Males average two more lamellae than females. Significant geographic variations and clines are not noted (Table 3).

In *sagrei* the *canthus rostralis* is well defined. The number of scales within the *canthus rostralis* constitutes the character.

The mean of population 12, greater than those of other populations, is closely approached by the means of populations 13-14 and overlapped in standard deviations by others (Table 3). Sexual dimorphism and clinal variation are insignificant.

The interparietal-rostral distance includes the number of scales intercepted by a straight line projected from the anterior edge of the interparietal to the posterior edge of the rostral. Its primary objective is to ascertain the degree of fragmentation of the cephalic scutes.

Significant geographic variation, clines, and sexual dimorphism do not obtain (Table 3).

The population samples are characterized by strongly differentiated frontal ridges. The configuration of, and the scales contained within, the frontal ridges are of taxonomic significance. Barbour (1914) distinguished *A. nelsoni* and *A. greyi* from *A. sagrei* primarily on the conformation of the frontal ridges.

The mean number of scales in the frontal ridges is relatively constant (Table 3). Neither clines, geographic variation, nor sexual dimorphism is indicated. Emphasis is placed upon the configuration of the frontal ridges.

The number of scales on the free edge of the dewlap is counted at a point anteriorly at which the dewlap scales are distinguishable from adjacent gular scales to a point posteriorly at which the dewlap scales merge with adjacent scales.

The mean number of scales is not significantly variable (Table 4).

In the ratio s-v/hl, hl is defined as the distance from the anterior edge of the auricular depression to the tip of the rostral. S-V is standard: from the anteriormost point of the rostral to the anterior lip of the vent. Smith and Burger (1947) reported the character to be non-diagnostic in the separation of *mayensis* and *sagrei.*

The mean geographic variations among the populations are not significant (Table 4). Neither clines nor sexual dimorphism is evident within the geographic entities.

In the ratio s-v/tl, tl is measured from the articulation of the

TABLE 3: *Geographic variation in mean number of digital lamellae, scales of the* Canthus rostralis, *scales in the interparietal-rostral distance, and scales in the frontal ridges among selected population samples of Cuban and Mesoamerican populations of* Anolis sagrei.

