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A Summary of Mexican Lizards of the Genus *Ameiva*

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ABSTRACT: The eleven forms of *Ameiva* known in México are summarized with a key, diagnosis, statements of ranges, lists of localities, tabulations of variation, and discussion of intergradation and characteristics. A possible phylogeny of the races of *Ameiva undulata* is suggested.

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PREFACE

ANY observer of the trend of recent literature upon Ameivas would not fail to notice that interest in the Mexican forms of *Ameiva undulata* has been rising to a crescendo whose peak surely could soon be anticipated. The present summary certainly cannot claim the finality of such heights, but does add considerable new information and a number of interpretations to the growing mass of knowledge and theory regarding Mexican Ameivas.

We have attempted here to summarize briefly the previous contributions to the knowledge of Mexican *Ameiva undulata*. We have reëvaluated and recorded some of the variations of the subspecies on the basis of more specimens than any other authors have had available. Diagnoses of all the forms of *undulata* occurring in México, at least to the extent now known, are included. It has been our aim to establish more precisely than has been done before the ranges and areas of intergradation of the several forms involved. A possible course of phylogeny of all forms of *undulata* is discussed, and we present a key which may facilitate identification of Mexican specimens.

Since there is little variation in most features of scutellation of the species we have not described them in detail for all forms. For the benefit of those interested we have included a more or less complete description of one form, *A. u. dextra*. Other forms differ little from this description save in the characters receiving special note.

For the sake of completeness we have added the only other *Ameiva* of México, *A. festiva edwardsii*.

HISTORICAL SUMMARY

When *Ameiva undulata* was first described over 100 years ago, Wiegmann (1834) recognized the existence of a related form, which he called variety A. Bocourt (1874: 254-259) also recognized a variety A (by his statement the same as Wiegmann's variety A) and a variety B. Both varieties appear to belong to the race now known as *Ameiva undulata hartwegi*.

For some time no further attempt was made to distinguish the Mexican races of Mexican *Ameiva undulata*. Neither Boulenger (Catalog of Lizards) nor Günther (Biologia Centrali-Americana) recognized any variants in 1885. And in 1915 Barbour and Noble, in their monograph of *Ameiva*, still placed all Mexican specimens in *Ameiva undulata undulata*. They recognized two Central Amer-

ican races, one of which (*u. parva*) has since been recorded in México, while the other *u. quadrilineata*, is now known by the earlier name of *u. pulchra*. In 1934 Stuart tentatively (and incorrectly) allocated the name *A. u. parva* with specimens from the Petén área of Guatemala, although in 1935 he reverted to "*Ameiva undulata*" for them. Not until 1937 was there a further advance toward the understanding of Mexican races. In that year (1) Hartweg and Oliver cited the need for revision, and stated that specimens from the Yucatán and Petén areas are different from Tehuantepec specimens; and (2) Smith recognized an "*Ameiva undulata parva*" from Yucatán and an "*Ameiva undulata undulata*" from Campeche and Veracruz. Smith's allocation of both names was incorrect; in reality neither of his races possessed a name at that time.

In 1940 Smith corrected his previous erroneous allocation of the name *parva*, proposing *A. u. hartwegi* for the race; restricted the type locality of *undulata* to Tehuantepec, and named as *A. u. stuarti* the Campeche form which he had previously called *A. u. undulata*. Thus at that time three forms of *Ameiva undulata* were known in México. Dunn, later in the same year, hesitated to segregate races of *Ameiva undulata* either in México or in Central America, holding his decisions in abeyance for the appearance of Stuart's summary. In the following year, 1941, Schmidt and Stuart commented further upon the races of *Ameiva undulata*, accepting the races proposed previously, correctly allocating the name *u. parva* for the first time with the Pacific coast race ranging from the Isthmus of Tehuantepec to Guatemala, and pointing out the proper use of the name *u. pulchra* for the race Barbour and Noble had called *u. quadrilineata*.

Stuart's review of the entire *unduluta* group of *Ameiva* appeared in 1942. In it he recognized four Mexican subspecies of *undulata*. He regarded the Pacific coast material from west of Tehuantepec as probably distinct from typical *u. undulata*, but refrained from defining it. His discussion of diagnostic characters, variation and phylogeny of the group is the only attempt that has been made along such lines.

