MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 138

The Evolution and Geographical Origin of the New World *Hemidactylus mabouia-brookii* Complex *(Gekkonidae, Sauria)*

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ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
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INTRODUCTION

In a recent study of the evolution of higher taxonomic categories in the lizard family Gekkonidae (Kluge, 1967; also see Kluge, 1964, pp. 4–6), I postulated that most of the relatively few endemic New World gekkonine genera evolved from Old World ancestors. In the context of that thesis I stated that the majority of the stocks were very likely African in geographical distribution and that their access to the New World might be accounted for by trans-Atlantic dispersal. The basis for these suppositions is the greater degree of independent affinity, as suggested by morphological similarity, of most New World genera with different genera or groups of genera which today exhibit a predominantly African geographical distribution. It was for these same reasons that I also stated that the endemic Neotropical subfamily Sphaerodactylinae probably had a similar, but much earlier origin.

The present paper on the genus *Hemidactylus* Oken is the first of a series which attempts to ascertain objectively the degree of affinity between Neotropical and Ethiopian taxa on the basis of morphological characters and thereby to infer the probable geographical origin of New World gekkos. I believe it is reasonable to assume that such studies will provide a better understanding not only of the taxonomic composition of the New World gekko fauna but also of the most likely method and route of dispersal. In addition, it is highly probable that approximate rates of evolution can be derived from the temporal spacing of the different dispersal lines.

According to Wermuth's (1965) recently published checklist of the Gekkonidae of the world there are 83 genera and 673 nominal species, and an additional 172 subspecies, recognized in the family. Of the number of species in the entire family, the genus *Hemidactylus* alone accounts for approximately 10% of the total (76 species, 13 subspecies). This index to the success of the genus would be further amplified if the comparison were restricted to the subfamily Gekkoninae to which *Hemidactylus* belongs (Kluge, 1967). The genus *Hemidactylus* contains the largest number of species in the family, excluding *Gymnodactylus* and *Phyllodactylus* which are obviously polyphyletic (Kluge, 1967; James R. Dixon, pers. comm.), and because of its extremely wide geographical distribution the contention that it is a modern expanding "dominant" (sensu Underwood, 1954) would appear to be strongly supported. However, an unqualified statement that *Hemidactylus* is a modern expanding dominant is misleading, not only to the evolutionist but also to the zoogeographer. For example, it cannot be denied that Africa has been the major center for speciation and southcentral Asia the secondary center. Approximately 70% of all Old World species and subspecies of *Hemidactylus* are found in central and northeastern Africa and of these 91% are endemic to that area. Central and southern India, including Ceylon, has approximately 29% of all Old World species and subspecies, and of these 77% are restricted to that region.

Most of the species of *Hemidactylus* exhibit relatively small geographical ranges. There are only eight species, *bowringii, brookii, flaviviridis, frenatus, garnotii, mabouia, persicus,* and *turcicus,* that exhibit wide ranges (viz., occur on geographically distant islands, continents and islands, major portions of continents, and on more than one continent). These eight species contribute the most to the circumtropic distribution of the genus. *Brookii, frenatus, garnotii, mabouia* and *turcicus* are found in both the Old and New Worlds. The remaining species, *bowringii, flaviviridis* and *persicus* are restricted to the Old World. The species *brookii, frenatus, garnotii, mabouia* and *turcicus* appear to exhibit the greatest degree of dispersal ability and ecological plasticity and they are often referred to as the "weedy" species. This study is restricted to the highly problematical *mabouia-brookii* complex in the New World. The details of the research on *garnotii* will be published elsewhere (Kluge and Eckardt, 1969) and the research on *frenatus* and *turcicus* is in preparation.

ACKNOWLEDGMENTS

I gratefully acknowledge the loan of materials and assistance in other ways from the following persons and institutions: Charles M. Bogart and Richard G. Zweifel, American Museum of Natural History (AMNH); James E. Böhlke and Edmond V. Malnate, Academy of Natural Sciences of Philadelphia (ANSP); Albert Schwartz of Miami, Florida (ASFS); Garth Underwood, formerly at the British Museum of Natural History (BMNH); Joseph R. Bailey, Duke University; Robert F. Inger and Hymen Marx, Field Museum of Natural History (FMNH); William E. Duellman, University of Kansas Museum of Natural History (KU); James R. Dixon, formerly of the Los Angeles County Museum of Natural History (LACM); Douglas A. Rossman, Louisiana State University Museum of Zoology (LSUMZ); Janis A. Roze, formerly of the Museo de Biologia, Universidad Central de Venezuela, Caracas (MBUCV); Ernest E. Williams, Museum of Comparative Zoology, Harvard University (MCZ); Hermano Nicéforo María, Instituto de la Salle, Bogotá (MLS); Jean Guibé, Musée National d'His-

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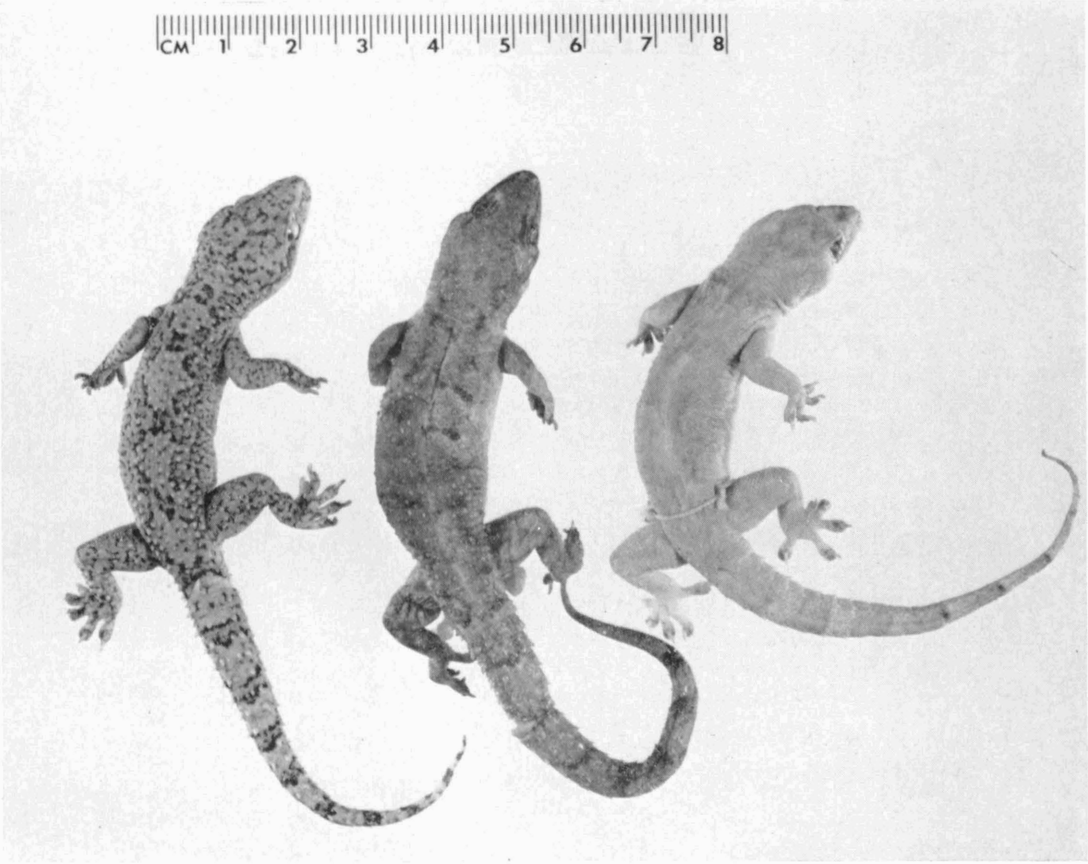

FIG. 1. Left—*brookii haitianus*, UMMZ 73557, adult male from San Juan, Puerto Rico. Center—*palaichthus*, AMNH 60931 (holotype), adult male, from Kurupukari, Guyana. Right—*mabouia*, UMMZ 73570, adult male, from Vieques Island.

A very special vote of thanks is extended to James S. Farris, State University of New York at Stony Brook. He alone has been responsible for developing the algorithms and computer programs of the Prim Network and Wagner Diagram that were used in this research. I gratefully acknowledge the time that he has given to me in discussing the procedures of quantitative phyletics.

TERMINOLOGY AND MATERIALS

To insure correct interpretation and to facilitate the description of the taxa, the meristic and morphometric characters used in the text are defined as follows:

(LS) *Number of loreal scales*—loreals are located between the postnasal scale and the anteromost margin of the bony ocular orbit; the count is taken along an imaginary straight line between these two points.

(CT) *Number of cheek tubercles*—cheek tubercles are the conspicuously enlarged scales located within the area bounded by the anterior margin of the external auditory meatus and the posteromost extreme of the angle of the mouth, and the dorsomost margin of the external auditory meatus and the throat (Fig. 2); tubercles located on any part of the margins of this rectangular area are included in the count.

(AS) *Number of auricular scales*—auriculars are enlarged scales located on the anterior margin of the external auditory meatus; only the conspicuously enlarged scales that project posteriorly into the meatus are counted.

(SL) *Number of supralabials*—supralabials are the conspicuously enlarged scales located along the margin of the upper lip between the rostral plate and the angle of the mouth.

(IL) *Number of infralabials*—infralabials are the conspicuously enlarged scales located along the margin of the lower lip between the mental plate and the angle of the mouth.

(RT) *Number of rows of body tubercles*—body tubercles are the conspicuously enlarged scales forming relatively straight longitudinal rows on the dorsal and lateral surfaces of the body; the number of longitudinal rows is counted as they intersect a transverse plane located half way between the axillae and the inguinal regions.

(TR) *Number of tubercles in paravertebral row*—the paravertebral row of tubercles is the relatively continuous longitudinal series of enlarged scales located immediately adjacent to the midline; the number of tubercles in the paravertebral row is counted between the transverse planes of the axillae and the inguinal regions.

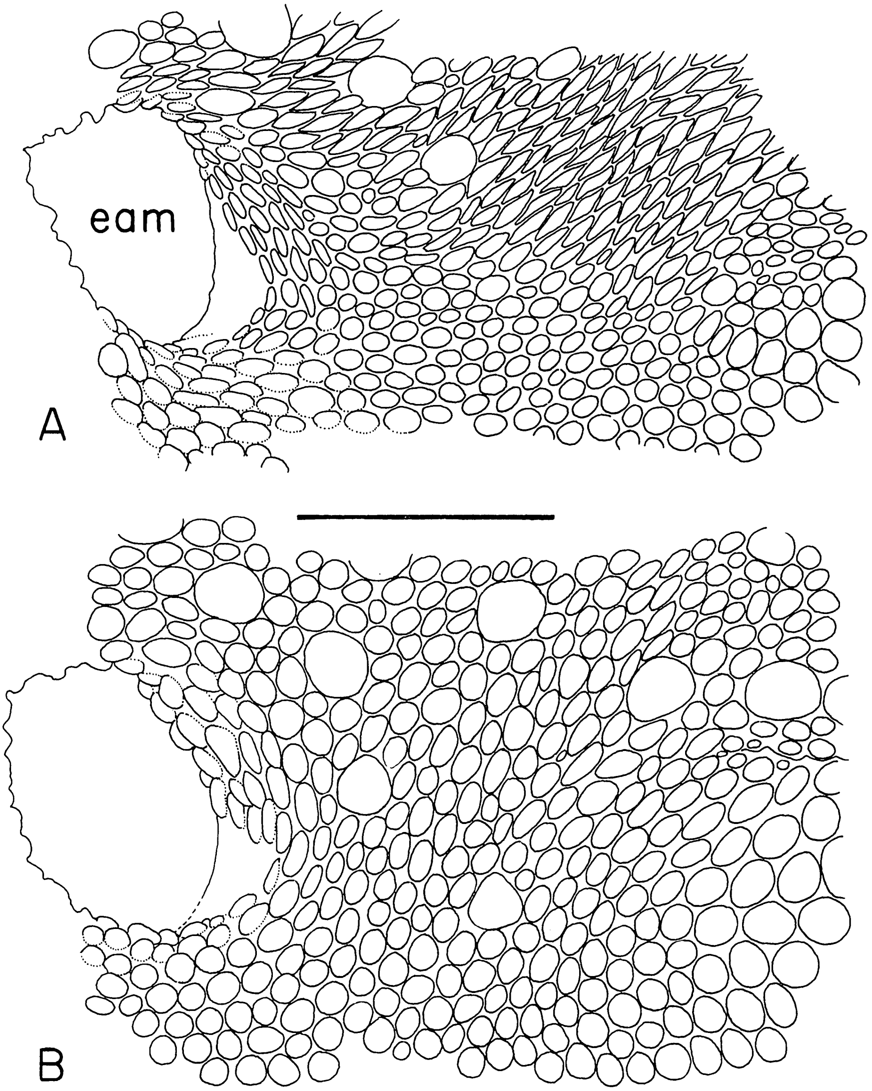

FIG. 2. Right lateral view of the region between the anterior margin of the external auditory meatus (eam) and the posteromost extreme of the angle of the mouth. Scale equals 1.55 mm. (A) *mabouia,* AMNH 64856, from Manaos, Brazil. Two cheek tubercles are present. (B) *brookii haitianus,* UMMZ 73553, from Mayagüez, Puerto Rico. Five cheek tubercles are present.

(TW) *Number of tubercles in caudal whorl*—caudal whorl consists of conspicuously enlarged scales arranged in a transverse row on the dorsal and lateral surfaces of the tail; this meristic character includes only those tubercles on one side of the fourth complete row distal to the level of the posterior margin of the vent.

(SW) *Number of scales between caudal whorls*—this meristic character includes those small scales between the innermost enlarged tubercles of the fourth and fifth caudal whorls.

(SD) *Number of subdigital lamellae*—subdigital lamellae include a single row of scales from the distal-most extreme of the dilated portion of the digit to its origin from the sole of the foot; only those of the fourth toe are presented.

(PP) *Number of preanal pores*—preanal pores refer to the external preanal glands in scales anterior to the vent; counts include the total number of pores in both right and left rows in males.

(IP) *Number of interpreanal pore scales*—this meristic character is the number of poreless scales located on the ventral midline between the right and left rows of preanal pores.

(TD) *Type of digit*—this refers to two conditions; namely, dilated proximal portion wide and enlarged subdigital lamellae replaced by granules at origin of digit from sole (type A), and dilated proximal portion narrow and enlarged subdigital lamellae continue to level of origin of digit from sole (type B). This character applies to the fourth toe (Fig. 3).

(SVL) *Maximum snout to vent length*—taken from the tip of the snout to the anteromost extreme of the vent; given in millimeters for the largest male examined.

(SEL) *Snout to eye length*—measured from the tip of the snout to the anteromost extreme of the bony ocular orbit; the measurement is given as a percentage of the snout to vent length.

(EEL) *Eye to ear length*—measured from the posteromost extreme of the orbit to the anteromost extreme of the external auditory meatus; the measurement is given as a percentage of the snout to vent length.

The characters SEL and EEL are used only in the general descriptions of the taxa. They were not used in the phyletic analysis owing to the absence of significant mean differences (Tables 21–22).

Where possible all measurements and counts were taken on the right side, and on "normal," well preserved individuals. The snout and eye to ear lengths were measured with a pair of dial calipers and were read to two decimal places. The snout to vent length was measured with a plastic ruler to one decimal place.

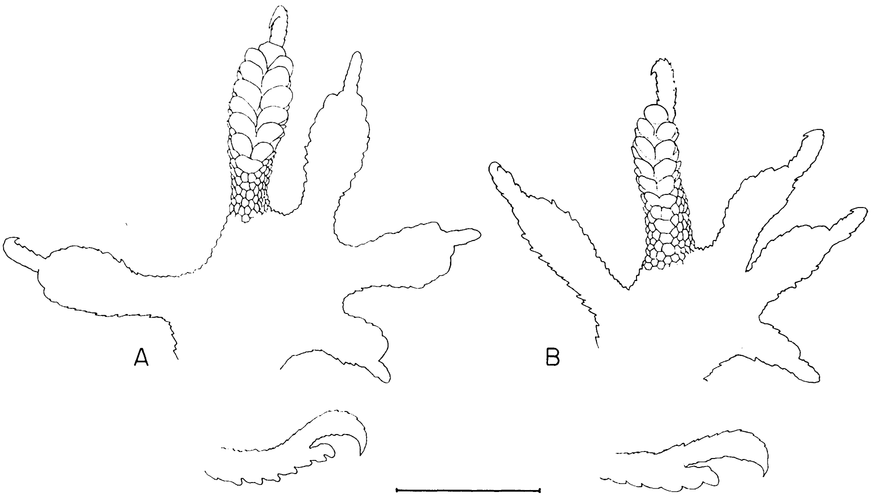

FIG. 3. Ventral view of the hind foot; the fourth toe is shown in detail. The distalmost portion of the fourth toe is also drawn separately from a lateral view. Scale equals 3.5 mm. (A) *mabouia*, AMNH 64856, from Manaos, Brazil. (B) *brookii haitianus*, UMMZ 73553, from Mayaqüez, Puerto Rico.

In the species diagnoses (pp. 29–39) the observed range of variation of the meristic and morphometric data are followed by the mean in parentheses. In the species descriptions (pp. 29–39), the meristic and morphometric data (except the SVL) are presented as the observed range of variation, and the mean and one standard deviation in parentheses; the number of individuals examined follows the parentheses. In Tables 9–23, the statistical notations are n = number of specimens in sample; ORV = observed range of variation; $\bar{x}$ = sample mean; s = sample standard deviation; $\text{SE}_{\bar{x}}$ = standard error of the sample mean. The sample standard deviations were computed as $\sqrt{(n - 1)^{-1} \sum_{i}^{n} (x_i - \bar{x})^2}$, where n is the sample size, $\bar{x}$ is the sample mean, and the x_i are observations. Figures 4–8 are modified Hubbs-Perlmutter diagrams; horizontal lines are observed ranges of variation; the mean is indicated by a vertical line; the open rectangles mark one standard deviation on each side of the mean; the solid rectangles are twice the standard error on each side of the mean.

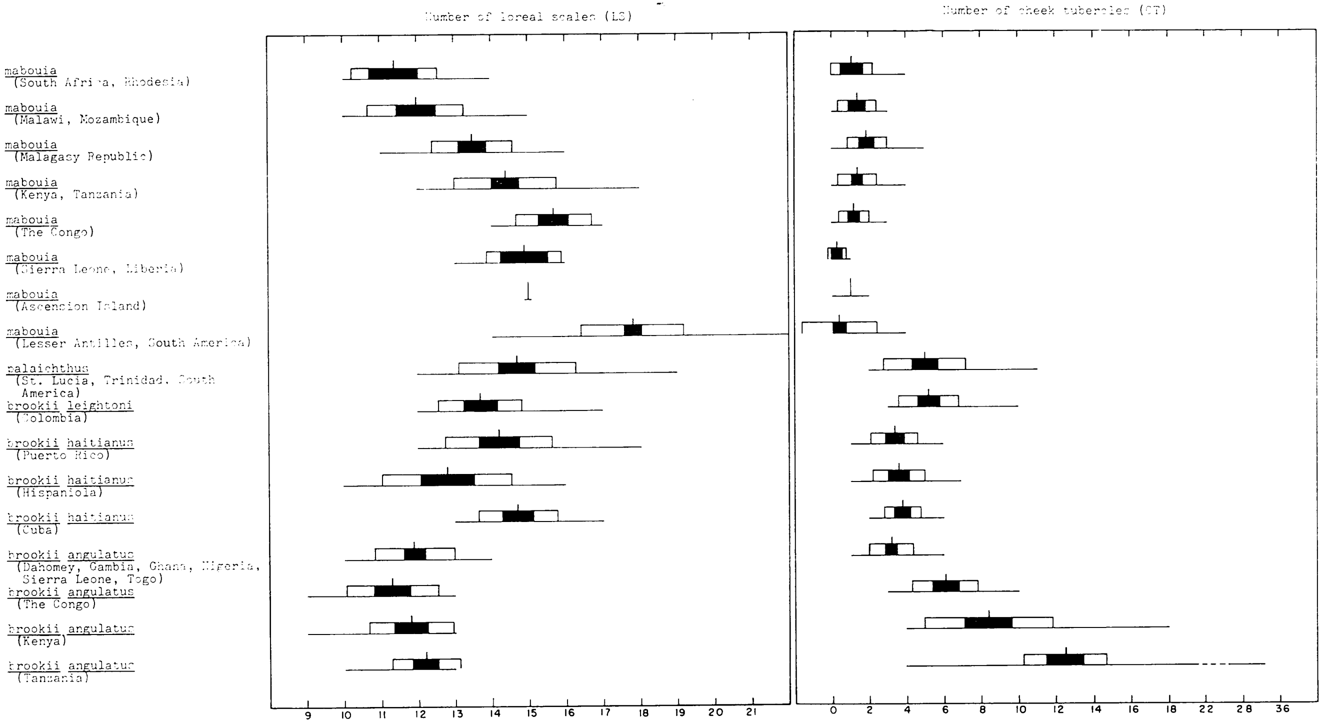

FIG. 4. Hubbs-Perlmutter diagrams of the data presented in Tables 9–10.