| Population Number | Digital Lamellae | Scales of Canthus Rostralis | Interparietal-Rostral Distance | Frontal Ridges |
|---|---|---|---|---|
| 1 | 37.2±2.2±0.3(32-41)38 | 4.0±0.0±0.0(3-5)75 | 14.0±3.8±0.6(12-17)38 | 5.6±0.0±0.0(4-7)75 |
| 2 | 39.7±2.2±0.3(34-45)47 | 3.9±0.0±0.0(3-6)126 | 14.6±1.0±0.1(12-19)51 | 5.8±0.0±0.0(4-8)102 |
| 3 | 37.0±0.0±0.0(32-42)37 | 4.1±0.1±0.0(3-5)60 | 13.7±1.5±0.2(11-18)48 | 5.2±0.7±0.1(4-7)92 |
| 4 | 36.5±2.4±0.4(32-41)30 | 4.1±0.3±0.0(3-5)59 | 14.1±1.8±0.3(12-21)30 | 5.6±0.8±0.1(4-9)92 |
| 5 | 37.0±2.4±0.5(30-41)20 | 4.3±0.0±0.0(4-6)32 | 14.2±1.0±0.2(12-17)17 | 5.5±0.6±0.1(5-7)32 |
| 6 | 35.4±2.8±0.7(31-40)13 | 4.1±0.0±0.0(4-5)26 | 14.8±1.0±0.2(12-17)13 | 6.1±0.6±0.1(5-7)26 |
| 7 | 37.5±2.0±0.2(33-43)71 | 4.6±0.0±0.0(3-6)131 | 14.8±1.0±0.1(12-19)63 | 5.5±0.1±0.0(5-7)126 |
| 8 | 36.2±2.0±0.4(26-42)194 | 4.1±0.0±0.0(3-6)375 | 15.0±1.0±0.0(10-19)195 | 5.8±0.1±0.0(5-8)390 |
| 9 | 35.9±2.2±0.5(32-41)17 | 4.0±0.0±0.0(3-5)34 | 14.1±1.1±0.2(13-16)17 | 5.7±0.1±0.0(5-7)34 |
| 10 | 37.0±1.4±0.4(34-40)11 | 4.5±0.0±0.0(4-5)20 | 15.6±0.8±0.2(14-17)10 | 6.4±0.1±0.0(5-8)18 |
| 11 | 36.5±1.0±0.1(33-40)38 | 4.2±0.0±0.0(4-6)76 | 16.8±1.0±0.1(14-18)38 | 5.6±0.1±0.0(4-7)76 |
| 12 | 40.5±2.4±0.1(33-45)369 | 6.0±0.0±0.0(4-8)728 | 16.1±1.3±0.4(12-27)362 | 6.0±0.1±0.0(5-8)626 |
| 13 | 40.1±1.8±0.2(37-44)47 | 5.7±0.9±0.1(4-7)79 | 16.6±2.2±0.3(14-19)42 | 6.0±0.1±0.0(5-7)91 |
| 14 | 40.5±1.9±0.1(35-47)304 | 5.8±0.1±0.0(4-8)603 | 16.9±1.2±0.0(13-21)302 | 5.8±0.2±0.1(4-8)498 |
| 15 | 37.6±2.2±0.2(31-42)68 | 5.7±0.4±0.0(5-7)121 | 17.0±1.5±0.2(13-23)60 | 5.8±0.1±0.1(4-7)122 |
| 16 | 40.4±1.7±0.4(37-44)15 | 4.8±0.7±0.1(4-6)29 | 15.2±1.0±0.3(14-17)12 | 6.0±0.5±0.1(5-7)26 |
| 17 | 39.5±2.7±0.7(35-44)12 | 5.1±0.9±0.2(4-6)19 | 14.6±1.3±0.3(12-17)12 | 6.5±0.7±0.1(5-8)22 |
| 18 | 38.[illegible]±2.2±0.3(34-43)36 | 4.7±0.5±0.0(4-6)67 | 15.1±1.1±0.2(13-17)31 | 5.9±0.6±0.1(5-7)67 |
| 19 | 40.7±2.4±0.4(35-44)34 | 4.6±0.5±0.0(4-6)65 | 14.6±1.3±0.2(13-17)34 | 5.9±0.6±0.1(4-7)68 |
| 20 | 40.0±2.1±0.1(35-45)172 | 5.1±0.7±0.0(3-7)344 | 15.2±2.0±0.1(12-19)170 | 5.9±0.6±0.0(4-8)336 |
| 21 | 4[illegible]±2.2±0.5(36-45)19 | 5.2±0.4±0.1(5-6)38 | 16.7±1.6±0.3(14-20)17 | 6.2±1.2±0.2(5-8)38 |
| 22 | 41.4±1.8±0.5(39-43)10 | 5.5±0.5±0.1(5-6)19 | 15.7±1.6±0.2(13-18)9 | 5.9±0.3±0.1(5-6)18 |

Explanation of Table: Mean ± 1 Standard Deviation ± 1 Standard Error (Range of Character) Number of Specimens, Counts, or Ratios

tibia with femur and pes when both are placed at right angles to the tibia.

The observed geographic variation merits comment (Table 4). Populations 3 and 11 are longer-legged than adjacent populations. Those of the cays of Belize are also longer-legged than their mainland conspecifers. The aforementioned are also divergent from the insular Mexican populations. Nevertheless, the geographic variation observed in these populations is either closely approximated by or similar to the means of one or more Cuban populations. Ontogenetic variation and sexual dimorphism are not noted when the components of the ratio are plotted separately.

The ratio vsr/ves is used to avoid subjective evaluation of relative sizes of scales. In numerous descriptions and diagnoses of *sagrei* (Rosen, 1911; Barbour, 1914, 1931; Smith and Burger, 1947; Stuart, 1955, 1963) the size of scales is subjectively compared.

The vertebral scales are consistently larger than the ventral scales (Table 4). The mean of population 12, greater than all others, is overlapped in standard deviational variance by those of populations 11-13. Clines and sexual dimorphism are not observable.