MATERIALS

The present study is based chiefly upon the Mexican specimens of *Ameiva undulata* in the Walter Rathbone Bacon collection secured by Smith from 1938 to 1940; in the E. H. Taylor-H. M. Smith collection; in the collection of the Museum of Zoölogy of the University of Michigan (part only); and in the U. S. National Museum collection (part only). These collections are indicated by the ab-

breviations HMS (uncatalogued specimens only; all Bacon specimens are on deposit at the U. S. National Museum and those entered in the permanent collection of that institution bear regular USNM numbers), EHT-HMS, UMMZ and USNM, respectively. The entire series includes some 875 specimens, and according to our interpretations represents 10 forms.

The material examined of *A. festiva edwardsii* includes some 50 specimens in the Bacon collection. No other Mexican specimens have been recorded in other U. S. collections.

CHARACTERS

As Stuart (1942: 146) has emphasized, in diagnosing the forms of the *undulata* group "a number of characters prove useful but few are infallible and, for the most part, they can be applied only to populations rather than to individuals."

PRIMARY CHARACTERS

There are a few characters which almost all students who have dealt critically with this group have realized are of primary significance. These are: (1) size and arrangement of the median gular scales, (2) arrangement of the preanals, and (3) separation of the third supraocular from the median head scales and, by two rows of granules, from the superciliary scales.

Gulars. The median gulars may be small and irregular, merging gradually with adjacent scales (Fig. 1C), abruptly enlarged and irregular (Fig. 1D), or abruptly enlarged and arranged in a single longitudinal row (Fig. 1B). Between these extremes variations do occur, although the usual condition in any one race as a whole places that race rather definitely in one of these groups. As one example of intermediate type, we may cite the occurrence of occasional specimens of *u. gaigeae* which have the central gulars aligned in a single row much as in Fig. 1B, although they are usually irregular as shown in Fig. 1C. In *u. podarga* two or three scales may be aligned at times, instead of all being irregular.

Preanals. The preanals are paired in most races (as in Fig. 2A), but in one (*u. undulata*) there is a single median row and on each side a smaller row (Fig. 2B). A specimen in which the former condition exists is said to have two rows of preanals, while those like *u. undulata* are said to have one row. In *u. sinistra* occasionally, and in *u. dextra* usually, the posterior preanal is paired as in Fig. 2C. In these latter two races the preanals are otherwise arranged in a single row.