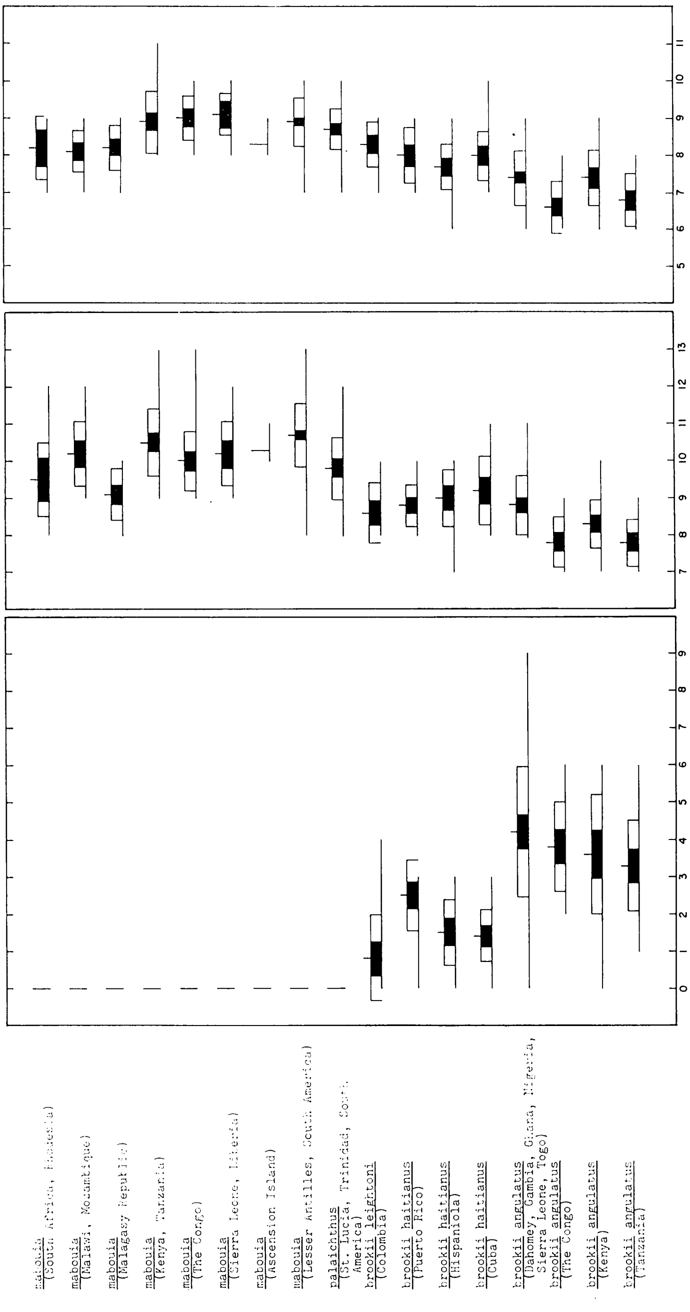

FIG. 5. Hubbs-Perlmutter diagrams of the data presented in Tables 11–13.

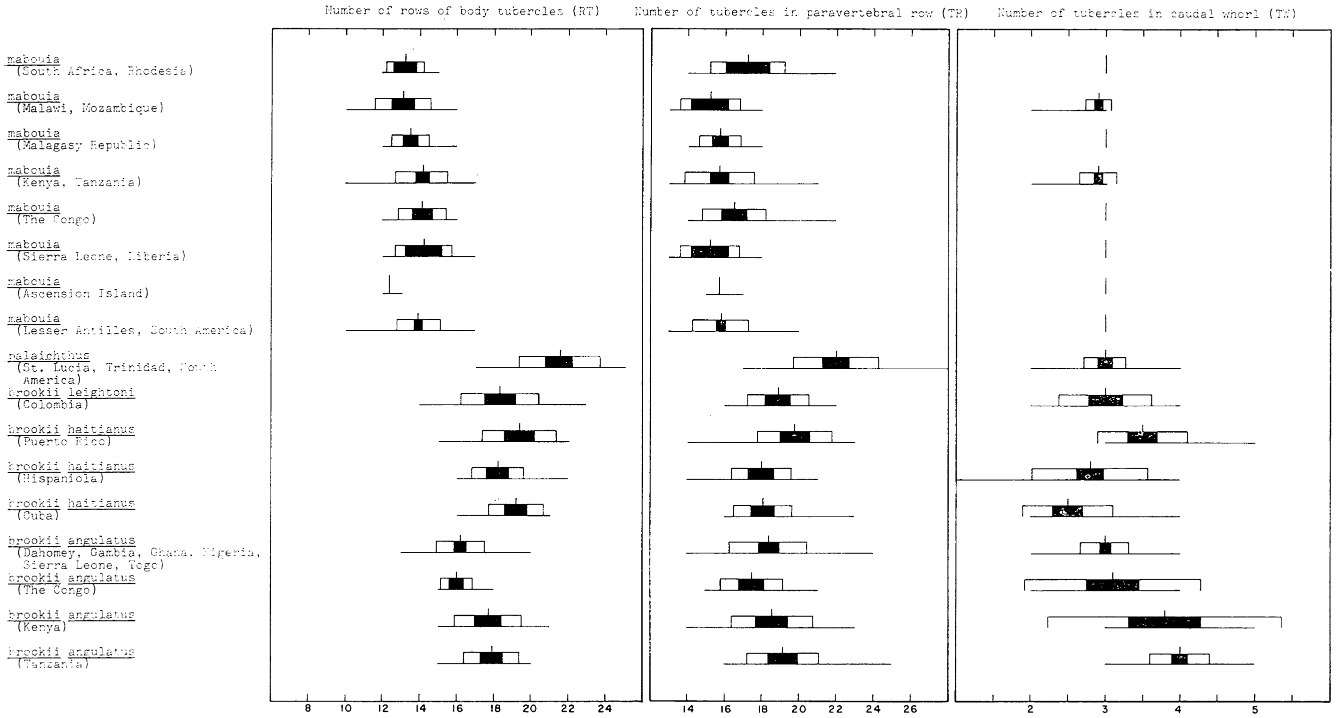

FIG. 6. Hubbs-Perlmutter diagrams of the data presented in Tables 14-16.

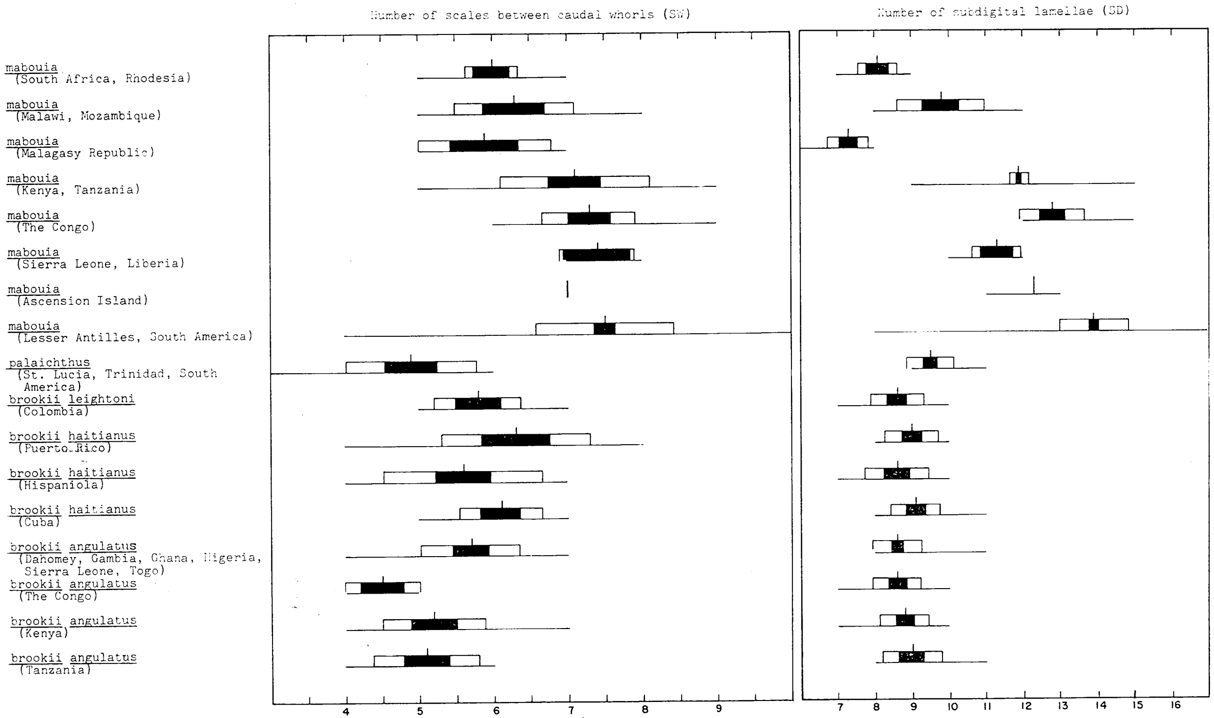

FIG. 7. Hubbs-Perlmutter diagrams of the data presented in Tables 17–18.

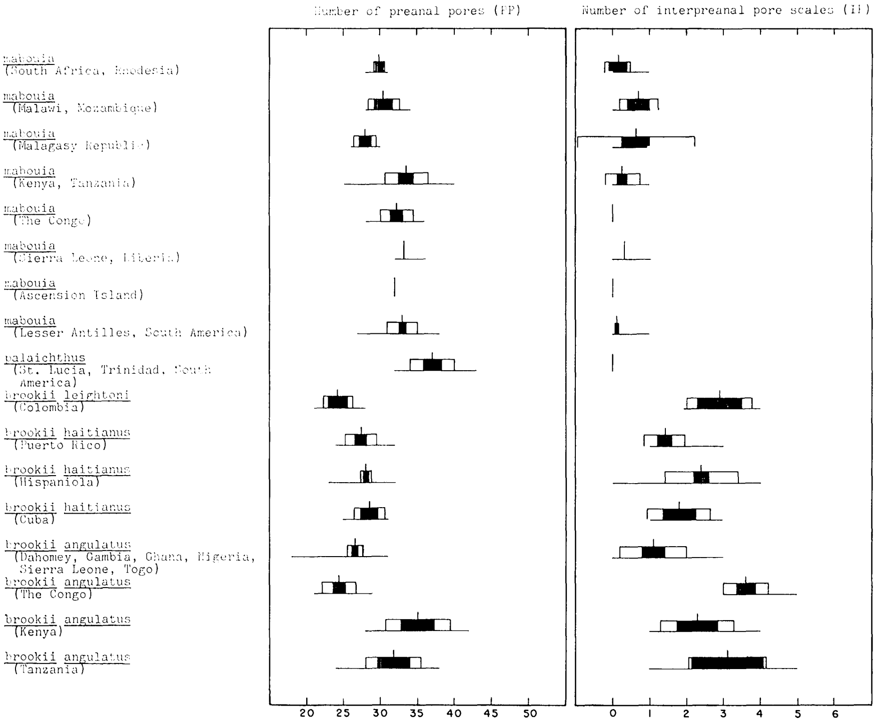

FIG. 8. Hubbs-Perlmutter diagrams of the data presented in Tables 19–20.

The data used in the species descriptions were taken from New World material only. With the exception of *mabouia,* more specifically two individuals from St. Lucia, the descriptions of the color and color pattern are based on preserved specimens. There does not appear to be any sexual dichromatism or difference in color pattern in any of the New World populations. The color pattern in juveniles, when present, seems to be a better defined version of that of the adults. The ventral surfaces of all New World populations are nearly devoid of color; only a very fine scattering of pigmentation is present.

TAXONOMIC PROCEDURE AND METHODOLOGY

One of the most consistently voiced criticisms of taxonomic research is the large degree of subjectivity and personal bias that is usually involved at all levels of study, data gathering, manipulation of data, and, in particular, interpretation of data (Kluge and Farris, 1969). I believe the procedure that satisfies the majority of these criticisms to be as follows: Accept some taxonomic unit as monophyletic wherein observations are made on the individuals. The acceptance of a taxonomic unit of some kind may be viewed as a deductively reasoned first premise which is justified only as a time-saving device. It is on the basis of the observations on the individuals that they are grouped into infraspecific populations (clusters). These populations are then used as the basis of the phyletic construct. And, lastly, it is this construct that provides the estimate of taxonomic boundaries, of the relatedness of the individuals examined and of the populations recognized.

I have adhered closely to this procedure in the present research in an attempt to escape the subjectivity and personal bias that so often accompany such a study. The formal part of this research began with a review of all literature known to me that mentions New World *Hemidactylus,* as well as their nominal Old World counterparts. The review and a preliminary examination of some of the specimens referred to in the literature (mainly holotypes and paratypes) indicated that most of the taxonomic controversy involved populations that at some time in the past had been called *mabouia* and *brookii.* The specimens shown in Figure 1 exemplify the degree of general external morphologic similarity of the most divergent individuals involved in the controversy. The literature survey and the preliminary study of typical material were used to construct the morphologic diagnosis (see below) that I believe encompasses all of the populations involved in the controversy. Only the material that conformed to this diagnosis was examined in detail and it was studied without direct reference to prior taxonomic conclusions. Samples of the material examined were used in the phyletic reconstruction, which in turn was used to establish the limits of species boundaries. It was only after this delimitation that nomenclature was applied to the samples. A slightly more direct, but considerably more time-consuming, approach would have been to examine all New World specimens of *Hemidactylus;* however, even here one is faced with the practical restraint of starting with the acceptance of the taxonomic unit called *Hemidactylus.* It seems likely that taxonomic research will always rest on some deductively reasoned first premise which can be justified only as a practicality.

The taxonomic method used herein, quantitative phyletics, was originally formulated by Wagner (1961) and later expanded upon by Farris (1966, 1967, 1968, 1969) and by Kluge and Farris (1969). The method was chosen for its quantitative and objective approach to the study of evolutionary relationships. Owing to the very confusing taxonomic history of the *mabouia-brookii* complex, it seemed most appropriate to use this methodology because it appears to be the one least predicated on prior conclusions.

Initially, only those specimens that conformed to the following diagnosis were studied in detail:

1. moderate sized gekkonid lizards of the genus *Hemidactylus* (sensu Kluge, 1967; also see Loveridge, 1947, Smith, 1935, and Wermuth, 1965). See Figure 1.
   a. snout to vent length less than 85 mm.
   b. snout to eye length 9.50–13.00% of snout to vent length
   c. eye to ear length 7.25–11.00% of snout to vent length
2. supralabials 7–13
3. infralabials 6–10
4. dorsal surfaces of body covered with small, relatively flat granules and enlarged, keeled or strongly striate tuberculate scales
   a. all dorsal body scales juxtapose, not obviously imbricate
   b. tubercles arranged in 7–26 relatively straight longitudinal rows
   c. a few enlarged tubercles on occiput (Fig. 2)
5. original tail oval in cross-section, not obviously dorsoventrally depressed; not obviously constricted at its origin from the body or swollen more distally
   a. covered dorsally and dorsolaterally with regularly spaced whorls of granules and enlarged tubercles
   b. 3–12 granules separating fourth and fifth caudal whorls of tubercles
   c. lateroventral edge of tail not denticulate
   d. median subcaudal scales greatly enlarged transversely
6. digits moderately dilated proximally, covered with divided subdigital lamellae (Fig. 3)
   a. compressed distal portion of digit extending beyond dilation
   b. 6–17 fourth toe subdigital lamellae
   c. subdigital lamellae not extending on to palm or sole
   d. no interdigital webbing
   e. all digits well developed and clawed
7. males with preanal pores
   a. total number of pores 14–59
   b. 0–6 poreless scales on midline separating row of pores under each thigh
8. dorsal body color pattern absent or consisting of a fine reticulation of dark brown or gray in adults. No regular pattern of bands or stripes (Fig. 1).

Over 2000 specimens which fit this diagnosis were borrowed from United States repositories alone. The phyletic construct based on samples of the material, as well as a small number borrowed from Western European museums, delimited monophyletic clusters of OTUs (Operational Taxonomic Units, *cf.* Sokal and Sneath, 1963), which corresponded reasonably well to the original and most of the subsequent, descriptions of *mabouia, brookii* (and its various subspecies, *fide* Loveridge, 1941), *leightoni, platycephalus* and *tasmani,* and various forms which appear to be unnamed. For the purposes of this study only those clusters of OTUs that were New World in distribution and their most similar African samples are considered. All of the Old World *mabouia* and *brookii* and the remaining species in the complex will be discussed in greater detail in another paper.

The storage capacity of the computer (I.B.M. 7090 with 32K storage) that was used in the phyletic analysis of the information collected in this research was not large enough to realize the ideal taxonomic procedure where each specimen is treated separately as an OTU. The physical condition of many of the 2000 specimens that were examined was very poor, and the preservation was found to be responsible for much of the experimental error present in the data (Kerfoot, 1969). The effects of this artificial variance should be minimized because of the method of character weighting that was employed in the phyletic reconstruction. It is because of both of the above reasons that only relatively small samples of well preserved specimens were studied in further detail. The samples were obtained by lumping those individuals from what I considered to be physiographically natural regions which, taken together, represented most of the total geographic range of that part of the complex studied. The specimens from which data were taken and used in the phyletic construct are marked with an asterisk in the Specimens Examined section of the Appendix (pp. 72–75). The geographic regions sampled (labeled according to country or island) and the maximum sample size of each are given in Table 1. In some geographic areas two samples were distinguished on the basis of the type of digit (Fig. 3). The occurrence of the type of digit among the samples is also given in Table 1 (see footnote) and the remaining twelve nonbinary coded characters that were employed are listed there as well. The data collected on the twelve characters for each of the samples are presented in Tables 9–20, and the corresponding graphic representation of these data are presented in Figures 4–8. The scientific names that are believed to apply to the samples are presented along with the geographic label of each OTU in these tables and figures. It must be emphasized that the names were recognized after the taxonomic analysis, and they have been applied to the tables and figures only to facilitate their interpretation by the reader.

The first step in the quantitative phyletic analysis was the determination of the overall similarity of the sixteen OTUs (geographic samples; see Table 1). The Ascension Island sample was not included because of the small number of specimens available for study. The character states that were used to describe the OTUs were the sample means of the thirteen characters. The type of digit is exceptional in that it was recorded as a binary character, either type A or type B (Fig. 3), and encoded as 0 and 1, respectively. The two types of digits are distinguished on the basis of the relative width of the expanded proximal portion, the relative length of the compressed distal-most portion, and whether or not the undivided subdigital lamellae have been replaced by granules at the origin of the digit from the sole of the foot. An algorithm very similar to the one used in this initial step of the analysis was described by Prim (1957; also see Edwards and Cavalli-Sforza, 1964). The graphic product of the computer analysis of the sixteen OTUs considered herein is presented in Figure 9. The set of relationships derived from this analysis will be referred to as the Prim Network in the following discussion. The Prim Network is an expression of the phenetic relationship of OTUs based on all characters considered; the characters are not weighted, and hypothetical intermediate taxa are

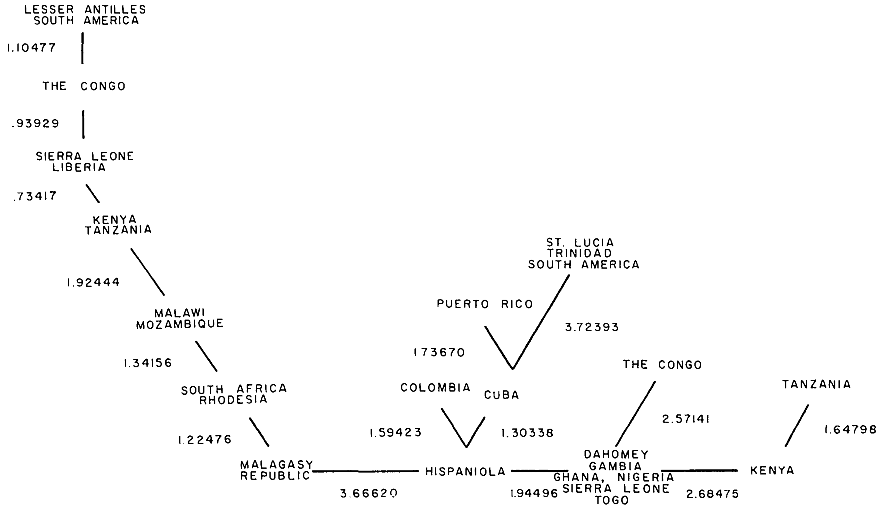

FIG. 9. A Prim Network. See pp. 20–21 for discussion of the procedure used in constructing the Network and for the interpretation of the Network. The OTUs, sample size and characters used in its construction are listed in Table 1.

not used in the construction of the Network. The relative primitiveness of the character states is not specified when the data are analyzed by the computer, and the construction of the Prim Network does not depend on designating a particular OTU (or set of character states) as the most primitive. In Figure 9, the patristic difference (Farris, 1967), viz., the length of the line connecting two OTUs, and the corresponding numerical value, represents the proportional overall differences that separate the OTUs. The angles between the cladistic (= branching) events are arbitrary. The total computer time required to analyze these OTUs and thirteen characters was 18.3 seconds. The consistency index of the data is .506. This value is the product of the sum of the ranges of characters divided by the total length of the Network (see Farris, 1968 for further explanation). A value of 1.000 indicates no homoplasy (sensu Simpson, 1962a) present in the characters; values less than 1.000 indicate the relative degree of homoplasy present. Based on this Network, the unit character consistencies are given in Table 2. The rank order of the characters based on these consistencies is also presented in Table 2. The total length of the Network is 28.143.