In agreement with Ruibal's observations (1964), the vertebral scales are strongly carinate in all populations.

The nature of the supraorbital semicircles exhibits several variations considered diagnostic in subspecific allocations of *sagrei* populations. Two primary conditions prevail: (a) supraorbital semicircles in contact medially (b) supraorbital semicircles separated by one or more rows of intervening scales. Contact may occur between the anterior, the posterior, or both pairs of scales. The intervening rows vary from one to three.

In all population samples analyzed, a high percentage of specimens possess separated supraorbital semicircles (Table 5). In three populations (3, 6, 18), 70% or fewer of the individuals have separated supraorbital semicircles. However, the percentage is either closely approached by other populations or the popula-

TABLE 4: *Geographic variation in mean number of scales defining the free edge of the dewlap and ratios of snout-vent length (S-V) to head length (HL), S-V to tibia length (TL) and vertebral scale rows (VSR) to ventral scale rows (VeSR) among selected population samples of Cuban and Mesoamerican populations of* Anolis sagrei.

| Population Number | Scales Defining Free Edge of Dewlap | Ratio of S-V to HL | Ratio of S-V to TL | Ratio of VSR to VeSR |
|---|---|---|---|---|
| 1 | 35.6±4.5±0.9(27-43)25 | 3.3±0.0±0.0(2.9-3.8)38 | 4.0±0.0±0.0(3.3-4.5)38 | 1.2±0.0±0.0(0.9-1.5)34 |
| 2 | 35.8±3.8±0.6(30-44)40 | 3.5±0.2±0.0(3.1-4.3)51 | 4.3±0.3±0.0(3.7-5.0)51 | 1.2±0.1±0.0(0.9-1.5)50 |
| 3 | 36.2±4.1±1.2(29-44)11 | 3.2±0.3±0.0(2.2-3.9)49 | 3.7±0.3±0.0(2.5-5.1)47 | 1.2±0.1±0.0(0.9-1.6)47 |
| 4 | 36.3±4.3±1.3(29-42)11 | 3.4±0.2±0.0(3.0-4.0)30 | 4.4±0.3±0.0(3.9-5.3)30 | 1.3±0.1±0.0(1.0-1.7)29 |
| 5 | 35.3±3.3±0.9(28-43)13 | 3.2±0.0±0.0(2.7-3.7)16 | 4.0±0.0±0.0(3.6-4.9)16 | 1.2±0.0±0.0(0.8-1.8)15 |
| 6 | 29.0±5.4±1.7(24-41)10 | 3.5±0.0±0.0(3.4-3.8)13 | 4.3±0.2±0.0(4.0-4.8)13 | 1.3±0.0±0.0(1.2-1.6)13 |
| 7 | 33.6±3.3±0.5(24-43)38 | 3.4±0.0±0.0(2.2-4.8)63 | 4.0±0.0±0.0(2.8-5.4)63 | 1.3±0.0±0.0(1.0-2.1)61 |
| 8 | 38.3±5.4±0.4(26-56)150 | 3.5±0.0±0.0(2.8-4.1)199 | 4.1±0.0±0.0(3.2-5.1)195 | 1.3±0.0±0.0(1.0-1.8)192 |
| 9 | 29.4±3.3±0.1(22-38)17 | 3.6±0.0±0.0(3.4-4.1)17 | 4.4±0.0±0.0(4.1-4.8)17 | 1.2±0.0±0.0(1.0-1.4)17 |
| 10 | 27.3±3.0±1.0(26-30)10 | 3.6±0.0±0.0(3.2-4.3)11 | 4.1±0.0±0.0(3.9-4.7)11 | 1.5±0.0±0.0(1.3-1.9)11 |
| 11 | 35.3±4.4±0.9(25-45)21 | 3.1±0.0±0.0(2.3-3.7)38 | 3.8±0.0±0.0(2.7-4.6)38 | 1.6±0.0±0.0(1.3-2.1)38 |
| 12 | 32.4±1.5±0.0(15-41)200 | 3.6±0.4±0.0(2.4-7.0)372 | 4.5±0.1±0.0(3.5-8.7)372 | 2.0±0.2±0.0(1.6-3.8)361 |
| 13 | 30.6±4.4±0.8(23-39)27 | 3.5±0.2±0.0(3.1-4.3)47 | 4.2±0.3±0.5(3.7-5.2)47 | 1.3±0.1±0.0(1.0-1.8)45 |
| 14 | 32.1±3.1±0.2(23-41)174 | 3.5±0.0±0.0(2.8-4.4)304 | 4.4±0.1±0.0(3.5-8.8)303 | 1.2±0.1±0.0(1.0-1.8)302 |
| 15 | 33.5±2.5±0.4(28-39)34 | 3.6±0.2±0.0(2.3-4.3)68 | 4.4±0.3±0.0(2.9-5.3)64 | 1.3±0.1±0.0(1.1-1.6)64 |
| 16 | 37.3±6.8±2.0(24-47)11 | 3.2±0.1±0.0(3.0-3.6)14 | 3.7±0.2±0.0(3.3-4.3)14 | 1.0±0.1±0.0(0.8-1.4)13 |
| 17 | | 3.4±0.2±0.0(3.0-3.7)12 | 3.9±0.2±0.0(3.6-4.2)12 | 1.0±0.1±0.0(0.9-1.4)11 |
| 18 | 32.3±4.3±1.0(25-42)16 | 3.3±0.2±0.0(2.8-4.2)30 | 3.8±0.2±0.0(3.2-4.5)30 | 1.1±0.1±0.0(0.8-1.4)25 |
| 19 | 35.3±3.8±0.7(29-44)24 | 3.2±0.2±0.0(2.6-3.7)34 | 3.6±0.2±0.0(3.2-4.3)31 | 1.0±0.1±0.0(0.8-1.4)31 |
| 20 | 33.8±4.1±0.4(26-46)104 | 3.2±0.2±0.1(2.6-5.0)173 | 3.7±0.5±0.0(3.0-4.6)172 | 1.[illegible]±0.2±0.0(0.8-1.6)172 |
| 21 | 36.3±3.9±1.0(29-40)13 | 3.4±0.3±0.0(2.9-4.6)19 | 3.8±0.8±0.1(3.1-4.2)19 | 1.1±0.1±0.0(0.9-1.4)18 |
| 22 | 33.1±2.4±0.9(30-38)8 | 3.7±0.1±0.0(3.6-3.9)10 | 4.1±0.4±0.1(3.2-4.5)10 | 1.2±0.1±0.0(1.1-1.5)10 |