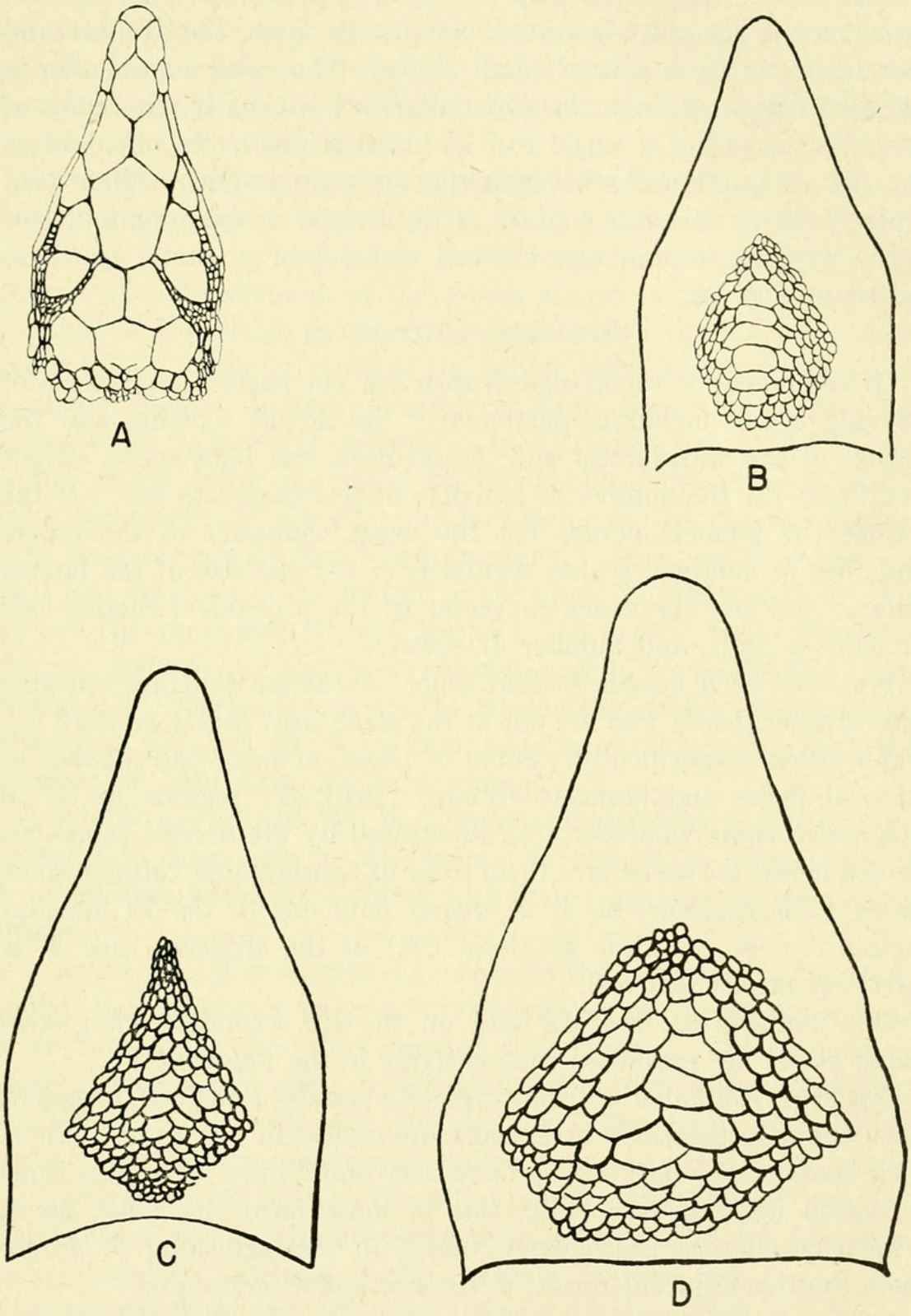


FIG. 1. A. Dorsal view of head scales of *A. u. parva,* HMS No. 14256, La Esperanza, Chiapas.
B. Gulars of *A. u. stuarti,* EHT-HMS No. 11952, San Ricardo, Chiapas.
C. Gulars of *A. u. gaigeae,* EHT-HMS No. 11927, Progreso, Yucatán.
D. Gulars of *A. u. podarga,* HMS No. 1597, Huichihuayán, San Luis Potosí.

Supraocular scales. In only one race, *u. parva,* the posterior supraocular is usually separated completely from the frontal and frontoparietal by a row of small scales. The same supraocular is likewise separated from the superciliaries by, usually, two rows of granules instead of a single row as in other races. In other forms the row of small scales between the supraocular and median head scales is short, allowing contact of the frontal or frontoparietal (or both) with the supraocular. These features in *u. parva* are illustrated in Fig. 1A.

SECONDARY CHARACTERS

Of secondary or racial significance are (1) pattern characters of varying types, including particularly the dorsal spotting and the nature of the dorsolateral and lateral dark and light spots, stripes and bars; (2) the number of lamellae under the fourth toe; (3) the number of femoral pores; (4) the exact character of the gulars (number of enlarged scales, regularity); (5) the size of the lateral gulars; and (6) the exact character of the preanals (whether one or more is split, and number of rows).

We have been unable to find other characters that are variable intersubspecifically and are not at the same time nearly equally variable intrasubspecifically. Some of these, in fact—the number of femoral pores and lamellae—Stuart (1942: 47) regards as of no diagnostic value whatever. As illustrated by the several tables included herewith, we believe them to be of considerable value in some cases. For example, in *A. u. stuarti* only one of the 72 lamellar counts is over 28, while all those (97) of the adjacent race *A. u. hartwegi* are 29 or over.