The Prim Network provides a useful and objective framework for the inference of sets of primitive character states. These of course must be decided upon before any kind of objective evolutionary dendrogram can be derived. In most research, particularly those involving external meristic and morphometric data, the investigator almost always finds it difficult, if not impossible, to defend logically and objectively his choice of which character state of a multistate character is primitive. This would be quite in contrast, for example, to the objective and logical arguments that could be raised for the presence of a bone being considered primitive, and its absence being considered derived (Kluge, 1967, p. 15; Kluge and Farris, 1969, p. 5). With external meristic and morphometric data, where the direction of evolution cannot be inferred directly, I have turned to the Prim Network for an indirect best estimate. Given no information about the direction of change of a set of characters, the best choice would make the fewest assumptions about their directionality. This reasoning is completely in accord with the generality that the evolution of an individual character can, at least theoretically, be in more than one direction. For all external morphometric and meristic character states this seems almost certain to be true. Therefore, for a given set of data, the minimum assumption that can be made for all character states of all characters, within the cladistic constraint of the Prim Network, is to choose the cladistic center of that Network. For this choice, I select that OTU of the Network that has the smallest mean and standard deviation of the interval lengths (where each length is set to 1.0), that is the point from which the largest number of different evolutionary directions can be realized.

Farris (1968) gives another rationale for inferring the most probable ancestral condition from a Prim Network. His thesis rests on the premise that there is a constant average rate of evolutionary change in major phyletic lines. He proposes that the patristic center of a Network is equivalent to the set of character states from which the most OTUs can be derived with the same rate of change, and therefore, this set of states is designated the ancestral form. Owing to the fact that the angles between cladistic events of the Prim Network are not fixed, the patristic center cannot be computed without some reference to the OTUs. I have chosen to define the patristic center as that OTU which has the smallest mean and standard deviation of the interval lengths between OTUs. In contrast to the method of finding the cladistic center, the actual patristic distances are used as the values of the interval lengths.

For the set of data described by the Prim Network in Figure 9, the Hispaniola OTU might be considered equivalent to the set of states of the ancestral form. It is directly linked to the most OTUs, Malagasy Republic, Colombia, Cuba, and Dahomey-Gambia-Ghana-Nigeria-Sierra Leone-Togo, and it is the cladistic center. In addition, the patristic center, that is the smallest combination of mean and standard deviation, is exhibited by Hispaniola ($\bar{x} = 5.339$, $s = 2.990$) and Malagasy Republic ($\bar{x} = 5.888$, $s = 2.384$). In this particular study, however, Hispaniola itself as a New World OTU seems unlikely to have been relatively more similar to the ancestor than other OTUs in the complex. This conclusion follows from the fact that the genus *Hemidactylus* almost certainly had its origin in the Old World, more specifically Africa, as inferred from its species and geographic radiation there (see pp. 5–6). For this reason alone the most probable ancestor was reconstructed according to the median character states of the two Old World OTUs, Malagasy Republic and Dahomey-Gambia-Ghana-Nigeria-Sierra Leone-Togo, that immediately surround Hispaniola in the Prim Network. (Here the sample size is two and the median is equivalent to the mean.) This course of action still keeps the ancestor very close to the cladistic and patristic centers of the Prim Network and it is consistent with zoogeographic facts. The reconstructed hypothetical OTU is hereafter referred to as the Ancestor, and its character states of the thirteen characters are given in Table 3. In the case of the type of digit, which was encoded in a binary form as either 0 (type A) or 1 (type B) the Ancestor was given a state of .5. With this form of notation the state of the binary character did not bias the set of evolutionary relationships that were derived subsequently.

The next step in the quantitative phyletic analysis is to obtain a Wagner Diagram, viz., most parsimonious dendrogram. This dendrogram expresses the relationships of the OTUs in terms of amount of evolution (patristic distance) and divergence (cladistic events). The dendrogram has orientation, that is, primitive and derived character states are explicitly considered; the orientation is established by using the estimated set of primitive states derived from the Prim Network (see above) as the ancestor. In addition, the characters are weighted according to the concept of conservatism (Farris, 1966), and hypothetical intermediate taxa are generated to effect the most parsimonious phylogeny (Farris, 1969). The most parsimonious phylogeny, namely the tree with the shortest total length, has been demonstrated to be the most probable one (Farris, 1969). Also, the most parsimonious tree gives the best fit to the data. A computerized version of the method for constructing most parsimonious trees (see Kluge and Farris, 1969) was used. The algorithm for the program was formulated by Farris (1969). The Ancestor, and the sixteen real OTUs listed in Table 1 (Ascension Island excluded), were used in the analysis, and the phyletic construct that was generated is presented in Figure 10. The scientific names that are believed to correspond to the OTUs, or groups of OTUs shown in that construct, have been included in order to facilitate later reference to the dendrogram; they do not reflect any prior (before the phylogeny was constructed) taxonomic decisions on the part of the author. The character states of the intermediates are listed in Table 3. The intermediates were generated by the computer to effect the most parsimonious tree and they must be considered hypothetical. The total computer time required to analyze these data was 19.4 seconds. The number of iterations required to produce the most parsimonious tree was two with a computer default value of .0005 to terminate the iterative process. In each iteration the characters are reweighted according to their variances and a new dendrogram is constructed. The iterative process continues until the specified default value is reached.

The consistency index of the data is .590. In contrast to the method for determining the consistency index of the Prim Network from unweighted data, in this calculation the weighted ranges of the characters and the weighted total length of the tree are used. The relative weight of the thirteen characters is given in Table 4. The rank order based on these weights is also presented and indicates that the type of digit embodies the greatest information content (1.000) relative to the phylogeny produced and the

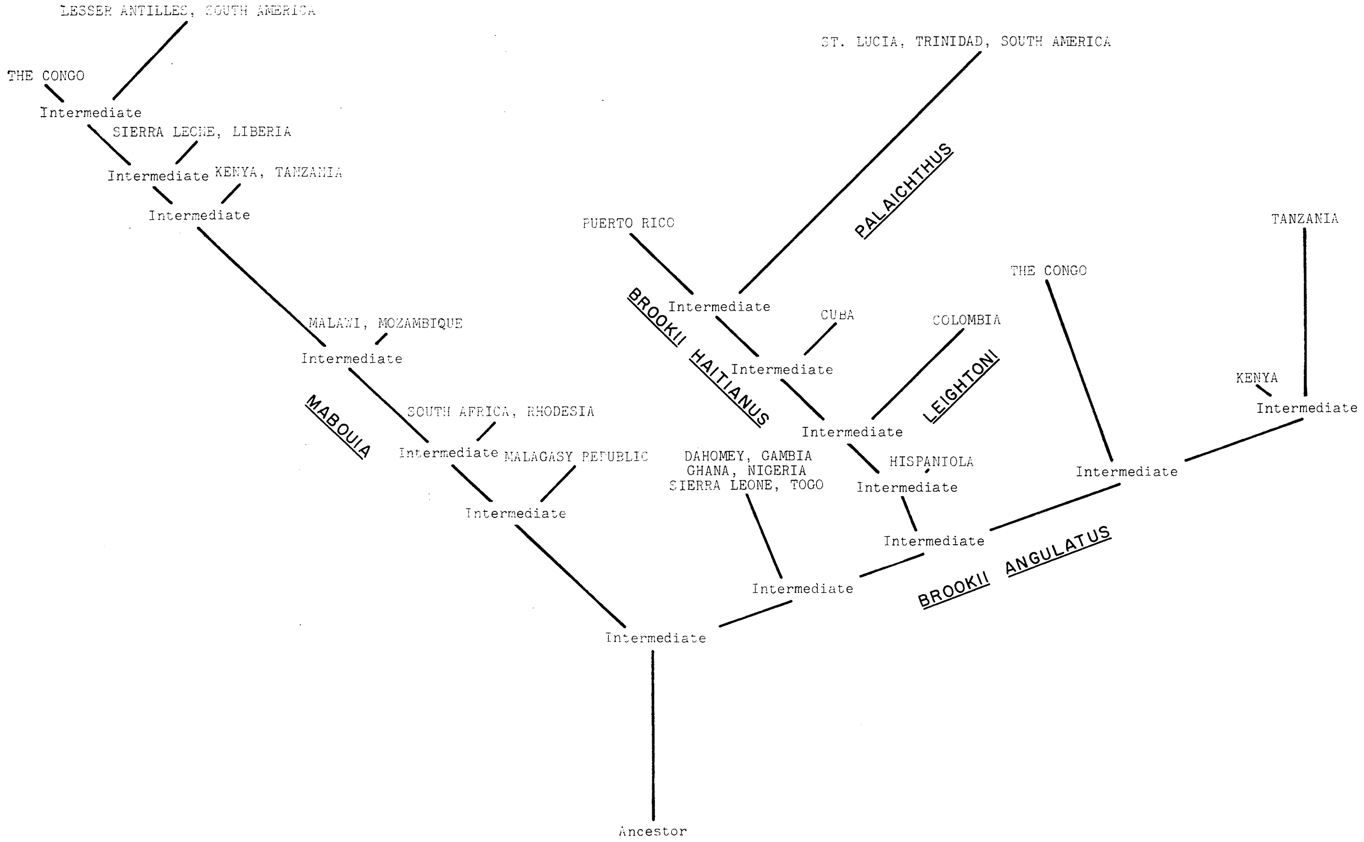

FIG. 10. A Wagner Diagram. See pp. 23–25 for discussion of the procedure used in constructing the dendrogram and for the interpretation of the dendrogram. The OTU's, sample size and characters used in its construction are listed in Table 1. The character states of the Ancestor and the Intermediates are listed in Table 3.

total number of preanal pores has the least information content (.386).

A matrix of the sums of the patristic differences (cf. Farris, 1967) of the phylogeny given in Figure 10 is presented in Table 5. These data are used to rank all of the OTUs according to degree of evolutionary relationship (Table 6). For example, the South Africa-Rhodesia OTU is most closely related to the Malagasy Republic OTU, and it is least closely related to the St. Lucia-Trinidad-South America OTU.

HISTORICAL PERSPECTIVE AND BINOMIAL NOMENCLATURE

Du Tertre appears to have been the first traveler to the New World to have conclusively documented the presence of a hemidactyl there. In his narratives on the general history of the Lesser Antilles (1654; 1667), particularly of Saint Christophe [Saint Kitts], Guadeloupe and Martinique, he describes a "Maboüya" lizard in some detail and provides a drawing of the animal which in my opinion conclusively relates his field observations and written description to a species of *Hemidactylus.* Although the color pattern of his "Maboüya" is different from the presently recognized New World *Hemidactylus* it is certainly within the limits of the artistic license taken by other workers of that period. The presence of hemidactyl-type digits, viz. expanded proximally, elevated and compressed distally and with exposed claws (Fig. 3), and the enlarged tubercles on the dorsal surfaces of the body cannot be related to any other Antillean gekko but *Hemidactylus.* Rochefort (1658) and Hughes (1750) also appear to have described the same type of lizard. It should be noted, however, that Rochefort may have plagiarized from the earlier work of Du Tertre (Grant, 1932a).

It was not until Moreau de Jonnès' description of *Gecko mabouia* in 1818 that more formal attention was given to a New World species of *Hemidactylus.* Shortly thereafter, Raddi (1823) referred his Brazilian hemidactyls to Daudin's *Gecko tuberculosus* (see p. 32). In 1824 and 1825, Wied-Neuwied and Spix, respectively, described two species of gekkos, all of which now appear to be synonyms of Moreau de Jonnès' *mabouia.* Following these early descriptions, *"mabouia"* was recorded frequently from many different localities on the mainland of South America and from many of the islands of the Greater and Lesser Antilles.

In 1901, Meerwarth described the Haitian hemidactyl population as a variety [= subspecies] of Gray's (1845) *Hemidactylus brookii,* a species which until then had never been recognized from the New World. Since 1901, however, most investigators have considered Meerwarth's *haitianus* to be indistinguishable from Old World *brookii.* Moreover, the species *brookii* and *mabouia* appear to have been very difficult to distinguish from each other since numerous misidentifications (post 1901) exist in the literature on the Antillean herpetofauna.

Boulenger (1911) recognized the third tuberculate *Hemidactylus* from the New World when he described *leightoni* from Colombia. In 1936, Shreve described *neotropicalis,* also from Colombia, which he thought was most closely related to *brookii.* Shreve acknowledged (1938) later that he had overlooked Boulenger's description of *leightoni* and that the two species were probably conspecific.

Numerous authors, e.g., Underwood (1962), Dunn (1944), Loveridge (1941), Cochran (1931), and in particular Grant (1932b, and other papers), have attempted to discern those characteristics which would consistently permit the taxonomic separation of *mabouia* from *brookii.* If any consensus is to be drawn from this vast literature it must relate to the digits as being the best diagnostic character. This is supported by the rank order shown in Table 4. A majority opinion also suggests that both species are believed to have been accidentally introduced into the New World concomitant with the slave trade from Africa, and that the New World forms are indistinguishable from their African progenitors. The former point will be discussed in detail later (pp. 41–50), while the latter point will be considered below.

The last step in the quantitative phyletic procedure is the inference of what taxonomic categories are present and the application of the nomenclature that best describes these units. With the brief historical résumé given above for nomenclatural perspective, the phylogeny shown in Figure 10 can be used in this inference. Sympatry of OTUs in different monophyletic clusters and relative sums of patristic differences between OTUs, or monophyletic clusters of OTUs, are the two objective criteria that I have used to delimit the specific and infraspecific categories. It is certain that at least two species (sensu Mayr, 1963) are present in the complex shown in Figure 10. This follows from the fact that most of the OTUs that diverge from the primary branch on the left side of the tree are sympatric with those that diverge directly from the primary branch on the right side (see Table 1); no morphological intermediates between the two groups are known to me. The specific names *mabouia* and *brookii* appear to be the correct ones to apply to these monophyletic clusters of OTUs (left and right sides of the tree, respectively; Fig. 10). This application follows from the fact that they seem to be the oldest names available in the literature whose original descriptions (along with subsequently collected information) are the most similar in morphologic detail to the OTUs that make up the two primary lines. It is important to note that the Malagasy Republic and the Dahomey-Gambia-Ghana-Nigeria-Sierra Leone-Togo OTU's of the species *mabouia* and *brookii,* respectively, are the two most closely related, and that they are separated by a sum of patristic differences of 1.7712; see Tables 5 and 7.

When all of the most closely related samples of the tree are compared in terms of the sum of the patristic differences that separate them, two distinct classes of differentiation can be readily discerned (.4273–.9690 and 2.0504–2.2895; see Table 7). Owing to the fact that the minimum patristic difference that separates the species *mabouia* and *brookii* is 1.7712, and because the St. Lucia-Trinidad-South American OTU differs from its closest relative, Puerto Rico, by a much larger sum, 2.0504, it seems only reasonable that the former OTU be treated as a species as well. That this OTU is sympatric with New World *mabouia* on Chacachacare Island, Trinidad, is partial support for this conclusion (p. 41). The St. Lucia-Trinidad-South American OTU appears to have gone unrecognized nomenclaturally prior to this publication and therefore a new name, *palaichthus* sp. nov., must be given to it (see p. 39 for formal description). The nomenclatural status of the other two sets of OTUs (Table 7) with sums of patristic differences greater than 1.7712 will be discussed by me in another publication. In the present paper these OTUs will be treated tentatively as conspecific with *brookii,* and further defined by the subspecific combination *brookii angulatus.*

The relatively small patristic difference that separates Hispaniola *(brookii haitianus)* and Dahomey-Gambia-Ghana-Nigeria-Sierra Leone-Togo *(brookii angulatus),* .9690, supports the contention that the two lineages should be considered subspecifically distinct (Table 7). Similarly, in the absence of other information, the Colombia OTU *(leightoni)* appears to be more appropriately referred to as a subspecies of *brookii.* It is derived from the *brookii haitianus* line, and it differs from its closest relative, Hispaniola, by a sum of patristic differences of .8276 (Table 7). It is not sympatric with any congener.

In summary, the known cases of sympatry and the different levels of differentiation suggest that the following nomenclature most accurately describes the groups of monophyletic clusters of OTUs shown in Figure 10:

Hemidactylus mabouia (Malagasy Republic, South Africa-Rhodesia, Malawi-Mozambique, Kenya-Tanzania, Sierra Leone-Liberia, The Congo, Lesser Antilles-South America).

Hemidactylus brookii angulatus (Dahomey-Gambia-Ghana-Nigeria-Sierra Leone-Togo, The Congo, Kenya, Tanzania).

Hemidactylus brookii haitianus (Hispaniola, Cuba, Puerto Rico).
Hemidactylus brookii leightoni (Colombia).
Hemidactylus palaichthus sp. nov. (St. Lucia-Trinidad-South America).

TAXONOMIC CONCLUSIONS

In this section of the paper only the New World taxa of the *mabouia-brookii* complex are considered in detail. Their synonomy is reviewed and the geographic range, diagnosis and description are given for each form. Additional remarks on nomenclature and geographic distribution are also presented. The list of specimens examined of each taxon is given in the Appendix.

Hemidactylus mabouia (Moreau de Jonnès)

1818. *Gecko mabouia* Moreau de Jonnès, Bull. Sci. Soc. Philom. Paris, ser. 3, 1818, p. 138. Type locality: Saint Vincent Island, Lesser Antilles (restricted by Stejneger, 1904).

1824. *Gekko incanescens* Wied-Neuwied (syn. *fide* Duméril and Bibron, 1836), *In* Isis von Oken, vol. 14, p. 662. Type locality: Brazil; Wied-Neuwied, 1825, Beitr. Naturgesch. Brasil., vol. 1, p. 101, restricted type locality to Rio de Janeiro, Cabo Frio, Campos des Goaytacases and Espirito Santo, Brazil.

1824. *Gekko armatus* Wied-Neuwied (syn. *fide* Duméril and Bibron, 1836), *In* Isis von Oken, vol. 14, p. 662. Type locality: Brazil.

1825. *Gecko aculeatus* Spix (syn. *fide* Cuvier, 1829), Spec. Nov. Lacert. Brasil., p. 16, pl. 18, fig. 3. Type locality: Rio de Janeiro, Brazil.

1825. *Gecko cruciger* Spix (syn. *fide* Boulenger, 1885), Spec. Nov. Lacert. Brasil., p. 16, pl. 13, fig. 3. Type locality: Province of Bahia [= State], Brazil.

1829. *G*[*ecko*] *mabuia* Cuvier (substitute name for *Gecko mabouia* Moreau de Jonnès), Règne Anim., ed. 2, vol. 2, p. 54.

1836. *Hemidactylus mabouia,* Duméril and Bibron, Erpét. Gén., vol. 3, p. 362.

1842. *Hemidactylus mercatorius* Gray (syn. *fide* Boulenger, 1885), Zool. Misc., p. 58. Type locality: Malagasy Republic.

1843. *Hemidactylus (Tachybates) mabuya* Fitzinger (substitute name for *Gecko mabouia* Moreau de Jonnès), Syst. Rept., fasc. 1, p. 105. [*mabuya* Fitzinger type of subgenus *Tachybates* Fitzinger (*non Tachybates* Guerin-Meneville, 1844 = Arachnomorpha), by original designation].

1878. *Hemidactylus frenatus* var. *calabaricus* Boettger (syn. *fide* Mertens, 1922), Jahresber. Offenbach. Ver. Naturk., 17–18, p. 1. Type locality: Old Calabar, Nigeria.

1893. *Hemidactylus benguellensis* Bocage (syn. *fide* Loveridge, 1947), Jour. Sci. Math. Phys. Nat. Acad., Lisbon, ser. 2, vol. 3, p. 115. Type locality: Cahata, Benguela, Angola.

1909. *Hemidactylus gardineri* Boulenger (syn. *Hemidactylus mercatorius* Gray, *fide* Loveridge, 1953), Trans. Linn. Soc. London, Zool., ser. 2, vol. 12, pt. 4, p. 296, pl. 11, fig. 4. Type locality: Farquhar Island (restricted by Loveridge, 1942).

1928. *Hemidactylus persimilis* Barbour and Loveridge (syn. *Hemidactylus gardineri* Boulenger, *fide* Loveridge, 1942), Mem. Mus. Comp. Zool., Cambridge (Massachusetts), vol. 50, no. 2, p. 140, pl. 4, figs. 1, 3. Type locality: Dar es Salaam, Tanzania.

1936. *Hemidactylus mandanus* Loveridge (syn. *Hemidactylus gardineri* Boulenger, *fide* Loveridge, 1942), Proc. Biol. Soc. Washington, vol. 49, p. 60. Type locality: Kitau, Manda Island, Kenya.

RANGE.—In the New World, *mabouia* is known from the eastern coast of South America from Montevideo, Uruguay to Georgetown, Guyana. It has been recorded from along most of the length of the Amazon river in Brazil, and from its head waters in Ecuador and Peru. It is known from most of the islands in the Lesser Antilles and from two widely separated localities in the Greater Antilles (Figs. 11–12).

DIAGNOSIS.—*Mabouia* differs from all other gekkos in the New World in the following combination of characters: (1) hemidactyl type of digit with enlarged subdigital lamellae of fourth toe not reaching origin of digit from sole (Fig. 3A), (2) dorsal surfaces of body covered with minute granules and small trihedral tubercles, (3) PP 27–38 (32.9), (4) IP 0 or 1 (0.10), and (5) AS absent.