Explanation of Table: Mean ± 1 Standard Deviation ± 1 Standard Error (Range of Character) Number of Specimens, Counts, or Ratios

tions are geographically adjacent to populations in which a high percentage obtains.

The character evidences neither geographic variation, clines, nor sexual dimorphism.

Non-meristic and non-mensurable characters in the Cuban populations are analyzed by provincial rather than by intra-population samples. The geographic grouping for the study of these characters is arbitrary.

The degree of carination of the vertebral and ventral scales is considered diagnostic. Garman (1888) distinguished *sagrei* from *luteosignifer,* in part, on the stronger carination of *sagrei.* Barbour (1914) associated *nelsoni* with *sagrei* on the basis of stronger ventral carination, noting that the carination is weaker in *A. greyi.* Conversely, he referred *A. bremeri* to the *sagrei* complex on its pronounced ventral carination.

Except for a single population, the ventral scales are strongly carinate and mucronate. A series of specimens from Trinidad, Provincia de Las Villas, exhibits a marked reduction in ventral carination, confirming the observation of Ruibal and Williams (1961). On this character, they referred *sagrei* to the *homolechis* complex. Such divergence is not observed in other populations. Neither ontogenetic nor sexual dimorphism is present.

The extent and intensity of mottling of the scales of the free edge of the dewlap has been accorded diagnostic significance (Smith and Burger, 1947; Oliver, 1948).

The incidence of mottling of the scales of the anterior one-half of the dewlap is consistently low, with the exception of the sample from Tom Owen's Cay (38%). The incidence of mottling of the scales of the posterior one-half of the dewlap is highly variable. Mottling of the entire free edge of the dewlap is of low frequency, except for several Mesoamerican populations. The immaculate condition is encountered in all population samples.

TABLE 5: *Geographic variation in the nature of the supraorbital semicircles among selected population samples of Cuban and Mesoamerican populations of* Anolis sagrei.

| Population Name | % Supraorbital Semicircles in Contact | % Supraorbital Semicircles Separated | Number of Specimens in Sample |
|---|---|---|---|
| 1 | 0 | 100 | 33 |
| 2 | 6 | 94 | 52 |
| 3 | 31 | 69 | 67 |
| 4 | 3 | 97 | 30 |
| 5 | 14 | 86 | 21 |
| 6 | 31 | 69 | 13 |
| 7 | 6 | 94 | 62 |
| 8 | 7 | 93 | 196 |
| 9 | 0 | 100 | 17 |
| 10 | 0 | 100 | 11 |
| 11 | 3 | 97 | 38 |
| 12 | 0.3 | 99.7 | 367 |
| 13 | 20 | 80 | 50 |
| 14 | 6 | 94 | 296 |
| 15 | 2 | 98 | 63 |
| 16 | 0 | 100 | 13 |
| 17 | 17 | 83 | 12 |
| 18 | 36 | 64 | 36 |
| 19 | 29 | 71 | 34 |
| 20 | 10 | 90 | 173 |
| 21 | 6 | 94 | 18 |
| 22 | 0 | 100 | 11 |

The character is neither geographically nor ontogenetically variable.

No single character has been accorded greater diagnostic significance in determining inter-populational relationships than the color of the interstitial skin of the dewlap.

Garman (1888) observed that *A. luteosignifer* differed from Cuban *sagrei* in possessing a yellow rather than a red dewlap. Stejneger (1905) remarked that Bahamian and Cuban specimens are separable only on the basis of dewlap color. Rosen (1911) claimed that differences in dewlap color are ontogenetic. Barbour (1914) noted that *A. nelsoni* ("deep olive-colored dewlap") is immediately distinguishable from *sagrei* ("flaming orange") in life. He further noted that *A. bremeri* (maroon dewlap) of Cuba is readily distinguishable from Cuban *sagrei.* Grant (1940) concluded that *A. luteosignifer* is unquestionably differentiated from Cuban *sagrei,* primarily on the character of dewlap color. Oliver (1948) determined that dewlap color in preserved males is one of the two diagnostic characters distinguishing three geographic races of *sagrei.* Smith and Burger (1947) also accorded taxonomic importance to the character in the diagnosis of *mayensis.* Stuart (1955) wrote that ecologic data and accurate color descriptions of the dewlap are necessary to unravel the systematics of *sagrei.* Duellman and Schwartz (1958) concluded that the populations of the Bahamas, Cuba, and Florida could be diagnosed, in part, on the color of the gular appendage in preserved specimens.

In the preserved individuals examined, the color of the interstitial skin varies from light- to dark-gray. Ruibal (1964) noted a greater variance, from almost colorless to black. He commented that the strength of the preservative, the length of time in preservation, and the specific preservative will influence the color of the dewlap.

Many preserved males retain vestiges of red, orange, and yellow, the presumed colors in living males. Field observations confirm that the red-orange-yellow polychromatism in living males is expressed as light- to dark-gray in preserved material.

In preserved Cuban males, traces of red and orange dewlaps vary from 25% to 90% of the population samples (Table 6) and yellow-tinged dewlaps from 4% to 9%. Light-gray (absence of pigment), present in all populations, varies from 4% to 11%. Dark-gray dewlaps occur in 1% of the males comprising the sample from the Province of Pinar del Río. On the assumption that light-gray interstitial skin originally contained red, orange, or yellow pigment, 99% of the Cuban population samples are referrable to the previously defined color spectrum.