DESCRIPTION.—Scalation: LS 14–22 (17.8, 1.41) 170; CT 0–4 (0.4, 2.13) 169 (Fig. 2A); AS absent, 169; SL 8–13 (10.7, .84) 170; IL 7–10 (8.9, .67) 170; RT 10–17 (13.9, 1.20) 167; TR 13–20 (15.8, 1.50) 165; TW 3, 230; SW 4–10 (7.5, .92) 110; SD 8–17 (13.9, .94) 169; PP 27–38 (32.9, 2.22) 90; IP 0–1 (.10, .03) 90.

Measurements: SVL 67.9; SEL 9.90–12.73 (10.98, .45) 165; EEL 7.89–10.48 (8.81, .51) 166.

Color and color pattern: (Fig. 1) Ground color of dorsal surfaces grayish-white to light brown; pattern color light to dark brown. Color pattern of

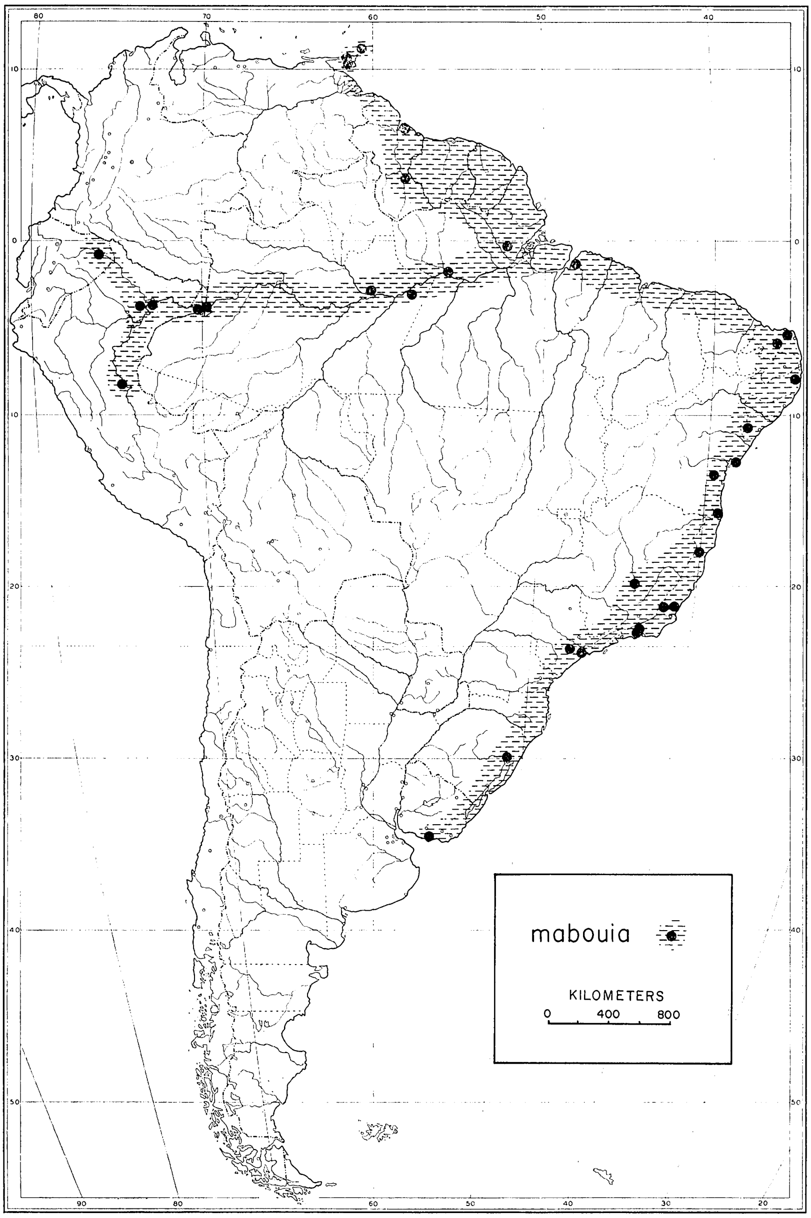

FIG. 11. The locality records of the South American specimens of *mabouia* that were examined in this study (see pp. 72–74). The stippling does not indicate the exact limits of the geographic range of the taxon.

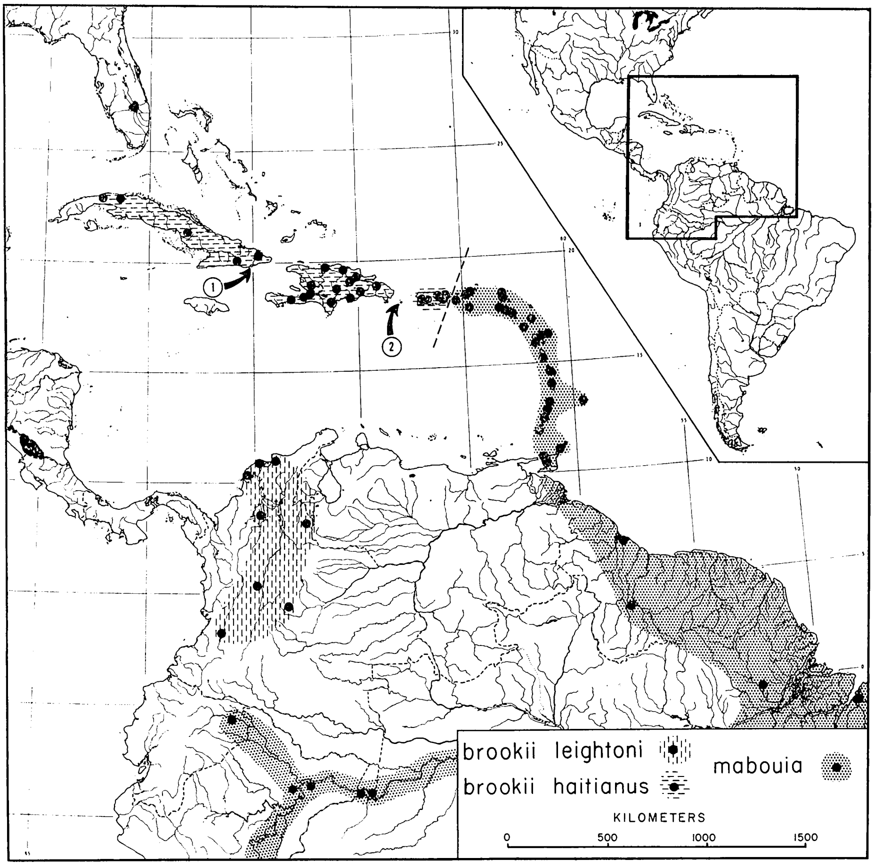

FIG. 12. The locality records of *brookii leightoni, brookii haitianus* and *mabouia* from northern South America and the Antilles that were examined in this study (see pp. 72–74). Arrow 1 points to Guantánamo Bay, Cuba, and arrow 2 points to Mona Island, Puerto Rico. These are two locality records for *mabouia* within the range of *brookii haitianus*. The stippling does not indicate the exact limits of the geographic ranges of the taxa. The heavy dashed diagonal line between Puerto Rico and Vieques Island separates the ranges of *brookii* and *mabouia*.

dorsal body surfaces absent to consisting of 3–6 V-shaped bands; apex of band directed posteriorly; bands vary in width; posterior margin of band darker brown. Dorsal surface of tail covered with 10–13 faint to conspicuous, relatively wide bands; posterior margin of band darker brown. Metachrosis appears to be well developed—from grayish-white and no pattern to light brown and a conspicuous pattern.

REMARKS ON NOMENCLATURE.—*"Gecko Mabouia"* was described as a new species in 1818 by Moreau de Jonnès on the basis of a single adult male (holotype PM 6573, *fide* Duméril and Bibron, 1836, Aug. Duméril, 1851, and Guibé, 1954 and pers. comm., 1967). It should be noted that Cuvier (1817, p. 49, footnote) first used the latinized name *mabouia,* but not in a binomial form, in reference to this gekko. Although the exact geographical origin of Moreau de Jonnès' holotype was not given in the original description and cannot be derived directly or indirectly from other available information, Moreau de Jonnès stated that his new species was widely distributed throughout the Greater and Lesser Antilles and on the continent of South America. Since that time, *mabouia* has been placed in the genus *Hemidactylus* (first by Duméril and Bibron, 1836), and the type locality restricted to "Antilles" (Aug. Duméril, 1851) and more precisely to Saint Vincent Island, Lesser Antilles (Stejneger, 1904; also see Smith and Taylor, 1950). Examination of the holotype reveals that *mabouia* is a typical member of the genus *Hemidactylus,* as defined by Loveridge (1947, p. 96), but that it is not conspecific with Lesser Antilles populations as has been generally accepted for so long. I have noted elsewhere in this paper that the size and arrangement of the subdigital lamellae (p. 23, Fig. 3A), and the number of enlarged cheek tubercles (p. 23, Fig. 2A; Table 4), are the most reliable characters with which to distinguish the species populations of *Hemidactylus* in the New World. The presence of the *brookii*-type digit and six cheek tubercles in the holotype of *mabouia* strongly suggest that its affinities are much closer to the Greater Antilles and Colombia populations of *Hemidactylus,* particularly the latter. The presence of 27 preanal pores (total) and of four interpreanal poreless scales in the holotype of *mabouia* confirms this conclusion. The specific name *mabouia* (Moreau de Jonnès) has for so many years, and so frequently, been associated with the Lesser Antilles and far eastern South American hemidactyls, as well as with their presumed African parental stock, that I believe it is in the best interest of nomenclatural stability to ignore the first use of the name *mabouia* by Cuvier, and the true identity and probable geographic origin of Moreau de Jonnès' holotype (probably Cartagena, Colombia). I recommend that the name *mabouia* (Moreau de Jonnès) be retained for the Lesser Antilles and South American *Hemidactylus* species populations which are diagnosed on page 29.

Daudin described *Gecko tuberculosus* in 1802 (p. 158). The moderately detailed description was based on a single male of unknown geographic origin which Daudin stated was deposited in the "Museum d'Historie de Paris." In the original description of the genus *Hemidacty*[*lus*] (= *Hemidactylus),* Oken (1817) was contrasting his own latinized classification with that of Cuvier (1817), who designated "G. Tuberculeux de Daud." as the type species. Various authors have ignored Daudin's nomenclaturally valid description of *tuberculosus,* while occasionally recognizing other uses of the name (e.g., Duméril and Bibron, 1836; Boulenger, 1885; Wermuth, 1965). Some workers have treated *tuberculosus* as an East Indies representative of the genus *Gekko* (e.g., as a synonym of *G. gecko, fide* Cuvier, 1817, and as a distinct species, *fide* Merrem, 1820), while others considered *tuberculosus* to be a distinct species of *Hemidactylus* (e.g., Raddi, 1823, and Peters, 1877—in Brasil; Fitzinger, 1826, 1843—in the Oriental Region; Gray, 1825—in the "Old Continent"). Loveridge (1947, p. 95) further complicated the issue by synonymizing, without comment as to reason, Daudin's *tuberculosus* with *Hemidactylus mabouia* (Moreau de Jonnès).

The fact that Moreau de Jonnès (1818), Duméril and Bibron (1836), and Guibé (1954 and pers. comm., 1967) failed to mention the holotype of *tuberculosus* as still extant in the herpetological collection of the Musée d'Histoire Naturelle de Paris, strongly suggests that the specimen was lost relatively soon after its description. Therefore, in the absence of the holotype, the original description is the only evidence that can be used to reinterpret the status of *tuberculosus.* Daudin's explicit reference to the absence of keels on the enlarged tubercles on the dorsal surfaces of the body, limbs and base of the tail, and to the presence of a total of 44 preanal pores and pairs of chestnut-brown spots on the back clearly excludes *tuberculosus* from being considered a member of the *mabouia-brookii* complex (including *palaichthus* and the African *platycephalus* and *tasmani;* see Vanzolini, 1968). If *tuberculosus* can be shown to represent a species of *Hemidactylus,* its affinities may be found to be with forms like *karenorum* (see Loveridge, 1947, and Smith, 1935). It seems much more probable, however, that Daudin was correct in his original generic assignment of *tuberculosus.* For example, the original description in its entirety is indistinguishable from the Oriental *Gekko monarchus* Schlegel. Loveridge's (1957, p. 181, footnote) statement that *tuberculosus* cannot be considered a synonym of *Gekko gecko* because of the latter's small quadrangular subcaudals, and therefore conspecific with *mabouia,* does not hold for *Gekko monarchus* which exhibits enlarged ventral caudal plates (see Rooij, 1915).

Of the list of probable synonyms of *mabouia* given on page 28, I know of no reason to question the opinion of earlier workers as to the conspecificity of *Gekko incanescens, Gekko armatus, Gecko aculeatus,* and *Gecko cruciger.* The additional synonyms, *Hemidactylus mercatorius, H. frenatus* var. *calabaricus, H. benguellensis, H. gardineri, H. persimilis,* and *H. mandanus,* will be discussed by me in a separate paper dealing with African *mabouia.*

Remarks on Geographic Distribution.—The list of specimens examined which is provided in the Appendix (see also the corresponding Figures 11–12) requires further discussion with reference to the generally accepted thesis that *mabouia* was accidentally introduced into the New World with the slave trade which began in the early part of the sixteenth century. In South America, the distribution of *mabouia* is restricted largely to a narrow margin along the eastern coast, from the strand to over two hundred miles inland. If it were not for the fact that most (but certainly not all) of these locality records suggest some association with human habitation, the coastal distribution pattern could be interpreted logically as the result of nonhuman-assisted trans-Atlantic rafting founder population(s) (see later discussion, p. 47). The distribution of *mabouia* along most of the length of the Amazon River seems to indicate a close correspondence to the large amount of human-related up-river water traffic. The "naturalness" of most of the Ecuador and Peru records, however, considerably lessens this supposed direct association with human activity. Vanzolini (1968) lists other locality records for *mabouia* in South America. I have not cited these because he did not distinguish *palaichthus* from *mabouia.*

Mabouia is known from all of the larger islands, and many of the smaller ones, from Trinidad to Vieques Island (essentially the Lesser Antilles). In the Greater Antilles *mabouia* is known definitely only from the two widely separated localities, Guantánamo, Cuba and Mona Island, and also apparently from Isabela, Puerto Rico. The specimens from Guantánamo are without question of the species *mabouia,* and the locality record seems certain. The following data on the two males and one female from Cuba indicate that they are not significantly different from either the Lesser Antillean or the mainland South American populations of *mabouia:* LS 15–17 (16.0); CT 0–1 (.30); AS 0; SL 11; IL 8–9 (8.7); RT 14–15 (14.3); TR 15–16 (15.3); TW 3; SW 8; SD 13–14 (13.3); PP 33–35 (34.0); IP 0; SVL 52.2; SEL 8.58–9.18 (8.87); EEL 11.00–11.38 (11.21). The single specimen from Mona Island is a juvenile and my species identification is given with considerably less confidence in that many of the diagnostic features are difficult to discern. It may be significant that the genus was not collected on the island during earlier surveys (Grant, 1932a; Weaver, Heatwole, Gorham and Rolle, 1961), and that there has relatively recently been established commerce between Mona and the Virgin Islands where *mabouia* is common (Heatwole, Torres and Heatwole, 1965). I have not been able to see the material described as *mabouia* from Isabela, Puerto Rico (Garcia-Diaz, 1967). Further discussion of their status must await their reexamination. There are two additional records of *mabouia* from the Greater Antilles:

Port-au-Prince, Haiti (MCZ 1327) and "Hassul," Puerto Rico (MCZ 34704). Information, either directly accompanying these specimens or in the original catalogue, casts considerable doubt on the authenticity of their places of origin (E. E. Williams, pers. comm., 1966). For example, "Hassul" appears to refer to Hassel Island, St. Thomas. These two records are not considered valid.

Levins and Heatwole (1963) considered the largely allopatric distribution pattern of *mabouia* and *brookii,* particularly on Vieques Island and Puerto Rico, respectively, as an example of competitive exclusion. They believed both species were introduced into the New World tropics through the agency of man, and that they are transported and have become established with "apparent ease." The large amount of commerce between Vieques Island and Puerto Rico coupled with the factors noted above led them to conclude that competitive exclusion was responsible for the species' allopatry. Levins and Heatwole have almost certainly overemphasized the ease with which the two species are transported and become established; also, the fact that *mabouia* and *brookii* occur together at many localities across the continent of Africa would tend to negate their argument for competitive exclusion in the New World.

In an attempt to ascertain the likelihood that more than one Old World founder "population" of *mabouia* (by either natural rafting or human agency) gave rise to New World *mabouia* I have analyzed intraspecific variability in the following manner: individual island and mainland samples in the New World were lumped into six geographically contiguous units to effect adequate sample sizes. These six samples consist of (I) Brazil; (II) Grenada, The Grenadines, St. Vincent, and St. Lucia; (III) Martinique, Dominica, and Guadeloupe; (IV) Antigua, St. Christopher, St. Eustatius, and Saba; (V) Tortola, St. John, and St. Thomas; and (VI) Vieques. Table 23 is a summary of the raw data of the ten characters (LS, CT, SL, IL, RT, TR, SW, SD, PP, IP) used in the comparisons, and Table 8 indicates the number of characters in which two samples exhibit significantly different means ($P \leq .05$). The coefficient of variability of each character of the lumped samples I–V were compared to those of the single island sample VI. With the possible exception of character CW, this comparison indicates that lumping of data has almost certainly had little relevant effect on sample variability. Two of the ten characters (LS, SD) did not exhibit significantly different means between any of the samples compared. The remaining eight characters used in the comparison of geographically adjacent samples indicates that there is a nearly uniform progression in the number of significant differences from mainland South America to Vieques

Island (Table 8; I:II = 1, II:III = 2, III:IV = 3, IV:V = 4, V:VI = 3).

The trend of increasing differentiation expressed by New World *mabouia* (Table 8) is consistent with the following hypothesis: where there is occasional emigration from the mainland, and subsequently along a chain of islands, those islands that are the most distant from the mainland will possess usually the most differentiated organisms (Simpson, 1962b). New World *mabouia* seems to be a likely candidate for natural rafting; the direction of the ocean currents favor the hypothesis that it emigrated naturally (non-human associated) from the mainland out along the Lesser Antilles, and there is a trend of differentiation which is correctly orientated and sustained with respect to distance from the mainland.

If one accepts the thesis that human transport was responsible for bringing *mabouia* to the New World, and specifically to the Lesser Antilles, he must also assume (in a probabilistic sense) some transport by human agency within the New World from island to island (see p. 44). Given the seemingly random pattern of shipping, both in the past and the present, one must explain the observed trend of character differentiation in Lesser Antilles *mabouia* as coincidental, and this seems highly unlikely. That *mabouia* was transported to the mainland of South America by human agency, e.g., those ships associated with the slave trade, appears to be geographically inconsistent with this human endeavor. If *mabouia* was brought to mainland South America on slaving ships, why not also to the Greater Antilles? The fact that Jamaica and the Bahama Islands do not have any hemidactyls is even more difficult to explain (p. 44). For example, Jamaica had some of the biggest and most frequently and longest used slaving ports in the New World. It is possible that hemidactyls have not been able to establish a population on Jamaica or the Bahamas because of some limiting factor or competitive interaction. However, neither of these situations seems very probable owing to the fact that *mabouia* (and *brookii*) occurs on other islands with similar physical and climatic features and which have at least similar faunal and floral elements.

Hemidactylus brookii haitianus Meerwarth

1901. *Hemidactylus brookii haitianus* Meerwarth, Mitt. naturhist, Mus., vol. 18, p. 17. Type locality: Port-au-Prince, Haiti (restricted by Cochran, 1941).

RANGE.—Known only from Cuba, Hispaniola and Puerto Rico (Fig. 12).

DIAGNOSIS.—*Haitianus* differs from all other gekkos in the New World in the following combination of characters: (1) hemidactyl type of digit with enlarged subdigital lamellae of fourth toe reaching origin of digit from sole (Fig. 3B), (2) dorsal surfaces of body covered with small granules and large trihedral tubercles, (3) PP 23–32 (28.0), (4) IP 0–4 (2.1), and (5) AS 0–3 (1.8).

DESCRIPTION.—Scalation: LS 10–18 (13.8, 1.61) 73; CT 1–7 (3.6, 1.22) 73 (Fig. 2B); AS 0–3 (1.8, .97) 73; SL 7–11 (8.99, .79) 74; IL 6–10 (7.9, .67) 74; RT 15–22 (16.9, 1.73) 73; TR 14–23 (18.6, 1.92) 73; TW 1–5 (2.9, .78) 140; SW 4–8 (5.9, .97) 69; SD 7–11 (8.9, .70) 73; PP 23–32 (28.0, .49) 129; IP 0–4 (2.1, .99) 132.

Measurements: SVL 67.5; SEL 9.66–11.75 (10.65, 2.77) 73; EEL 7.45–10.42 (8.90, 2.31) 73.

Color and color pattern: (Fig. 1) Ground color of dorsal surfaces brownish-white to relatively dark brown; pattern color light to dark brown. Color pattern of dorsal body surfaces absent to consisting of 3–6 butterfly-shaped marks; these may be broken up into numerous irregularly shaped spots on midline and along lateral body surfaces. Dorsal surface of tail covered with 9–11 irregularly shaped bands or numerous irregularly shaped and randomly located small spots.

Hemidactylus brookii leightoni Boulenger comb. nov.

1911. *Hemidactylus leightoni* Boulenger, Ann. Mag. Nat. Hist., London, ser. 8, vol. 7, art. 3, p. 19. Type locality: Honda, Río Magdalena, 300–400 feet, Colombia.