Observations on living males confirm those noted on preserved specimens. Gundlach (1880) reported the dewlap to be orange-brown in Cuban specimens. Stejneger (1905) recorded crimson and scarlet-crimson in the island populations. Barbour and Ramsden (1919) reported brick-red; Barbour (1930) reported orange or reddish-orange dewlaps. Duellman and Schwartz (1958) stated that the interstitial color is orange in Cuban males.

The dewlap color is preserved Mesoamerican males in polychromatic, paralleling that observed in Cuban populations. Red, orange, and yellow occur in approximately the same frequencies as in Cuban males. Light-gray dewlaps attain a high frequency.

Living males from Belize and Stann Creek possess reddish dewlaps. A male from El Cayo, near the Guatemalan frontier, also has a reddish dewlap. Specimens from South Water Cay have yellow dewlaps (personal observations).

The interstitial skin of males from Isla del Carmen, Isla Cozumel, and Isla Mujeres are reported to be either red-yellow or yellow (personal communication, Clarence McCoy). Duellman (1965) noted that Yucatecan males have orange dewlaps.

The character evidences neither clines, geographic variation, nor ontogenetic variation.

TABLE 6. *Geographic variation in polychromatism of the dewlaps among selected populations of Cuban and Mesoamerican populations of* Anolis sagrei.

| Locality | Red | Orange | Yellow | Light Gray | Dark Gray |
|---|---|---|---|---|---|
| CUBA | | | | | |
| Pinar del Río | 0% | 87% | 9% | 3% | 1% |
| Habana | 5% | 70% | 8% | 17% | 0% |
| Camaguey | 25% | 0% | 7% | 68% | 0% |
| Matanzas | 75% | 0% | 0% | 25% | 0% |
| Oriente | 56% | 34% | 4% | 6% | 0% |
| MEXICO | | | | | |
| *Campeche* | | | | | |
| Cd. del Carmen | 70% | 3% | 3% | 24% | 0% |
| Cd. Campeche | 100% | 0% | 0% | 0% | 0% |
| *Yucatan* | | | | | |
| Isla Contoy | 93% | 0% | 0% | 7% | 0% |
| Isla Mujeres | 18% | 6% | 6% | 70% | 0% |
| Isla Cozumel | 95% | 0% | 0% | 5% | 0% |
| BELIZE | | | | | |
| Belize | 18% | 1% | 0% | 81% | 0% |
| Manatee | 18% | 0% | 0% | 82% | 0% |
| Stann Creek | 0% | 0% | 0% | 100% | 0% |
| Turneffee Id. | 15% | 0% | 0% | 85% | 0% |
| Glovers Reef | | | | | |
| Middle Cay | 33% | 25% | 0% | 42% | 0% |
| SW Cays | 33% | 33% | 0% | 34% | 0% |
| Tom Owens Cay | 0% | 0% | 0% | 100% | 0% |
| HONDURAS | | | | | |
| Puerto Cortes | 0% | 50% | 0% | 50% | 0% |

## DISCUSSION

The populations of *A. sagrei* inhabiting Cuba, Mesoamerica, and the off-shore islands of Mesoamerica exhibit relatively wide latitudes of mean variation in most characters analyzed. No single character or complex of characters serves to delineate the Cuban populations taxonomically from each other or from those of the coastal versant of Mesoamerica and its attendant islands and cays.

Except for certain numerically small population samples from eastern Cuba, the extent of mean variation within the Cuban populations is as great as that within the Mesoamerican populations. The total variation recorded for the Cuban population is not significantly divergent from that observed in the Mesoamerican populations. In those populations in which the means are greater than the means of contiguous or distant populations, a high percentage of standard deviational overlap obtains. The mean number of middorsal scales, scales in the *canthus rostralis*, and scales in the frontal ridges exhibits the greatest divergence.

Greater variation occurs in the non-meristic characters. However, no individual or combination of characters delimit the Cuban populations from each other. Similarly, the Mesoamerican populations are not individually recognizable. Moreover, the total variation of the Cuban population is approximated by that of the Mesoamerican population.

Of cardinal importance is the variation of two non-meristic characters: degree of carination of the ventral scales and polychromatism of the interstitial skin of the dewlap. Ruibal and Williams (1961) observed that the population from Trinidad, Provincia de Las Villas, exhibits a marked reduction in the carination of the ventral scales. They thereby referred *A. sagrei* to the *A. homolechis* complex. Although such taxonomic allocations are not within the scope of the study, it is noteworthy that the reduction in carination is not observed in other populations.

Polychromatism in dewlaps is characteristic of the Cuban and Mesoamerican populations. Within one population are evidenced red, orange, yellow and intermediate shades. Consequently, the separation of a population based on this criterion is invalid. Ruibal (1964) wrote that the dewlap may be bright red, dark red, or ochraceous in the Cuban population of Camaguey. Similar polychromatic variation has been noted among the Mesoamerican populations. Ruibal (1964) also remarked that little reliance can be placed on the color of the dewlap in preserved males. However, field observations and remnants of color in preserved dewlaps confirm that high reliance may be given to the character.

Mesoamerican populations tend to be greater in s-v length than those of Cuba and of other populations currently allocated to *sagrei,* with the exception of the Swan Island population. In the coastal lowlands of Mesoamerica, no other anoline species is known to occupy areas inhabited by *sagrei.* Elsewhere throughout the geographic range of *sagrei,* a number of anoles occur sympatrically with *sagrei.* The larger size of Mesoamerican *sagrei* may be the result of the absence of competition.

## CONCLUSIONS

*Anolis sagrei* of Cuba, México, and Central America consist of a large number of distinct and divergent populations allocateable to a single subspecies, *A. s. sagrei.* Other studies have recognized geographic races in the Bahamas, the Swan Islands, and possibly southern Florida and the Florida Keys.

The Mesoamerican populations may have originated independently through repeated introductions from Cuba and from other islands of the West Indies. Differentiation of the Mesoamerican populations from their insular parental stock is so slight that the arrivals may be of recent origin, perhaps post-Columbian in time.

## SPECIMENS EXAMINED

The abbreviations used hereinafter designate to the following institutional collections: American Museum of Natural History (AMNH), Chicago Museum of Natural History (CMNH), United States National Museum (USNM), University of Michigan Museum of Zoology (UMMZ), Academy of Natural Sciences of Philadelphia (ANSP), University of Colorado Museum (UCM), Museum of Michigan State University (MSU). CUBA. *Province of Pinar del Río.* 8½ mi. SE Cabanas, AMNH 79734-42; Cueva de los Indios, San Vicente, AMNH 7943-46; San Vicente, AMNH 79747, 79755-59, 79782-87, CNHM 60266-67; 1 mi. S San Vicente, AMNH 79748-52; 4.4 mi. NW San Vicente, AMNH 79753-54; Cueva de Santo Tomás, 10 kms. N Cabezas, AMNH 79770; 2.9 mi. E Isabel Rubio, AMNH 79772-73; 7.6 mi. E. Isabel Rubio, AMNH 79771; 6.1 mi. N Punta de Cartas, AMNH 7974-77; 10 kms. S San Juan y Martinez, AMNH 79778-81; ca. 8 kms. NE Puerto Esperanza, AMNH 79788-89; San Diego de los Banos, USNM 26681-82, 26702, 26717-18, 26727-28, 26737-38, 26748-50; near San Diego de los Banos, USNM 75771-89; Guanajay, USNM 27505-13, 27520-21, 27524, 27539-44, 27549-56, 27563-72, 27577-92; Caimito, USNM 27606-07. 27609; Mariel, USNM 27619-23, 27672-74, Cabanas-Ing. Varila, USNM 27684-92, 27702-18; Cabanas, 27877; Quemadas, USNM 27351-54; Dimas Bay, USNM 52007-11; ¼ mi. S La Guira Mansion, USNM 75759-65; S Bahia Honda, USNM 134322-25; Mercereta, USNM 134328; Santa Lucía, USNM 51809-10; Pinar del Río (no specific locality), USNM 27341, 27345-46, 27359, 27362-66, 27378. *Province of Habana.* Habana, UMMZ. 70952, ANSP 7824-25, UMMZ 128112-16, USNM 134320; near Tapaste, CMNH 60193; near Caimito, USNM 134317-18; Calabazar, USNM 138352-53, 137358-59, 138361-62; Santiago de las Vegas, USNM 26771, 26774, 26781-90.