1936. *Hemidactylus neotropicalis* Shreve, Occ. Pap. Boston Soc. Nat. Hist., vol. 8, p. 270. Type locality: Puerto Wilches, Department of Santander, Colombia (corrected by Shreve, 1938).

RANGE.—Restricted to Colombia, from the northwestern coast to the central highlands. It probably occurs in western Venezuela (Fig. 12).

DIAGNOSIS.—*Leightoni* differs from all other gekkos in the New World in the following combination of characters: (1) hemidactyl type of digit with enlarged subdigital lamellae of fourth toe reaching origin of digit from sole (similar to Fig. 3B). (2) dorsal surfaces of body covered with small granules and large trihedral tubercles, (3) PP 21–28 (24.3), (4) IP 2–4 (2.9), and (5) AS 0–4 (.80).

DESCRIPTION.—Scalation: LS 12–17 (13.7, 1.13) 26; CT 3–10 (5.2, 1.63) 27 (similar to Fig. 2B); AS 0–4 (.80, 1.18) 25; SL 8–10 (8.6, .83) 26; IL 7–9 (8.3, .60) 26; RT 14–23 (18.3, 2.15) 27; TR 16–22 (18.9, 1.68) 27; TW 2–4

(3.0, .62) 30; SW 5–7 (5.8, .58) 13; SD 7–10 (8.6, .71) 27; PP 21–28 (24.3, 2.07) 8; IP 2–4 (2.9, .84) 8.

Measurements: SVL 63.4; SEL 10.17–12.33 (11.89, 1.33) 27; EEL 7.67–9.71 (8.81, 1.69) 25.

Color and color pattern: Similar to *haitianus*; see page 37.

REMARKS ON NOMENCLATURE.—I have examined the holotype of *neotropicalis,* MCZ 39706. It is an adult female with the following characteristics: LS 14; CT 7; AS ?; SL 9; IL 9; RT 17; TR 19; TW 3; SW 6; SD 8; SVL 60.5; SEL 10.75; EEL 8.04. Although I have not seen the holotype of *leightoni,* BMNH 1946.8.25.65, I believe the two named forms to be conspecific. My conclusion is based on morphological data taken from the two holotypes and included in correspondence between Benjamin Shreve of the Museum of Comparative Zoology and J. C. Battersby of the British Museum. The data on both specimens do not differ significantly from any character mean of the Colombian population that I have sampled.

REMARKS ON GEOGRAPHIC DISTRIBUTION.—With the single exception of ANSP 7440, all of the material of *brookii* that I have thus far examined from the New World was collected in Cuba, Hispaniola, Puerto Rico, or Colombia. The single exception noted above is recorded as having been collected at Rio de Janeiro, Brazil with a single specimen of *mabouia,* ANSP 7439. The date and place of collection of the *brookii* are probably in error. The two specimens were collected by the U. S. Exploring Expedition which visited numerous ports where *brookii* is known definitely to occur.

Like *mabouia, brookii* is generally thought to represent a recent introduction into the New World, probably in association with the transport of slaves from Africa. However, the following facts cause me to doubt this assumption: (1) the New World populations are significantly different from their supposed African progenitors in numerous morphological characteristics (see pp. 20–25), (2) some of the New World populations are significantly different from each other in numerous morphological characteristics (see pp. 20–25), and (3) the geographical distribution patterns in the Greater Antilles and in Colombia do not appear to correspond to ones resulting from human introduction (Mechler, 1968). Relative to this last point, the absence of *brookii* (and *mabouia* for that matter) from major slave trading ports once located on Jamaica and in the Bahama Islands and the Dutch West Indies (Curacao, Aruba, Bonaire and the Venezuelan islands, Hummelinck, 1940) may be added as very strong negative evidence against the hypothesis of a human related introduction. Garth Underwood (pers. comm.) spent twelve years on Jamaica and actively worked on the herpetofauna of that island. During that time he did not collect or observe *Hemidactylus*. Barbour (1930) listed *mabouia* as occurring on Jamaica, but specimens to which he might have been referring cannot be located. Furthermore, competitive exclusion does not appear to exist between the two species, as I reasoned on page 35. And, the nearly random routes of commerce that have been established between Africa and the New World tropics, and particularly within the latter area demand that the nearly completely discordant geographic ranges be explained in some other way.

Hemidactylus palaichthus sp. nov.

HOLOTYPE: AMNH 60931 (original field number L 18), adult male (SVL 63.1).

TYPE LOCALITY: Kurupukari, Guyana (4° N, 59° 25′ W), collected by R. Snedigar, on October 2–3, 1937.

PARATYPES: All specimens listed under "Specimens Examined," pages 74–75.

ETYMOLOGY: From the common Greek work *palaichthon,* meaning indigenous inhabitant.

RANGE.—Known from northern Brazil, Guyana, central and northeastern Venezuela, Trinidad and St. Lucia, Lesser Antilles (Fig. 13).

DIAGNOSIS.—*Palaichthus* differs from all other gekkos in the New World in the following combination of characters: (1) hemidactyl type of digit with enlarged subdigital lamellae of fourth toe reaching origin of digit from sole (similar to Fig. 3B), (2) dorsal surfaces of body covered with small granules and large trihedral tubercles, (3) PP 32–43 (37.1), (4) IP absent, and (5) AS absent.

DESCRIPTION.—Scalation: LS 12–19 (14.7, 1.59) 43; CT 2–11 (5.0, 2.20) 40 (similar to Fig. 2B); AS absent, 43; SL 8–12 (9.8, .82) 43; IL 7–10 (8.7, .58) 43; RT 17–25 (21.5, 2.24) 40; TR 17–28 (22.0, 2.29) 42; TW 2–4 (3.0, .28) 54; SW 3–6 (4.9, .88) 25; SD 9–11 (9.5, .63) 43; PP 32–43 (37.1, 3.09) 24; IP absent, 24.

Measurements: SVL 63.1; SEL 10.37–12.46 (11.34, 1.47) 39; EEL 8.55–9.96 (9.22, .97) 39.

Color and color pattern: (Fig. 1) Ground color of dorsal surfaces light brown to dark gray; pattern color dark brown to nearly black. Color pattern of dorsal body surfaces absent to consisting of a latticework of about 7–10

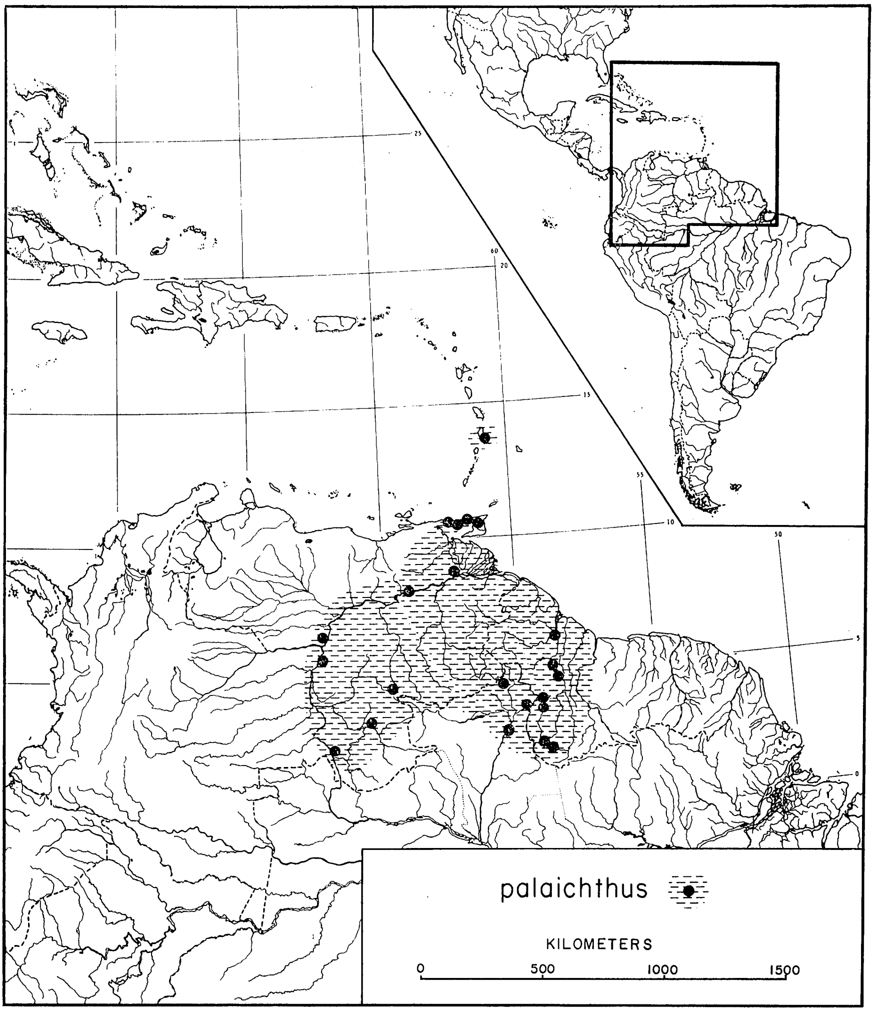

FIG. 13. The locality records of *palaichthus* from the Lesser Antilles and northern South America that were examined in this study (see pp. 74–75). The stippling does not indicate the exact limits of the geographic range of the taxon.

narrow dark reticulate marks and a pair of dorsal-lateral continuous or discontinuous narrow reticulate marks. Dorsal surface of tail covered with about 10 faint to conspicuous relatively wide bands or numerous irregularly shaped and positioned small spots.

REMARKS ON GEOGRAPHIC DISTRIBUTION.—There are two important features of the geographical distribution of *palaichthus* that must be emphasized. Firstly, the species has been collected far into the interior of the continent, and from environments that appear to have been little touched by "European Man." Secondly, the species occurs on Trinidad and St. Lucia (actually the adjoining Maria Island), but not on any of the intervening islands, Grenada, The Grenadines, or St. Vincent. This disjunction may not be entirely an artifact of lack of study, because Grenada, St. Vincent and many of the larger islands of The Grenadines have been visited by professional herpetologists who appear to have been effective collectors (see herpetofaunal lists given by Underwood, 1962).

At present, *mabouia* and *palaichthus* are known to be sympatric (sensu stricto) at only one locality; Underwood (pers. comm.) has collected both species in the same (or at least adjacent) palm tree on Chacachacare Island, Trinidad. On Trinidad proper, the two species have been collected relatively near one another, and it seems likely that other points of sympatry exist. At the northern disjunct extreme of its range *palaichthus* appears to be restricted to Maria Island, while *mabouia* covers most of the island of St. Lucia which is immediately adjacent to it. There is no indication that the two species will be found in sympatry.

GEOGRAPHIC ORIGIN AND MODE OF DISPERSAL

If the proposed time and place of origin of the four primary phyletic lines within the Gekkonidae, late Mesozoic and southeast Asia, respectively (Kluge, 1967), are reasonably accurate estimates, then there appear to have been only two major non-human assisted dispersal routes between the Old and New Worlds open to subsequent radiations. These routes are (1) by gradual geographic spread over the Bering Land Bridge from the Oriental Region during the Cenozoic (Repenning, 1967), and (2) by fortuitous trans-Atlantic dispersal, mostly from Africa (see below, pp. 42–43). The north Atlantic Land Bridge is generally thought to have become disrupted prior to the Tertiary (Hopkins, 1967), and therefore it may be excluded from the remainder of this discussion. Major movements of continents may be dismissed for similar reasons.

The Bering Land Bridge was almost certainly used by some gekkos, e.g., the progenitor of the New World eublepharine genus *Coleonyx*. The evidence in support of this example follows from the conclusion that within the Eublepharinae, *Coleonyx* is the most divergent genus and that it was derived from an Old World *Eublepharis*-like ancestor (Kluge, 1962, 1967). Further evidence comes from the present-day geographic distribution of the Oriental eublepharine species of *Eublepharis* (Kluge, 1967, see Map 1).

The northernmost form, *E. kuroiwae splendens* occurs on Toku no Shima, Riu Kiu Islands, approximately 28° N. lat. (Wermuth, 1965), and its presence there strongly suggests that the genus had a much wider geographic distribution in the past and certainly one from which a Bering Land Bridge propagule could have been derived readily during climatically more favorable times. No other group of gekkos appears to approximate this set of conditions closely and it is not unlikely that the *Eublepharis-Coleonyx* example is unique among the extant Gekkonidae.

The gekkonine genus *Tarentola* has been cited as an example of trans-Atlantic dispersal (Kluge, 1967). In the New World, there exists a single endemic species, *T. americana,* which is restricted to Cuba and the Bahama Islands. The species' insular differentiation has been studied recently by Schwartz (1968), and he believes that it has been significant. Its presence in the Late Pleistocene (New Providence Island, Bahama Islands; Etheridge, 1965) and in Recent deposits of probable pre-Colombian age (Cuba; Koopman and Ruibal, 1955) eliminates all possibility that the species was introduced initially into the New World by modern man, either intentionally or fortuitously. The general place of geographic origin of *T. americana* is suggested by the distribution of its Old World congeners from which it was almost certainly derived. *Tarentola annularis* is known from eastern Africa, from Egypt and Libya southward through the Sudan and Abyssinia to Somalia, and southwestern Asia (Arabia), *T. delalandii* (four subspecies) from the Canary and the Cape Verde Islands, *T. ephippiata* from western Africa (the drier parts of Mauritanica) southward to Cameroon, eastward to and including the Sudan, *T. mauritanica* (two subspecies) from southern Europe (eastward to Greece), the Canary Islands and northern Africa (eastward to Egypt), and *T. neglecta* from the Algerian Sahara eastwards to Libya. No one has studied in detail the interspecific relationships of *T. americana* and therefore a more restricted part of Africa of southern Europe cannot be suggested as the geographic place of origin of its ancestral stock.

Other likely examples of trans-Atlantic dispersal are the endemic New World Sphaerodactylinae (see Kluge, 1967, for discussion) and the *Lygodactylus* sp. reported from Brazil (Kluge, 1964). Recently, Vanzolini (1968) listed the unnamed *Lygodactylus* from Barreiras and Senhor do Bonfim, State of Bahia, and from Urucum, State of Mato Grosso. Joseph R. Bailey (pers. comm., 1968) discussed the likelihood that, of the 48 species and 16 additional subspecies presently recognized in the genus (sensu stricto, including *Microscalabotes* and *Millotisaurus),* it is a relatively primitive species and the only form restricted to the New World. In the Old World, the genus is confined to Africa, apparently south of the Sahara, and to the

Malagasy Republic and islands in between the two land masses. This distributional pattern, coupled with the kind and degree of speciation in the Ethiopian Region, suggests that the known Brazilian populations are derived and that they have not been transported there by human agency.

In any discussion of the method of dispersal of gekkonid lizards, the possibility of their transport by human conveyance must be taken into consideration, particularly of those species that frequent human habitation and refuse. In the case of *Coleonyx* (see above), the degree and kind of differentiation exhibited by the species strongly point to at least a pre-Pleistocene radiation in the New World and its existence there prior to the relevant period of the evolution of modern man. *Tarentola americana* shows some intraspecific morphologic differentiation, and the presence of fossils referred to that species clearly substantiates it as resident in the New World before the evolution of modern man. In contrast to these examples, the New World hemidactyl *mabouia* and *brookii* populations have almost always been cited as the product of human transport, more specifically of the slave trade that existed between Africa and the New World tropics. And, with the exception of a few authors, the New World *mabouia* and *brookii* were stated to be morphologically indistinguishable from their Old World counterparts.

The kind of phylogenetic and biogeographic information that supports a thesis of over-water natural dispersal by *mabouia* and *brookii* (see below) is conspicuously absent in the case of two other New World hemidactyls, *frenatus* and *turcicus*. The evidence that these other two species were brought to the New World on ships across the Pacific and Atlantic, respectively, and on more than one occasion, is as follows: (1) they do not appear to differ significantly from their Old World progenitors (Smith and Taylor, 1950; Loveridge, 1941, 1947; Kluge, in prep.); (2) their geographic distribution is almost entirely within, or very near, human settlements, particularly on wharves and buildings in ports, or along major routes of commerce; (3) most of the locality records in the New World are coastal, and they do not form a continuous geographic range (with the possible exception of *turcicus* on Cuba); and (4) the dates of introduction have been relatively accurately established (for review see Stejneger, 1922; Leavitt, 1933; Burt and Myers, 1942; Etheridge, 1952; Dixon, 1958, King, 1959).

The earlier sections of this paper have demonstrated the following points relative to morphologic differentiation of *mabouia* and *brookii:* (1) that New World *mabouia* are significantly different from their phyletically closest African ancestors (The Congo and Sierra Leone, Liberia) in four of the thirteen characters employed and there is increasing differentiation of island populations in the Lesser Antilles, proportionate to the distance of the islands from the mainland of South America; (2) that the Greater Antillean *brookii* are sufficiently different from their Old World progenitors to be labeled as a different subspecies, *brookii haitianus;* (3) that the Colombia hemidactyl is very different and consequently is considered an endemic New World subspecies, *brookii leightoni,* that was derived from *brookii haitianus;* and (4) that there exists an endemic New World species, *palaichthus* (St. Lucia, Trinidad and northeastern South America), which also evolved from *brookii haitianus.* This summary indicates that *brookii* and derived taxa, and probably *mabouia,* have undergone considerable differentiation in the New World. And, the degree of this differentiation probably required a period of time that predated the origin of modern man.

Previous students of *mabouia* and *brookii* biogeography appear to have inferred from the seemingly random distribution of locality records of the taxa recognized at those times that numerous propagules of different geographic origin were fortuitously transported to the New World on slaving ships. Grant (1959) even went so far as to propose that on Barbados, *mabouia* was purposely but clandestinely, introduced by sorcerers to terrify their subjects. With the reevaluation of the taxonomy of New World hemidactyls (pp. 28–41), the interpretation of the details, and even the general patterns of geographic distribution of the taxa, have changed markedly. These new patterns are now largely non-random (Figs. 11–15), and they appear better to support a thesis of a very small number of transportations from Africa to the New World, and gradual radiation therein, without the aid of man. The arguments based on phylogenetic evidence presented above most strongly substantiate this point of view while the following generalizations derived from biogeographic observations add further support: (1) hemidactyls were present in the Lesser Antilles in 1654 (Du Tertre, 1654), and therefore very early in the history of the slave trade; (2) at least some parts of the geographic ranges of all taxa lie outside the usual routes of commerce and places of human habitation, viz., they appear to be naturally distributed; (3) hemidactyls are not known from some islands which were major ports of entry for slave ships coming directly from Africa (e.g., Jamaica and the Bahamas); and (4) most of the geographic ranges of the species are allopatric and the locality records of each indicate contiguous ranges, conditions that seem totally inconsistent with the irregular routes taken by the slave traders from Africa to the West Indies and within the West Indies from island to island. The history of the Africa-New World slave trade relative to these four points can be discussed conveniently under two headings, namely temporality and intensity of slaving, and geographic patterns of the trade (Copley, 1839; Blanshard, 1947; Parry and Sherlock, 1957).

The first direct shipment of slaves from Africa to the New World was in 1513, and by 1518 the commerce was regular and organized. As early as 1540, 10,000 slaves per year were being sold to sugar planters in the West Indies, principally the Greater Antilles, and by the end of the Sixteenth Century about 100,000 in all had been imported. In contrast to the history of the Greater Antilles, the Lesser Antilles, wherein Du Tertre (1654) first noted a hemidactyl, was settled only 30 years prior to his observations and very few shipments of slaves had been received directly from Africa by then. These data are interpreted to mean that in terms of the early history of slaving and the number of slaves introduced, the probability of *mabouia* being introduced into the Lesser Antilles with the trade from Africa seems considerably more remote than the unlikely human assisted introduction of *brookii* into the Greater Antilles. It will be recalled that the phylogenetic evidence strongly rules against a slave trade introduction of *brookii*.

Few if any regular patterns of collection, transport and sale of slaves can be reconstructed that might explain the seemingly natural geographic ranges of New World *mabouia* and *brookii*. While it is true that the Portuguese suppled most of the slaves during the Sixteenth Century, and that the Dutch supplied them from 1640 to the end of the Seventeenth Century, and that most of the slaves came from the west coast of Africa between 15° N. lat. and the Equator, there are many exceptions. The pirating, capture and recapture, of slaves within Africa, enroute to and within the Americas produce an historical picture without any pattern. In addition, many slave coffles were brought from 500–600 miles inland, and there is one known case where slaves were captured on the east coast, marched across Africa, and shipped from the mouth of the Congo River. Furthermore, slaving was not limited to the west coast of Africa north of the Equator. Major slaving ports existed as far south as Mossamedes, Angola and along most of the east coast of Africa between Zanzibar and Quelimane. Here again, a definite historical pattern is absent. Most of the slaving was carried out by companies that were managed or subsidized by European governments, and therefore utilized the slave collection agencies of their nationality in Africa and sold only to the islands governed by their nationality in the Antilles. However, there were many slavers who had no government ties and therefore their purchase and sale of slaves cut across national lines. Moreover, it must be remembered that most of the islands in the Antilles were settled and governed by more than one nationality. Some of the islands have changed hands relatively frequently. One of the most difficult single pieces of negative evidence against the thesis of an introduction of *mabouia* and *brookii* with the slave trade is their absence from islands known to be major clearing houses for slaves coming directly from Africa. It seems impossible to resolve the fact that hemidactyls do not occur on Jamaica and yet, for example, 610,000 slaves were shipped to Port Royal alone between 1700–1786. This brief summary of the slave trade produces a historic background which is not concordant with the geographic distribution of *Hemidactylus* as it should be if they were brought to the New World with the trade.