*Province of Matanzas.* 8 9/10 mi. NE Varadero, AMNH 96967-68; Matanzas, USNM 26355, 27355; Bellemar, USNM 42185; Cayo Largo, Banco Jardines, ANSP 26017-19.

*Province of Las Villas.* 18 9/10 mi. SSW Jaguey Grande, Bahía de Cochinos, AMNH 96959-66; Rodas, ANSP 26050-53; Cienfuegos-Soledad, CMNH 12501-07; USNM 58452, 134330-33, 134349, 134352, 136146-65; 2 mi. N. Cienfuegos, ANSP 26040; Soledad, UMMZ 70045, 70732; Cienfuegos, UMMZ 76733-34, ANSP 26033-39. 26043-44: Trinidad-Soledad, AMNH 80279-310, UMMZ 72348, USNM 58451, 136169-88, 138155, 138198, 138225-29, 138231-350, 140445, 140447-50, 140452-61, 140463; near Trinidad, USNM 140463; Tope de Collantes, AMNH 96969, ANSP 26045-46; Arriero, 15 kms. S. Cabaiguan, UMMZ 75186; Sanctí Spíritus, ANSP 15910, 15912, 15914.

*Province of Camaguey.* 5½ mi. NE Banao, Paso de Lesca, AMNH 80479-99; 11.9 mi. NW Banao, AMNH 96976; Los Paredones, AMNH 96970-71; Cascorro, UMMZ 70958; 70962; Martí, UMMZ 70952-56; 6 mi. E Martí, UMMZ 70961; Tana, UMMZ 70959-60; Playa Santa Lucía, AMNH 96972; 3 mi. S.

Playa Santa Lucía, AMNH 96973-74; Playa Bonita, E and Cayo Sabinal, AMNH 96977-81; Cuatro Caminos, UMMZ 70955.
*Province of Oriente.* Las Mercedes, 27 kms. S Yara, AMNH 83660; Yara, AMNH, 138142-52; San Luis, USNM 29811-13; El Cobre, USNM 29814-20; mouth of Río Jumurí, CMNH 42186, USNM 36824-28, 36830-34; Guantanamo, San Carlos, USNM 63227; Puerto Portillo, USNM 81824; Ocujal, USNM 138096-99; Jucaral, USNM 138118-24; Puerto Bonito, near Santiago de Cuba, USNM 141627; Baracoa, UMMZ 94049; Santiago de Cuba, USNM 26774, 26781-90; Santiago de Cuba, Castillo Morro, UMMZ 92173.
MEXICO. *State of Campeche.* Ciudad del Carmen, CMNH 116726-30, 116733-34, 124122-23, UCM 18272-417, 20551-570, 20185-21100; Ciudad de Campeche, UCM 18425-428, UMMZ 113549.
*State of Yucatán.* Progreso, CMNH 116731, 116736; Merida, CMNH 116732, UCM 13423-24, 29550, 21521-26; Bahía de Ascensión, UMMZ 78584.
*Territory of Quintana Roo.* Isla Mujeres, UCM 21101-21400, UMMZ 78581-82; Isla Contoy, UCM 21401-450; Isla Cozumel, UMMZ 78583; San Miguel de Cozumel, UCM 21451-520.
BELIZE. Belize (city) UMMZ 56475; 1 mi. NW Belize, UMMZ 75185-88; vicinity of Belize, CMNH 4179-85, 4464-68 (117); Stann Creek (town) (9) CMNH 4469-77; Manatee (town), CMNH 5818 (19); Glovers Reef: Southwest Cays, CMNH 34602-10 (30); Middle Cay, CMNH 34611 (12), 24617-18 (22); Turneffe Islands, Grant Point, CMNH 34625-26 (9); Half Moon Cay, CMNH 36653, 121049; Tobacco Cay, not catalogued, MSU, South Water Cay, not catalogued, MSU; Tom Owens Cay, CMNH 4478 (8).

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