In contrast to the very low probability that seems to accompany the thesis that *mabouia* and *brookii* were introduced into the New World by man within the last 470 years, considerably greater likelihood is placed on the hypothesis of their natural trans-Atlantic dispersal. This likelihood obtains from the existence of certain biological characteristics which are absolutely necessary to, or at least would greatly facilitate, successful over-water dispersion and subsequent colonization, as well as the presence of requisite geographic land and ocean configurations. As a group, gekkos seem to have a very high probability for rafting for a terrestrial vertebrate, even closely approaching the aerial dispersal of bats and birds (Simpson, 1952). The following characteristics have been described for many gekkonines and they are almost certainly all present in *mabouia* and *brookii:* (1) small adult size, (2) young and adults are very adept at clinging to a moving structure, (3) largely insectivorous, occasionally ingest plant exudate, (4) can survive long periods without food, fat in tail appears to serve as a food reservoir, (5) do not require free water for long periods of time, (6) sperm retention exists, (7) skin is relatively impervious to water loss and to uptake of salts from a marine environment, (8) young and adults very secretive, frequently found in cracks and crevices and under bark of trees and larger shrubs, (9) gregarious, (10) population densities very high, (11) relatively broad habitat preference, (12) adults often occur in association with tidal debris, (13) communal egg laying site is common, (14) eggs are covered with a calcareous shell, (15) eggs have an adhesive glutinous covering when first laid which enables them to firmly adhere to each other and to other surfaces, either rock or plant material, (16) eggs can withstand long periods of exposure to sea water and still remain viable, (17) moderately long incubation period is typical, 40 to well over 70 days are common (122 days has been reported), and (18) sexual maturity may be attained within 30 to 40 days after hatching. In particular, *mabouia* has been observed to reside commonly in the hollows of trees, under loose bark, and in the crowns of palms, and to lay communally up to 50–60 eggs, which owing to their glutinous covering when first laid are stuck to each other and to the substrate (FitzSimons, 1943).

It is clear that the direction of the present surface winds and oceanic currents in the mid-Atlantic favor the dispersal of animals by rafting on floating objects from Africa to the Antilles and to the mainland of South America. Latitudinal compressions of winds and currents during the Pleistocene, and probably throughout the Tertiary, were not sufficiently great to have altered at least the important aspects of this pattern (Sverdrup, Johnson and Fleming, 1964). The North, Main, and South Equatorial Currents are those most likely to be involved in the east to west dispersal of terrestrial organisms. The distinction between the Main and South Equatorial Currents in the Southern Hemisphere is made on the basis of their different origins and destinations; however, they are contiguous in mid-ocean (Guppy, 1917). Darlington (1957) stated that much of the floating drift in the Atlantic is carried by the Main Equatorial Current and that at least some of it comes from the Niger and Congo Rivers and that it may be carried beyond the coast of Brazil to the West Indies by means of the Guiana Current. It seems unlikely, however, that the floating drift from the Niger River contributes as much to dispersal to the New World as does the Congo because of the main west to east flow of the East Counter and Guinea Currents (Guppy, 1917). It is certain that the Guiana Current, as an extension of the Main Equatorial Current north of Cape St. Roque, picks up additional drift from the Amazon and Orinoco and the rivers of the Guianas (see King, 1962, and references cited therein). It is important to recognize that the Main Equatorial Current at its origin in the Gulf of Guinea is fed by the Guinea Current on its north side, and on its south side by the slightly colder, northward flowing inshore waters of the Benguela Current. The South Equatorial Current may be regarded as fed principally by the offshore waters of the Benguela Current and therefore it probably carries less drift to the southern coast of South America by means of the Brazil Current. The direction of the East Counter and Guinea Currents and the colder water sources of the Main and South Equatorial Currents may indicate that they are not as important in dispersal to the New World as is the North Equatorial Current. The difference between the North and South Equatorial Currents may be even greater than that between the North and the Main Currents because of the South Equatorial Current's source in the Benguela Current. Along the Atlantic seaboard in Africa, *brookii* occurs farther north than does *mabouia,* 16° N. lat. (Cape Verde Islands) and 9° N. lat. (Sierra Leone), respectively (Figs. 14–15; Schmidt, 1919; Loveridge,

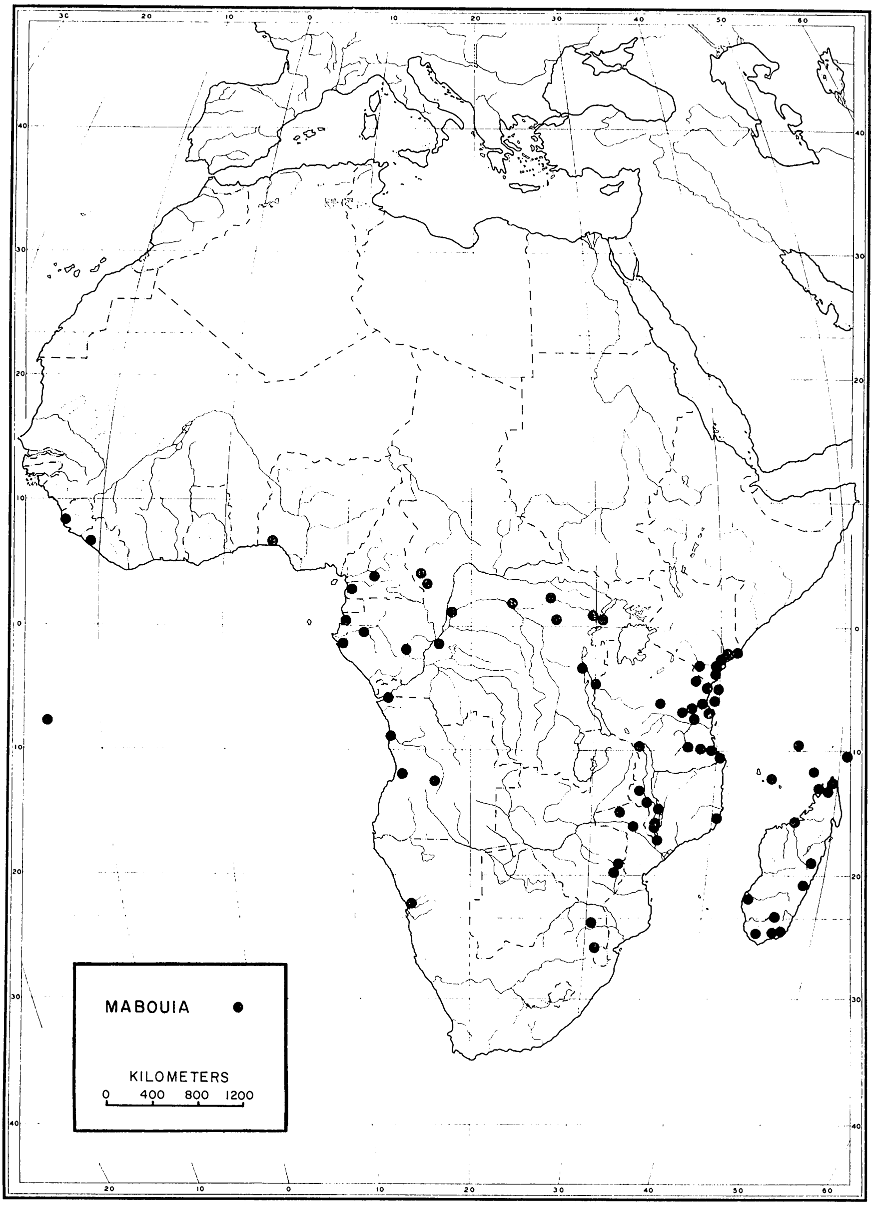

FIG. 14. The locality records of *mabouia* from Africa, Madagascar and offshore islands that were examined in this study (the locality data will be listed elsewhere).

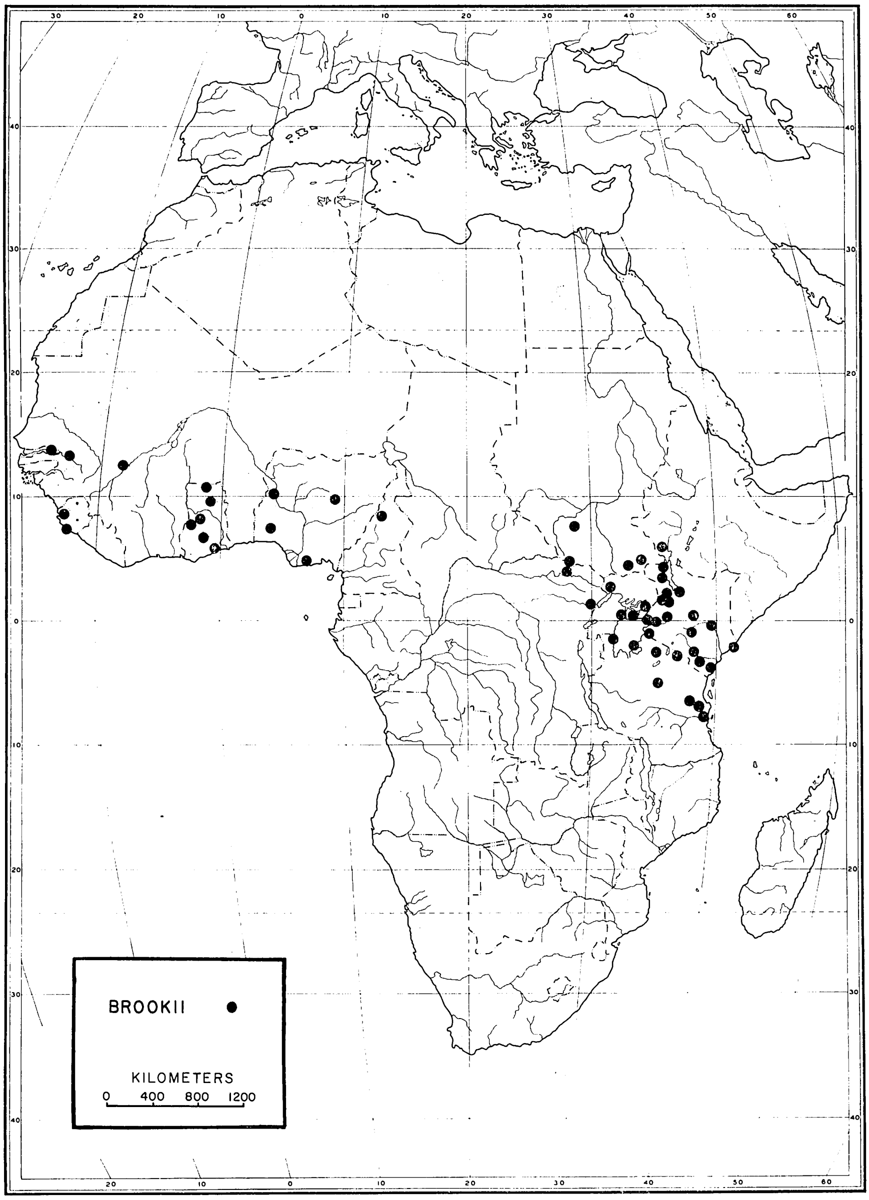

FIG. 15. The locality records of *brookii* from Africa that were examined in this study (the locality data will be listed elsewhere).

1947). If this difference is not an artifact of collecting, which it does not appear to be, then *brookii* could be ferried in the North and Main equatorial currents, whereas *mabouia* would probably have access only to the Main Equatorial Current. During more pluvial times in the Cenozoic both species would probably have extended their ranges farther to the north and *mabouia* would then have had access to both currents.

Guppy's (1917, pp. 46–82) monumental summary of drift bottle studies has not only helped to establish the details of the direction of the currents in the Atlantic and the Gulf of Mexico and their source and destination but has also provided data on the speed and time of the drift that might be equated to that of natural debris which could carry small organisms such as gekkos. He has shown that drift bottles in the North Equatorial Current end up in the Greater Antilles, Bahamas, and Lesser Antilles, north of Barbados and St. Vincent, with few exceptions. The distribution of 60 drift bottles placed in the Main Equatorial Current (and later passing into the Guiana Current) had the following destination by percent: Guiana (5), Trinidad, Tobago, coast of Venezuela (31), Lesser Antilles (26), Greater Antilles (13), Bahamas (2), Nicaragua and Honduras (7), Gulf of Mexico (11), and coast of Florida (5). It appears that about 6 percent of the drift from the Main Equatorial Current reaches the north coasts of the Greater Antilles, the Bahamas, the Florida Strait, and the Bermudas by way of the Antillean Stream.

The following approximate data on rate of bottle drift (miles per day) were given by Guppy (1917): (1) for the North Equatorial Current—(a) Canary Islands to the West Indies, 9, (b) Cape Verde Islands to the Grenadines, 13, and (c) mid-Atlantic (9° 51′ N, 32° W) to St. Vincent, 17; (2) for the Main Equatorial Current—(a) velocities as high as 60 in the mid-Atlantic to Cape San Roque, (b) along the coast of northern Brazil and the Guianas from 30 to 50, occasionally as high as 70 or 80; (3) Guiana Current—(a) Amazon to Florida, 17; (4) Brazil Current, 12 to 20. The importance of the velocity of drift to the dispersal of organisms can be better appreciated from the above data if one considers that starting in the Gulf of Guinea, a bottle would require an average of only about 12 weeks to reach the vicinity of Cape San Roque and 17 weeks to reach Trinidad. Guppy stated that the run to the coast of Brazil may be made even in as little as 2 months. The biological characteristics given above suggest that *mabouia* and *brookii* have the tolerance and adaptability to withstand a very long natural trans-Atlantic dispersal, almost certainly in excess of the average time that natural rafts take to make the crossing.

SUMMARY

Evolutionary relationships of samples belonging to the *Hemidactylus mabouia-brookii* complex were analyzed by quantitative phyletic methods. The 16 samples used in the study were selected without direct reference to prior taxonomic conclusions. The samples were described by 13 characters. Initially, the samples were clustered on the basis of their overall similarity. The cladistic and patristic centers of this phenetic product were used to estimate the most likely set of primitive character states. Next, the most parsimonious dendrogram was constructed. The set of primitive character states was included in the dendrogram as the ancestor to establish the direction of character change, and the characters were weighted according to the concept of conservatism. Sympatry of samples in different monophyletic clusters and relative sums of patristic differences between samples in the dendrogram were the criteria that were used to delimit specific and infraspecific categories. The oldest available name in the literature whose description is the most similar in morphologic detail to the specific or infraspecific category was applied to it.

The following points summarize the major taxonomic conclusions: (1) New World *mabouia* differ relatively little from their phyletically closest Old World ancestor which is located on the west coast of Africa; (2) the New World *brookii* populations on Cuba, Hispaniola and Puerto Rico differ considerably from their most similar ancestor which is also located on the west coast of Africa, and accordingly they are referred to a different subspecies, *brookii haitianus;* (3) the allopatric Colombian population is sufficiently different from its most similar relative *brookii haitianus* to be referred to as *brookii leightoni;* and (4) an extremely different lineage, derived from *brookii haitianus,* is restricted to St. Lucia, Trinidad and northeastern South America and it is described as a new species, *palaichthus.*

The new taxonomic arrangements and the concomitantly changed geographic ranges of the taxa require a reevaluation of the generally accepted thesis that *mabouia* and *brookii* were introduced into the New World along with the shipment of slaves from Africa. Cladistic and patristic relationships and geographic distribution in the New World strongly indicate that the progenitor of the *brookii* complex, *b. haitianus, b. leightoni* and *palaichthus,* was derived from a west coast Africa stock and was transported to, and radiated within, the New World independent of man. The evidence is considerably weaker for the same conclusion for *mabouia.* The biology of *mabouia* and *brookii,* as well as ocean current and land configurations, complement the proposal of a natural trans-Atlantic dispersal.

TABLE 1

POPULATIONS SAMPLED, SAMPLE SIZE AND THE CHARACTERS USED IN THE QUANTITATIVE PHYLETIC ANALYSIS

Populations Sampled	Sample Size	Characters (13)
South Africa, Rhodesia[1]	12	Number of loreal scales (LS)
Malawi, Mozambique[1]	23	Number of cheek tubercles (CT; see Fig. 2)
Malagasy Republic[1]	26	Number of auricular scales (AS)
Kenya, Tanzania[1]	55	Number of supralabials (SL)
Kenya[2]	26	Number of infralabials (IL)
Tanzania[2]	26	Number of rows of body tubercles (RT)
The Congo[1]	26	Number of tubercles in paravertebral row (TR)
The Congo[2]	25	Number of tubercles in caudal whorl (TW)
Sierra Leone, Liberia[1]	10	Number of scales between caudal whorls (SW)
Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo[2]	59	Number of subdigital lamellae (SD)
Ascension Island[1]	3	Number of preanal pores (PP)
Lesser Antilles, South America[1]	170	Number of interpreanal pore scales (IP)
St. Lucia, Trinidad, South America[2]	43	Type of digit TD; (see Fig. 3)
Colombia[2]	27	
Puerto Rico[2]	25	
Hispaniola[2]	24	
Cuba[2]	24	

[1] Type A digit

[2] Type B digit

TABLE 2

RELATIVE UNIT CHARACTER CONSISTENCIES

Character	LS	CT	AS	SL	IL	RT	TR
Consistency	.488	.565	.477	.446	.490	.600	.391
Rank	8	4	7	9	6	3	11

Character	TW	SW	SD	PP	IP	TD
Consistency	.405	.492	.629	.350	.279	1.000
Rank	10	5	2	12	13	1

TABLE 3

CHARACTER STATES OF HYPOTHETICAL OTUs

	LS	CT	AS	SL	IL	RT	TR	TW	SW	SD	PP	IP	TD
Ancestor	12.7	2.5	2.1	9.0	7.8	14.9	17.1	3.0	5.8	8.0	27.3	0.87	.5
Intermediate 1*	12.7	2.5	2.1	9.0	7.8	14.9	17.1	3.0	5.8	8.0	27.3	0.87	1
Intermediate 2	12.7	3.2	2.1	9.0	7.7	16.2	18.0	3.0	5.7	8.6	27.3	1.10	1
Intermediate 3	12.7	3.6	2.1	9.0	7.7	17.7	18.0	3.0	5.6	8.6	28.1	2.30	1
Intermediate 4	11.8	6.1	3.6	8.3	7.4	17.7	18.0	3.1	5.2	8.6	28.1	2.30	1
Intermediate 5	11.8	8.4	3.6	8.3	7.4	17.7	18.6	3.8	5.2	8.8	31.8	2.30	1
Intermediate 6	12.8	3.6	1.5	9.0	7.7	18.2	18.0	2.8	5.6	8.6	28.1	2.30	1
Intermediate 7	13.7	3.8	1.4	9.0	8.0	18.3	18.1	2.8	5.8	8.6	28.1	2.30	1
Intermediate 8	14.2	3.8	1.4	9.0	8.0	19.2	18.1	2.8	6.1	9.0	28.1	1.80	1
Intermediate 9	14.2	3.8	1.4	9.0	8.0	19.4	19.8	3.0	6.1	9.0	28.1	1.40	1
Intermediate 10	12.7	1.9	0.0	9.1	8.2	13.5	17.1	3.0	5.9	8.0	28.0	0.63	0
Intermediate 11	12.0	1.4	0.0	9.5	8.2	13.2	17.1	3.0	6.0	8.1	29.9	0.63	0
Intermediate 12	12.0	1.4	0.0	10.2	8.2	13.2	15.7	2.9	6.3	9.8	30.6	0.63	0
Intermediate 13	14.4	1.4	0.0	10.2	8.9	14.1	15.7	2.9	7.1	11.3	33.3	0.33	0
Intermediate 14	14.9	1.2	0.0	10.2	9.0	14.1	15.7	3.0	7.3	11.3	33.3	0.33	0
Intermediate 15	15.7	1.2	0.0	10.2	9.0	14.1	15.8	3.0	7.3	12.8	32.9	0.10	0

* See Figure 10. Intermediates 1–5 correspond to those of the *brookii angulatus* phyletic line, beginning with the one located at the primary cladistic event; Intermediates 6–9 correspond to those of the *brookii haitianus* phyletic line, beginning with the one located at the cladistic event leading to Hispaniola; Intermediates 10–15 correspond to those of the *mabouia* phyletic line, beginning with the one located at the cladistic event leading to Malagasy Republic

TABLE 4

RELATIVE WEIGHT OF CHARACTERS

Character	LS	CT	AS	SL	IL	RT	TR
Weight	.500	.739	.420	.509	.510	.730	.548
Rank	10	2	12	9	8	3	7

Character	TW	SW	SD	PP	IP	TD
Weight	.577	.588	.717	.386	.447	1.000
Rank	6	5	4	13	11	1

TABLE 5

Matrix of sums of patristic differences

	South Africa, Rhodesia	Malawi, Mozambique	Malagasy Republic	Kenya, Tanzania	The Congo	Sierra Leone	Lesser Antilles, South America	St. Lucia, Trinidad, South America	Colombia	Puerto Rico	Hispaniola	Cuba	Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo	The Congo	Kenya	Tanzania
South Africa, Rhodesia	x	.7514	.6530	1.6525	2.0614	1.8098	2.4337	4.4369	2.8526	3.2297	2.0498	2.7420	1.9232	3.4256	3.2076	3.9059
Malawi, Mozambique		x	1.1356	1.0573	1.4662	1.2146	1.8385	4.9195	3.3352	3.7123	2.5324	3.2246	2.4058	3.9082	3.6902	4.3885
Malagasy Republic			x	2.0367	2.4456	2.1940	2.8179	4.2849	2.7006	3.0777	1.8978	2.5900	1.7712	3.2736	3.0556	3.7539
Kenya, Tanzania				x	.6789	.4273	1.0512	5.8206	4.2363	4.6134	3.4335	4.1257	3.3069	4.8093	4.5913	5.2896
The Congo					x	.5388	.6163	6.2295	4.6452	5.0223	3.8424	4.5346	3.7158	5.2182	5.0002	5.6985
Sierra Leone						x	.9111	5.9779	4.3936	4.7707	3.5908	4.2830	3.4642	4.9666	4.7486	5.4469
Lesser Antilles, South America							x	6.6018	5.0175	5.3946	4.2147	4.9069	4.0881	5.5905	5.3725	6.0708
St. Lucia, Trinidad, South America								x	2.7975	2.0504	2.4119	2.1247	3.3561	4.1639	3.9459	4.6442
Colombia									x	1.5903	.8276	1.1026	1.7718	2.5796	2.3616	3.0599
Puerto Rico										x	1.2047	.9175	2.1489	2.9567	2.7387	3.4370
Hispaniola											x	.7170	.9690	1.7768	1.5588	2.2571
Cuba												x	1.6612	2.4690	2.2510	2.9493
Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo													x	2.3448	2.1268	2.8251
The Congo														x	1.5912	2.2895
Kenya															x	.8911
Tanzania																x

TABLE 6

Rank order of evolutionary relationship[1]

	South Africa, Rhodesia	Malawi, Mozambique	Malagasy Republic	Kenya, Tanzania	The Congo	Sierra Leone	Lesser Antilles, South America	St. Lucia, Trinidad, South America	Colombia	Puerto Rico	Hispaniola	Cuba	Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo	The Congo	Kenya	Tanzania
South Africa, Rhodesia	0	2	1	3	7	4	8	15	10	12	6	9	5	13	11	14
Malawi, Mozambique	1	0	3	2	5	4	6	15	10	12	8	9	7	13	11	14
Malagasy Republic	1	2	0	5	7	6	10	15	9	12	4	8	3	13	11	14
Kenya, Tanzania	5	4	6	0	2	1	3	15	10	12	8	9	7	13	11	14
The Congo	5	4	6	3	0	1	2	15	10	12	8	9	7	13	11	14
Sierra Leone	5	4	6	1	2	0	3	15	10	12	8	9	7	13	11	14
Lesser Antilles, South America	5	4	6	3	1	2	0	15	10	12	8	9	7	13	11	14
St. Lucia, Trinidade, South America	9	11	8	12	14	13	15	0	4	1	3	2	5	7	6	10
Colombia	9	11	7	12	14	13	15	8	0	3	1	2	4	6	5	10
Puerto Rico	9	11	8	12	14	13	15	4	3	0	2	1	5	7	6	10
Hispaniola	8	11	7	12	14	13	15	10	2	4	0	1	3	6	5	9
Cuba	9	11	8	12	14	13	15	5	3	2	1	0	4	7	6	10
Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo	5	9	3	11	14	13	15	12	4	6	1	2	0	8	7	10
The Congo	9	10	8	12	14	13	15	11	6	7	2	5	4	0	1	3
Kenya	9	10	8	12	14	13	15	11	6	7	2	5	4	3	0	1
Tanzania	9	10	8	12	14	13	15	11	6	7	2	5	4	3	1	0

[1] The relative degree of relationship of an OTU is found by reading across the appropriate row of the matrix, not down the column.

TABLE 7

COMPARISON OF SUMS OF PATRISTIC DIFFERENCES OF MOST CLOSELY RELATED SAMPLES AND GENERALLY RECOGNIZED TAXA

Divergence	Sum of Patristic Differences
A. Of Most Closely Related Samples	
South Africa, Rhodesia—Malagasy Republic	.6530
Malawi, Mozambique—South Africa, Rhodesia	.7514
Kenya, Tanzania—Sierra Leone, Liberia	.4273
The Congo—Sierra Leone, Liberia	.5388
Lesser Antilles, South America—The Congo	.6163
St. Lucia, Trinidad, South America—Puerto Rico	2.0504
Colombia—Hispaniola	.8276
Puerto Rico—Cuba	.9175
Hispaniola—Cuba	.7170
Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo—Hispaniola	.9690
The Congo—Kenya	2.1268
Kenya—Tanzania	2.2895
B. Relative to Previous Taxonomic Status	
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)—*mabouia* (Malagasy Republic)	1.7712
brookii haitianus (Hispaniola)—*brookii angulatus* (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	.9690
leightoni (Colombia)—*brookii haitianus* (Hispaniola)	.8276
palaichthus sp. nov. (St. Lucia, Trinidad, South America)—*brookii haitianus* (Puerto Rico)	2.0504

TABLE 8

COMPARISON OF SIX SAMPLES OF NEW WORLD *mabouia* IN TERMS OF THE MEANS OF TEN CHARACTERS[1]

Populations	I	II	III	IV	V	VI
I		1	0	2	1	3
II	9		2	3	1	4
III	10	8		3	2	4
IV	8	7	7		4	5
V	9	9	8	6		3
VI	7	6	6	5	7	

[1] See Table 23 for raw data; upper half of matrix represents number of characters with differences in means at $P \leq .05$ level of significance, the lower half of the matrix represents number of characters which do not exhibit significant differences in their means at $P \leq .05$. Two of the ten characters (LS, SD) exhibited no significant mean differences.

TABLE 9
NUMBER OF LOREAL SCALES (LS)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	$SE_{\bar{x}}$
mabouia (South Africa, Rhodesia)	12	10–14	11.4	1.17	.337
mabouia (Malawi, Mozambique)	23	10–15	12.0	1.28	.267
mabouia (Malagasy Republic)	26	11–16	13.5	1.10	.215
mabouia (Kenya, Tanzania)	55	12–18	14.4	1.39	.188
mabouia (The Congo)	26	14–17	15.7	1.02	.200
mabouia (Sierra Leone, Liberia)	10	13–16	14.9	1.00	.316
mabouia (Ascension Island)	3	15	15.0	—	—
mabouia (Lesser Antilles, South America)	170	14–22	17.8	1.41	.108
palaichthus (St. Lucia, Trinidad, South America)	43	12–19	14.7	1.59	.242
brookii leightoni (Colombia)	26	12–17	13.7	1.13	.222
brookii haitianus (Puerto Rico)	25	12–18	14.2	1.44	.288
brookii haitianus (Hispaniola)	24	10–16	12.8	1.74	.355
brookii haitianus (Cuba)	24	13–17	14.7	1.09	.233
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	59	10–14	11.9	1.08	.139
brookii angulatus (The Congo)	25	9–13	11.3	1.24	.248
brookii angulatus (Kenya)	26	9–13	11.8	1.15	.225
brookii angulatus (Tanzania)	26	10–13	12.2	.92	.180

TABLE 10
NUMBER OF CHEEK TUBERCLES (CT)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	$SE_{\bar{x}}$
mabouia (South Africa, Rhodesia)	12	0–4	1.1	1.18	.342
mabouia (Malawi, Mozambique)	23	0–3	1.4	1.03	.214
mabouia (Malagasy Republic)	26	0–5	1.9	1.08	.211
mabouia (Kenya, Tanzania)	55	0–4	1.4	1.04	.141
mabouia (The Congo)	26	0–3	1.2	.83	.162
mabouia (Sierra Leone, Liberia)	10	0–1	.3	.48	.152
mabouia (Ascension Island)	3	0–2	1.0	—	—
mabouia (Lesser Antilles, South America)	169	0–4	.4	2.13	.164
palaichthus (St. Lucia, Trinidad, South America)	40	2–11	5.0	2.20	.348
brookii leightoni (Colombia)	27	3–10	5.2	1.63	.313
brookii haitianus (Puerto Rico)	25	1–6	3.4	1.26	.252
brookii haitianus (Hispaniola)	24	1–7	3.6	1.41	.288
brookii haitianus (Cuba)	24	2–6	3.8	.99	.202
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	59	1–6	3.2	1.22	.158
brookii angulatus (The Congo)	25	3–10	6.1	1.78	.357
brookii angulatus (Kenya)	26	4–18	8.4	3.42	.670
brookii angulatus (Tanzania)	26	4–30	12.5	2.27	.445

TABLE 11

NUMBER OF AURICULAR SCALES (AS)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	SE$_{\bar{x}}$
mabouia (South Africa, Rhodesia)	12	0	0	—	—
mabouia (Malawi, Mozambique)	23	0	0	—	—
mabouia (Malagasy Republic)	26	0	0	—	—
mabouia (Kenya, Tanzania)	55	0	0	—	—
mabouia (The Congo)	26	0[1]	0	—	—
mabouia (Sierra Leone, Liberia)	10	0	0	—	—
mabouia (Ascension Island)	3	0	0	—	—
mabouia (Lesser Antilles, South America)	169	0[2]	0	—	—
palaichthus (St. Lucia, Trinidad, South America)	43	0	0	—	—
brookii leightoni (Colombia)	25	0–4	.8	1.18	.235
brookii haitianus (Puerto Rico)	25	0–3	2.5	.94	.188
brookii haitianus (Hispaniola)	24	0–3	1.5	.89	.182
brookii haitianus (Cuba)	24	0–3	1.4	.71	.145
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	59	0–9	4.2	1.75	.228
brookii angulatus (The Congo)	25	2–6	3.8	1.20	.240
brookii angulatus (Kenya)	26	0–6	3.6	1.61	.316
brookii angulatus (Tanzania)	25	1–6	3.3	1.21	.242

[1]—one specimen with 2; [2]—4 specimens with 1.

TABLE 12
NUMBER OF SUPRALABIALS (SL)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	$SE_{\bar{x}}$
mabouia (South Africa, Rhodesia)	12	8–12	9.5	1.00	.289
mabouia (Malawi, Mozambique)	23	9–12	10.2	.88	.183
mabouia (Malagasy Republic)	26	8–10	9.1	.72	.142
mabouia (Kenya, Tanzania)	55	9–13	10.5	.92	.124
mabouia (The Congo)	26	9–13	10.0	.80	.157
mabouia (Sierra Leone, Liberia)	23	9–12	10.2	.88	.183
mabouia (Ascension Island)	3	10–11	10.3	—	—
mabouia (Lesser Antilles, South America)	170	8–13	10.7	.84	.065
palaichthus (St. Lucia, Trinidad, South America)	43	8–12	9.8	.82	.125
brookii leightoni (Colombia)	26	8–10	8.6	.83	.162
brookii haitianus (Puerto Rico)	25	8–10	8.8	.58	.116
brookii haitianus (Hispaniola)	25	7–10	9.0	.79	.158
brookii haitianus (Cuba)	24	8–11	9.2	.93	.190
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	59	8–11	8.8	.77	.100
brookii angulatus (The Congo)	25	7–9	7.8	.69	.139
brookii angulatus (Kenya)	26	7–10	8.3	.66	.130
brookii angulatus (Tanzania)	26	7–9	7.8	.63	.124

TABLE 13
NUMBER OF INFRALABIALS (IL)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	SE$_{\bar{x}}$
mabouia (South Africa, Rhodesia)	12	7–9	8.2	.86	.247
mabouia (Malawi, Mozambique)	23	7–9	8.1	.57	.118
mabouia (Malagasy Republic)	26	7–9	8.2	.60	.118
mabouia (Kenya, Tanzania)	55	8–11	8.9	.83	.112
mabouia (The Congo)	26	8–10	9.0	.60	.118
mabouia (Sierra Leone, Liberia)	10	8–10	9.1	.58	.182
mabouia (Ascension Island)	3	8–9	8.3	—	—
mabouia (Lesser Antilles, South America)	170	7–10	8.9	.67	.051
palaichthus (St. Lucia, Trinidad, South America)	43	7–10	8.7	.58	.088
brookii leightoni (Colombia)	26	7–9	8.3	.60	.118
brookii haitianus (Puerto Rico)	25	7–9	8.0	.74	.148
brookii haitianus (Hispaniola)	25	6–9	7.7	.61	.122
brookii haitianus (Cuba)	24	7–10	8.0	.66	.135
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	59	6–9	7.4	.72	.094
brookii angulatus (The Congo)	25	6–8	6.6	.71	.141
brookii angulatus (Kenya)	26	6–9	7.4	.75	.147
brookii angulatus (Tanzania)	26	6–8	6.8	.72	.141

TABLE 14
NUMBER OF ROWS OF BODY TUBERCLES (RT)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	$SE_{\bar{x}}$
mabouia (South Africa, Rhodesia)	12	12–15	13.2	1.05	.303
mabouia (Malawi, Mozambique)	23	10–16	13.1	1.45	.302
mabouia (Malagasy Republic)	26	12–16	13.5	1.02	.200
mabouia (Kenya, Tanzania)	55	10–17	14.1	1.45	.195
mabouia (The Congo)	26	12–16	14.1	1.30	.254
mabouia (Sierra Leone, Liberia)	10	12–17	14.2	1.55	.490
mabouia (Ascension Island)	3	12–13	12.3	—	—
mabouia (Lesser Antilles, South America)	167	10–17	13.9	1.20	.093
palaichthus (St. Lucia, Trinidad, South America)	40	17–25	21.5	2.24	.354
brookii leightoni (Colombia)	27	14–23	18.3	2.15	.413
brookii haitianus (Puerto Rico)	25	15–22	19.4	2.02	.404
brookii haitianus (Hispaniola)	24	16–22	18.2	1.40	.286
brookii haitianus (Cuba)	24	16–21	19.2	1.47	.300
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	59	13–20	16.2	1.31	.170
brookii angulatus (The Congo)	25	15–18	16.0	.87	.173
brookii angulatus (Kenya)	26	15–21	17.7	1.81	.355
brookii angulatus (Tanzania)	26	15–20	17.9	1.49	.291

TABLE 15

NUMBER OF TUBERCLES IN PARAVERTEBRAL ROW (TR)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	$SE_{\bar{x}}$
mabouia (South Africa, Rhodesia)	12	14–22	17.2	2.05	.592
mabouia (Malawi, Mozambique)	22	13–18	15.2	1.62	.511
mabouia (Malagasy Republic)	26	14–18	15.7	1.10	.215
mabouia (Kenya, Tanzania)	55	13–21	15.7	1.84	.247
mabouia (The Congo)	26	14–22	16.5	1.70	.333
mabouia (Sierra Leone, Liberia)	10	13–18	15.2	1.62	.511
mabouia (Ascension Island)	3	15–17	15.7	—	—
mabouia (Lesser Antilles, South America)	165	13–20	15.8	1.50	.117
palaichthus (St. Lucia, Trinidad, South America)	42	17–28	22.0	2.29	.353
brookii leightoni (Colombia)	27	16–22	18.9	1.68	.332
brookii haitianus (Puerto Rico)	25	14–23	19.8	2.04	.408
brookii haitianus (Hispaniola)	24	14–21	18.0	1.71	.349
brookii haitianus (Cuba)	24	16–23	18.1	1.59	.325
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	59	14–24	18.4	2.11	.273
brookii angulatus (The Congo)	25	15–21	17.5	1.73	.347
brookii angulatus (Kenya)	26	14–23	18.6	2.21	.433
brookii angulatus (Tanzania)	26	16–25	19.1	2.00	.392

TABLE 16

NUMBER OF TUBERCLES IN CAUDAL WHORL (TW)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	SE$_{\bar{x}}$
mabouia (South Africa, Rhodesia)	18	3	3.0	—	—
mabouia (Malawi, Mozambique)	34	2–3	2.9	.17	.030
mabouia (Malagasy Republic)	36	3	3.0	—	—
mabouia (Kenya, Tanzania)	70	2–3	2.9	.25	.029
mabouia (The Congo)	42	3	3.0	—	—
mabouia (Sierra Leone, Liberia)	12	3	3.0	—	—
mabouia (Ascension Island)	6	3	3.0	—	—
mabouia (Lesser Antilles, South America)	230	3[1]	3.0	—	—
palaichthus (St. Lucia, Trinidad, South America)	54	2–4	3.0	.28	.039
brookii leightoni (Colombia)	30	2–4	3.0	.62	.113
brookii haitianus (Puerto Rico)	38	3–5	3.5	.59	.096
brookii haitianus (Hispaniola)	66	1–4	2.8	.78	.095
brookii haitianus (Cuba)	36	2–4	2.5	.61	.102
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	68	2–4	3.0	.32	.038
brookii angulatus (The Congo)	44	2–4	3.1	1.18	.178
brookii angulatus (Kenya)	42	3–5	3.8	1.56	.241
brookii angulatus (Tanzania)	46	3–5	4.0	.40	.058

[1] —one specimen with 2 on one side.

TABLE 17
NUMBER OF SCALES BETWEEN CAUDAL WHORLS (SW)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	$SE_{\bar{x}}$
mabouia (South Africa, Rhodesia)	9	5–7	6.0	.35	.118
mabouia (Malawi, Mozambique)	15	5–8	6.3	.80	.206
mabouia (Malagasy Republic)	15	5–7	5.9	.89	.230
mabouia (Kenya, Tanzania)	34	5–9	7.1	1.00	.171
mabouia (The Congo)	21	6–9	7.3	.63	.138
mabouia (Sierra Leone, Liberia)	5	7–8	7.4	.50	.223
mabouia (Ascension Island)	3	7	7.0	—	—
mabouia (Lesser Antilles, South America)	110	4–10	7.5	.92	.088
palaichthus (St. Lucia, Trinidad, South America)	25	3–6	4.9	.88	.176
brookii leightoni (Colombia)	13	5–7	5.8	.58	.159
brookii haitianus (Puerto Rico)	19	4–8	6.3	.99	.227
brookii haitianus (Hispaniola)	33	4–7	5.6	1.06	.184
brookii haitianus (Cuba)	17	5–7	6.1	.56	.136
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	31	4–7	5.7	.66	.118
brookii angulatus (The Congo)	20	4–5	4.5	.51	.114
brookii angulatus (Kenya)	20	4–7	5.2	.69	.153
brookii angulatus (Tanzania)	22	4–6	5.1	.72	.154

TABLE 18
NUMBER OF SUBDIGITAL LAMELLAE (SD)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	$SE_{\bar{x}}$
mabouia (South Africa, Rhodesia)	12	7–9	8.1	.52	.150
mabouia (Malawi, Mozambique)	23	8–12	9.8	1.19	.248
mabouia (Malagasy Republic)	26	6–8	7.3	.57	.111
mabouia (Kenya, Tanzania)	55	9–15	11.9	.26	.036
mabouia (The Congo)	26	12–15	12.8	.87	.171
mabouia (Sierra Leone, Liberia)	10	10–12	11.3	.66	.219
mabouia (Ascension Island)	3	11–13	12.3	—	—
mabouia (Lesser Antilles, South America)	169	8–17	13.9	.94	.072
palaichthus (St. Lucia, Trinidad, South America)	43	9–11	9.5	.63	.096
brookii leightoni (Colombia)	27	7–10	8.6	.71	.136
brookii haitianus (Puerto Rico)	25	8–10	9.0	.71	.142
brookii haitianus (Hispaniola)	24	7–10	8.6	.88	.180
brookii haitianus (Cuba)	24	8–11	9.1	.68	.139
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	59	8–11	8.6	.68	.088
brookii angulatus (The Congo)	25	7–10	8.6	.65	.130
brookii angulatus (Kenya)	26	7–10	8.8	.66	.130
brookii angulatus (Tanzania)	26	8–11	9.0	.80	.157

TABLE 19

NUMBER OF PREANAL PORES (PP)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	SE$_{\bar{x}}$
mabouia (South Africa, Rhodesia)	8	28–31	29.9	.84	.298
mabouia (Malawi, Mozambique)	12	28–34	30.6	2.11	.608
mabouia (Malagasy Republic)	16	26–30	28.0	1.51	.377
mabouia (Kenya, Tanzania)	35	25–40	33.5	2.96	.499
mabouia (The Congo)	19	28–36	32.3	2.22	.509
mabouia (Sierra Leone, Liberia)	3	32–36	33.3	—	—
mabouia (Ascension Island)	1	32	32.0	—	—
mabouia (Lesser Antilles, South America)	90	27–38	32.9	2.22	.234
palaichthus (St. Lucia, Trinidad, South America)	24	32–43	37.1	3.09	.631
brookii leightoni (Colombia)	8	21–28	24.3	2.07	.732
brookii haitianus (Puerto Rico)	27	24–32	27.4	2.17	.417
brookii haitianus (Hispaniola)	90	23–32	28.1	.84	.089
brookii haitianus (Cuba)	12	25–31	28.6	2.07	.598
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	34	18–31	26.6	1.23	.210
brookii angulatus (The Congo)	20	21–89	24.5	2.44	.493
brookii angulatus (Kenya)	14	28–42	35.0	4.37	1.171
brookii angulatus (Tanzania)	12	24–38	31.8	3.84	1.112

TABLE 20
NUMBER OF INTERPREANAL PORE SCALES (IP)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	SE$_{\bar{x}}$
mabouia (South Africa, Rhodesia)	8	0–1	.13	.35	.122
mabouia (Malawi, Mozambique)	12	0–1	.70	.52	.150
mabouia (Malagasy Republic)	16	0–1	.63	1.58	.400
mabouia (Kenya, Tanzania)	35	0–1	.24	.49	.083
mabouia (The Congo)	19	0[1]	—	—	—
mabouia (Sierra Leone, Liberia)	3	0–1	.33	—	—
mabouia (Ascension Island)	1	0	—	—	—
mabouia (Lesser Antilles, South America)	90	0–1	.10	.03	.003
palaichthus (St. Lucia, Trinidad, South America)	24	0	—	—	—
brookii leightoni (Colombia)	8	2–4	2.88	.84	.298
brookii haitianus (Puerto Rico)	28	1–3	1.36	.56	.106
brookii haitianus (Hispaniola)	92	0–4	2.37	.98	.102
brookii haitianus (Cuba)	12	1–3	1.83	.84	.241
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	32	0–3	1.10	.90	.159
brookii angulatus (The Congo)	20	3–5	3.55	.61	.136
brookii angulatus (Kenya)	14	1–4	2.29	1.07	.288
brookii angulatus (Tanzania)	12	1–5	3.08	1.71	.496

[1]—one specimen with 1.

TABLE 21

SNOUT TO EYE LENGTH (SEL)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	$SE_{\bar{x}}$
mabouia (South Africa, Rhodesia)	12	10.11–11.14	10.66	.30	.087
mabouia (Malawi, Mozambique)	23	10.24–11.87	10.75	1.15	.239
mabouia (Malagasy Republic)	26	10.48–11.87	11.21	1.34	.263
mabouia (Kenya, Tanzania)	55	9.86–11.87	11.26	1.45	.195
mabouia (The Congo)	26	10.32–13.24	11.03	1.13	.222
mabouia (Sierra Leone, Liberia)	10	10.56–11.55	11.05	.91	.288
mabouia (Ascension Island)	3	10.55–11.58	10.94	—	—
mabouia (Lesser Antilles, South America)	165	9.90–12.73	10.98	.45	.035
palaichthus (St. Lucia, Trinidad, South America)	39	10.37–12.46	11.34	1.47	.236
brookii leightoni (Colombia)	27	10.17–12.33	11.89	1.33	.256
brookii haitianus (Puerto Rico)	25	9.84–11.74	10.55	1.47	.294
brookii haitianus (Hispaniola)	24	9.66–11.38	10.67	1.46	.298
brookii haitianus (Cuba)	24	9.98–11.75	10.72	1.19	.243
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	59	9.93–11.81	10.67	1.24	.161
brookii angulatus (The Congo)	25	9.94–11.12	10.47	1.01	.201
brookii angulatus (Kenya)	25	9.68–11.53	10.54	1.75	.348
brookii angulatus (Tanzania)	26	10.12–11.23	10.74	.74	.144

TABLE 22
EYE TO EAR LENGTH (EEL)

Taxon (Population sampled)	n	ORV	$\bar{x}$	s	SE$_{\bar{x}}$
mabouia (South Africa, Rhodesia)	12	8.37–9.99	9.32	1.23	.355
mabouia (Malawi, Mozambique)	23	8.54–10.18	9.24	1.52	.316
mabouia (Malagasy Republic)	26	7.62–9.88	9.03	1.90	.371
mabouia (Kenya, Tanzania)	55	7.96–10.35	9.24	1.75	.236
mabouia (The Congo)	26	8.40–9.77	9.24	1.25	.246
mabouia (Sierra Leone, Liberia)	10	8.79–10.24	9.30	1.32	.416
mabouia (Ascension Island)	3	8.30–8.63	8.46	—	—
mabouia (Lesser Antilles, South America)	166	7.89–10.48	8.81	.51	.040
palaichthus (St. Lucia, Trinidad, South America)	39	8.55–9.96	9.22	.97	.155
brookii leightoni (Colombia)	25	7.67–9.71	8.81	1.69	.339
brookii haitianus (Puerto Rico)	25	7.45–9.67	8.77	1.92	.384
brookii haitianus (Hispaniola)	24	8.30–10.42	9.16	1.90	.388
brookii haitianus (Cuba)	24	8.34–9.42	8.79	.93	.189
brookii angulatus (Dahomey, Gambia, Ghana, Nigeria, Sierra Leone, Togo)	59	8.08–10.34	9.10	1.73	.225
brookii angulatus (The Congo)	25	8.29–10.11	9.08	1.41	.282
brookii angulatus (Kenya)	25	8.55–10.66	9.37	1.74	.348
brookii angulatus (Tanzania)	26	8.77–10.39	9.50	1.64	.322

TABLE 23

Populations of *mabouia*[1]	n	ORV	$\bar{x}$	s	$SE_{\bar{x}}$
		Number of loreal scales (LS)			
I	26	16–21	17.7	1.22	.239
II	17	16–22	18.5	1.62	.395
III	26	15–21	17.3	1.65	.324
IV	33	14–20	18.1	1.27	.223
V	21	16–19	17.7	1.12	.244
VI	24	15–21	17.9	1.37	.280
		Number of cheek tubercles (CT)			
I	26	0–4	1.20	1.18	.231
II	17	0–1	.06	.08	.020
III	26	0–3	.65	.85	.167
IV	33	0–2	.36	.55	.097
V	20	0–2	.10	.14	.031
VI	24	0–1	.08	.09	.018
		Number of supralabials (SL)			
I	26	9–12	10.8	.80	.157
II	17	8–12	10.2	.91	.222
III	26	10–12	10.4	.63	.124
IV	33	9–12	10.3	.71	.125
V	21	9–12	10.9	.59	.128
VI	24	10–13	11.5	.84	.171
		Number of infralabials (IL)			
I	26	8–10	8.9	.60	.118
II	17	8–10	9.1	.71	.173
III	26	7–10	8.8	.66	.129
IV	33	8–10	8.6	.71	.135
V	21	8–10	8.8	.67	.146
VI	24	8–10	9.2	.55	.112
		Number of rows of body tubercles (RT)			
I	26	12–17	13.9	1.13	.222
II	17	13–17	14.8	1.24	.303
III	24	13–16	14.4	.92	.180
IV	33	12–15	13.8	.81	.142
V	21	13–16	14.1	.89	.194
VI	23	10–16	12.9	.77	.160
		Number of tubercles in paravertebral row (TR)			
I	26	14–20	15.8	1.58	.310
II	17	14–19	16.7	1.41	.344
III	24	13–20	16.2	1.71	.335
IV	33	13–18	15.6	1.12	.197
V	21	14–19	16.1	1.67	.363
VI	23	13–19	15.3	1.32	.275

TABLE 23 (continued)

Populations of *mabouia*[1]	n	ORV	$\bar{x}$	s	SE$_{\bar{x}}$
Number of scales between caudal whorls (SW)					
I	11	7–9	7.6	.80	.242
II	10	6–9	7.4	.82	.256
III	18	6–10	7.9	.91	.217
IV	26	4–9	6.9	1.06	.208
V	14	6–9	8.0	.79	.214
VI	15	7–9	8.0	.54	.139
Number of subdigital lamellae (SD)					
I	26	12–16	14.0	.96	.188
II	17	11–15	13.7	1.06	.259
III	26	13–15	13.9	.60	.118
IV	32	13–15	13.7	.50	.088
V	21	13–15	14.1	.71	.154
VI	24	12–15	13.8	.78	.159
Number of preanal pores (PP)					
I	14	30–36	32.8	1.88	.508
II	7	30–36	32.9	2.48	.919
III	12	29–35	32.0	1.65	.471
IV	17	30–36	33.0	1.62	.395
V	13	27–35	31.5	2.27	.631
VI	15	31–38	34.7	1.91	.490
Number of interpreanal pore scales (IP)					
I	14	0–1	.14	.12	.032
II	7	0–1	.29	.15	.056
III	12	0–1	.08	.09	.026
IV	17	0	—	—	—
V	13	0–1	.15	.12	.033
VI	15	0–1	.07	.08	.021

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[1] The populations referred to above are as follows: I—Brazil; II—Grenada, The Grenadines, St. Vincent, St. Lucia; III—Martinique, Dominica, Guadeloupe; IV—Antigua, St. Christopher, St. Eustatius, Saba; V—Tortola, St. John, St. Thomas; VI—Vieques.

APPENDIX

SPECIMENS EXAMINED

Hemidactylus mabouia (total 517)

ANGUILLA—no loc (MCZ 59183*). **ANTIGUA**—Dutchman Bay (ASFS 19136–7*, 19146–7*, 19213–4*, 19215–7*, X470*, X7216–9*, X7369, X7576, X7710, X8710–11); Great Bird Is (MCZ 75828); Gunthorpes Dist (UMMZ 76097a–g); Mill Reef (MCZ 75378); St Johns (UF 11373, 11383; USNM 35751). **BARBADOS**—Bridgetown (AMNH 6574); St Michael (MCZ 75372–3*; UF 15088–9); St Philip (MCZ 75374–7*; UF 15090–92); no loc (FMNH 21096*; USNM 31001–2). **BRASIL**—Anapolis (UMMZ 103063); Atafona (MCZ 79015–22*); Baixa Verde (FMNH 64259–62); Bahia City (USNM 119119); Belem (MCZ

1012*, 3305*, 74146–8*); Belo Horizonte (UMMZ 103061); Ceara Mirim (FMNH 64264); base Corcovado, Mt Rio de Janeiro (USNM 52603); Extremoz (FMNH 64265); Fazenda de Sao Sabastio, Vazonas (MCZ 3440a–b*); Ilha Madre de Deus (KU 29429–37); Ipanema, Varnhagen (FMNH 69959–60); Manaos (AMNH 64263;FMNH 64263; MCZ 19539*; UMMZ 56854); Manguinhos (USNM 98573); Maues (AMNH 89781); Obidos, Amazon R (AMNH 77065–71); Porte Alegre (FMNH 80112–3); Recife (USNM 58947–8); Recreio dos Bandeirantes, Rio de Janeiro (USNM 98588–92); Rio de Janeiro (AMNH 17027; ANSP 7439, 7440; MCZ 1365*, 3312*, 3320*, 3443a–e*; UMMZ 103062; USNM 5679, 52601, 98587); Rondonia, Rio Momore (MCZ 74156); Sao Paulo (FMNH 83586–7); Santa Teresa (MCZ 79023); Santos (USNM 71076); Serra do Navio (FMNH 83586–7); St Clara, Rio Mucury (MCZ 3717*); Teresopolis, nr Rio Guapi (USNM 98602); Toco de Onca (USNM 52612); no loc (MCZ 2170a*, 3362*). **COLOMBIA**—Leticia (AMNH 91725–6, 95072–3; LACM a uncat; UF 8566). **CUBA**—Guantanamo (MCZ 68728–9, 68926–7). **DOMINICA**—Canefield Estate, nr Roseau (UMMZ 83326a–b, 122428); Roseau (MCZ 60813–4*); no loc (FMNH 3896–7*; UMMZ 83327). **ECUADOR**—Rio Napo, 850 ft (AMNH 57154). **GRENADA**—Point Saline (ASFS X7136–7*); Salt Pond (ASFS 11108*); St. Georges (ASFS 11053*, 17619–20*, 17628–30*, 17702–6*). **GRENADINES**—Mayero Is (USNM 103979–80); Petit Martinique Is (ASFS 17851–2*; MCZ 6069a–d); Tyrrell Bay, Carriacou Is (ASFS 17780*). **GUADELOUPE**—2 km SE Vieux Habitants (Basse Terre) (ASFS X5484–5*); Gosier, Grande Terre (ASFS X4992, X5045*); 1 km W Pointe des Chateaux, Grande Terre (ASFS X5023); 4 km W Pointe des Chateaux, Grande Terre (ASFS 5028–34*, X5898–900*, X5949, X6138–9, X6239–40, X6325–6, X6398–400, X6643–4); Iles de la Petite Terre, Terre de Bas (ASFS X6155*). **GUYANA**—Georgetown (MCZ 81215*); Malai (UMMZ 77817). **HAITI**—Port-au-Prince (MCZ 1327). **LES ILES DES SAINTES**—Fort Josephine, Ilet-a-Cabrit (ASFS X5791*); Pointe-a-Vache, Terre de Bas (ASFS X5789*); Terre de Haut (ASFS X5740–41*). **MARTINIQUE**—1 km NW Case-Pilote (ASFS 18516); Fond Boucher (AMNH 85376*); Fort-de-France (MCZ 6070a–d*); 3 km W Ste Luce (ASFS X6749, X7000–01); no loc (ANSP 7437). **PERU**—Cedro Is, nr Requena, 380 ft (AMNH 57151); Iquitos, 100 m (AMNH 56377, 57140, 57141, 57143–4, 57146, 57147, 57149, 57150, 57152, 57155, 57157, 57158; FMNH 45450); Nazareth (FMNH 5672); ca 5 mi W Pucallpa (LSUMZ 9602); Requena, 380 ft (AMNH 56414, 57139); Rio Itaya, nr Iquitos, 360 ft (AMNH 57138, 57142, 57145, 57148, 57153, 57156); Rio Maniti (FMNH 109822); Roaboya, 525 ft (AMNH 56220). **PUERTO RICO**—Desembarca Uvera, Mona Is (UPRRP 3001); "Hassul" (MCZ 34704). **SABA**—The Bottom (ASFS 19992–5*); no loc (USNM 104204). **ST CROIX**—Anguilla (ASFS V3629–30*); Cotton Valley (AMNH 90486–7*); Christiansted (ASFS V3352*, V3496–7*, V3566*, V3631–2*; MCZ 42367*; UMMZ 80780a–f); west cape, Prune Bay (ASFS V3495*); no loc (UMMZ 80579). **ST EUSTATIUS**—Oranjestad (ASFS 19673–85*, X370; MCZ 75379*, 75829*; UF 15169); no loc (MCZ 39739–40a–h, 54709). **ST JOHN**—Caneel Bay (ASFS V7563*); Cruz Bay (AMNH 88674–8*, 93090–91); Lameshur (KU 46678–83); .5 mi WSW Lameshur (KU 46684–6); Lovango Cay (KU 45632); no loc (KU 45673–87; MCZ 34740, 34742–3, 34747–50a–c*; UMMZ 73568a–i). **ST CHRISTOPHER**—Basseterre (UF 11392a–i, 11393); 1.5 mi N Basseterre (UF 11394a–f, 11397); nr Basseterre (UMMZ 83315); Brimstone Hill Fort (UF 11396); no loc (MCZ 10749*). **ST LUCIA**—Castries (ASFS 18294–5*, 18299, 18899–900, 19172–3; MCZ 6067*, 33379*); Reduit (ASFS X6642*; UMMZ 127382, 127944). **ST MARTIN**—Philipsburg (MCZ 74344*; UF 11401a); no loc (ANSP 7341–2, 7398–9; FMNH 57452–3*). **ST THOMAS**—Hassel (UMMZ 73569); Mosquito Bay (USNM 115856–7); Water Bay (ASFS V7289, V8035*); no loc (MCZ 34734–9*; UMMZ 73566–7a–d, 80574a–b; USNM 52538, 52540–41, 98945). **ST VINCENT**—8.5 mi SE Kingstown (ASFS 18153*). **TOBAGO**—Bacolet (AMNH 72897); Bucco Bay

(AMNH 94878); Scarborough (MCZ 55709–12). **TORTOLA**—Lloyds Pond (ASFS V7959–60*, V8071–2); 1 mi W Pasea Hall Estate (ASFS V7902–3*, V7936*); Peter Is (MCZ 34705*; UMMZ 73571, 80576a–b, 80578); W end Tortola (UMMZ 80575a); E end Tortola (UMMZ 80577a); no loc (MCZ 33380*). **TRINIDAD**—Pointe-a-Pierre (UF 16523–5, 16529); Port-of Spain (AMNH 72893, 94879); Santa Cruz Valley, 7.5 mi N San Juan (ASFS T106*). **URUGUAY**—Montevideo (UMMZ 59008). **VIEQUES**—Cayo de Tierra (ASFS V4070–71*); no loc (MCZ 34706–33a–g*; UMMZ 73570a–n, 73572a–i; USNM 84705).
Additional Records.—Bequia and Montserrat Ids. (Garth Underwood, pers. comm.)

Hemidactylus brookii haitianus (total 418+)

CUBA—Baracoa (AMNH 83587a–d*, 83588a*); 6.4 mi NE Camagüey (ASFS 9637); Casablanca, Habana (AMNH 65609); Habana (MCZ 8537, 38394*; UMMZ 78490a–f; USNM 75843, 100945); Jesús del Monte, Habana (AMNH 78223–5*, 81378*); Mariel (USNM 27630–31); Matanzas (USNM 136189); Santiago de Cuba (UMMZ 90722); 4 km N Santiago de Cuba (AMNH 83586*, 83825; ASFS 9809–28*); no loc (AMNH 58632; USNM 10420). **DOMINICAN REPUBLIC**—19 km NW Baní (MCZ 57756–7*); Barahona (ASFS V2920*, X9455*); 12 km NE Jarabacoa, 2000 ft (ASFS V1965*); Jovero (USNM 65783*); Pepillo Salcedo (ASFS V1138*, V1267*); Samaná (AMNH 41767*, 41769a–f*, 43853–7*, 44787–96* + numerous hatchlings, 50306–316*, 50345–8*, 50350–52*, 50374–93*, 50395–405*, 63032–3*, 63034–7*, 63038–42*, 63043–7*; MCZ 58408*); nr Samaná (AMNH 45247–50*, 45251–66*, 45268*); Samaná and Laguna (USNM 65782*); Samaná Prov (AMNH 39792*, 40820–30*, 44797–800*); San Francisco de Macorís (ASFS V2983*); San Juan (ASFS V588*); Santa Barbara de Samaná (FMNH 28232–4*; MCZ 43701–5a–b*; UMMZ 82913a*); Santiago (MCZ 57754*); Santo Domingo (ASFS X7781*, V2946*; MCZ 57755*, 57758*, 57964*, 75270–3*; UMMZ 83306a–f*; UF 6679–83*; USNM 49937*); no loc (AMNH 50336–43*). **HAITI**—Carrefour-feuille, Port-au-Prince (MCZ 59473*, 64928–9*); Miragoâne (MCZ 25423*); Mirebalais (MCZ 68481–2*); Morne de Cayette (MCZ 63607–8*, 64390*); Port-au-Prince (AMNH 22590*, 49617*; MCZ 63322–37*, 63630–49*). **PUERTO RICO**—Caguas (MCZ 34670–73; UMMZ 73559a–b); Casa Blanca (MCZ 34659; UMMZ 73565); Humacao (MCZ 34677–700a–c*, 58821*; UMMZ 73555, 73558, 73562–3a–v; USNM 84704); Isla Verde (ASFS X7370–74*, X7534–6*); La Parguera (ASFS 11964–5*); La Princesa (MCZ 34653–7*, 34701–3; UMMZ 73556, 73560); Mayagüez (UMMZ 73554a–c); Parguera Lajas (MCZ 57851); Ponce (UMMZ 73552a, 78471); Ponce Playa (MCZ 34660–69*; UMMZ 73554a–b); Punta Santiago (MCZ 58822–3); mouth Río Loco (MCZ 62180); Río Piedras (FMNH 130279–80*, 38543–9*; MCZ 34651–2*; UMMZ 67717a, 73561, 73565); San Cristóbal (MCZ 34658); San Juan (FMNH 130277–8*; MCZ 6068, 78755–6*; UMMZ 73557); Santurce (MCZ 78757–61*).

Hemidactylus brookii leightoni (total 46)

COLOMBIA—Barranquilla (MCZ 58781–2*; USNM 86482*); Barranquilla region (MCZ 78438–58*); Bocagrande (MCZ 78436–7); Cambao (MCZ 61148); Cartagena (FMNH 73801, 74915a–b); Cúcuta (MLS 34b); Cundinamarca (AMNH 91717–24*); Puerto Wilches (MCZ 39706*); Rio Frio (MCZ 29692–3*); San Felipe de Rio Negro (MCZ 53242–3*); Villavicencio (MCZ 77400).

Hemidactylus palaichthus (total 58)

BRAZIL—Boa Vista, Rio Branco (FMNH 5696); Frechal, Rio Surumu (AMNH

36306*). **GUYANA**—Bartica (MCZ 81214); Haiowa Fall (AMNH 61439–40*); Isherton (AMNH 60900–906*); Karanambo (AMNH 60925–6*, 61452–8*); Kurupukari (AMNH 60931–2*); Lethem (MCZ X23250–3*); Lower Kuyuwini River (AMNH 60919–20*); Yapukarri (AMNH 60912–3*); no loc (AMNH 61393*). **ST LUCIA**—Maria Is (ASFS X6727–8*; MCZ 59182*). **TRINIDAD**—Chacachacare Is (MCZ 66936*); Simla, nr Arima (USNM 146361*); no loc (MCZ 6066a–e*). **VENEZUELA**—Cerro de Ayacucho, Loja Venade (MCZ 83205*); Barrancas (LACM uncat); nr mouth of Cinaruco River (USNM 80627*); Ciudad Bolivar (FMNH 35115); Esmeralda (AMNH 36632*); Las Caramelitas (AMNH 99982*); Maroa (MBUCV 1279a*); Puerto Ayachucho (USNM 83952*); Puerto de Hierro (MBUCV 5036*, 5038*, 5041*; UMMZ 127942–3*); Yucua (MCZ 43855*).

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