Our methods of treating data on the six secondary characters listed above are explained consecutively in the following.

Pattern. A number of forms typically possess numerous, irregular, dark spots on the back, arranged more or less in two rows. Others lack spots completely or else have very small ones. There is some variation intrasubspecifically, but in most forms it is not great. This character is particularly useful in distinguishing *u. dextra* from the two adjacent forms, *u. sinistra* and *u. undulata.*

Of greatest significance so far as pattern is concerned, however, is the nature of the dorsolateral and lateral pattern. Light and dark stripes, transverse bars and spots are the chief components. Some forms appear rather distinctly striped, others barred, and combinations of both types of pattern with neither particularly prominent is common. As Stuart (1942: 147) has pointed out, ontoge-

netic changes and sexual dimorphism in pattern occur in most forms. Juveniles of both sexes and all females tend to have a more linear pattern than adult and subadult males, which tend to stress the barred elements of the pattern. Adult males are more brightly marked than other specimens.

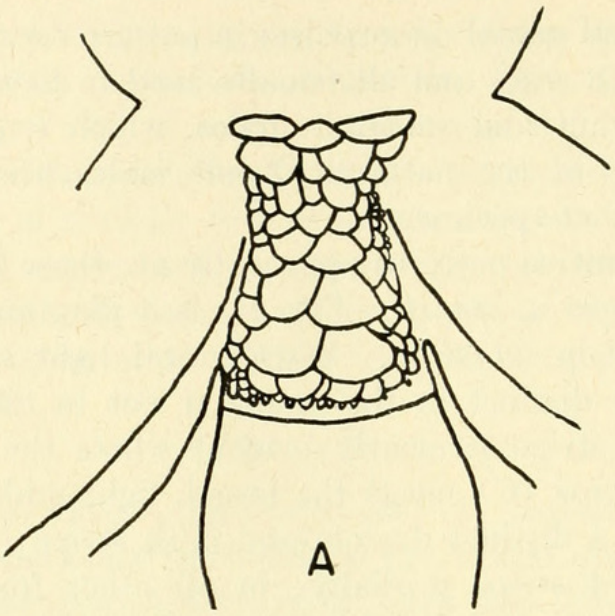
The most primitive patterns apparently are those in which stripes predominate, as in *u. stuarti*. Fig. 2D is a diagram of the stripes that may occur in *undulata*. Dorsolateral light stripes (D) are typical and are distinct in the young if not in the adult, or the position of the stripe is clearly evident where the adjacent dark upper lateral stripe (C) meets the broad, light middorsal area. In *u. stuarti* only, a distinct dorsolateral dark stripe (E) borders the dorsolateral light stripe medially; in all other forms the medial border of the latter is formed by the light middorsal area, which obviously meets the upper lateral dark stripe in case the dorsolateral light lines are poorly developed or absent. In *u. amphigramma* a light line develops in the middle of the upper lateral dark line; this we call the upper lateral light line (F). In several forms (particularly *u. podarga, u. dextra, u. sinistra,* and *u. thomasi*) the upper lateral light line is represented by large spots, which either remain isolated in the dark stripe (as in *u. podarga et al.*) or fuse with the dorsolateral light stripe (as in *u. thomasi*).

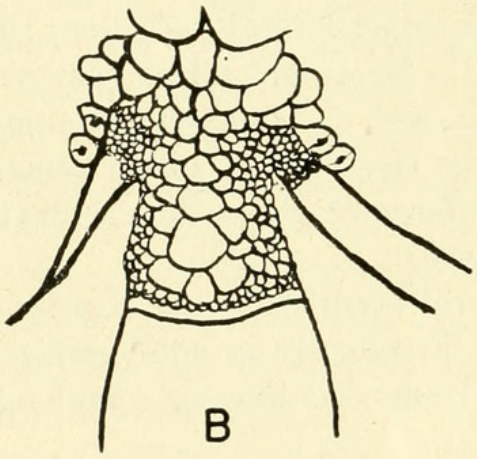
A lateral light stripe (B) is of general occurrence, but is usually broken into short lines or into spots. Frequently in adult males it is not evident, being either fused with transverse lines or completely absent.

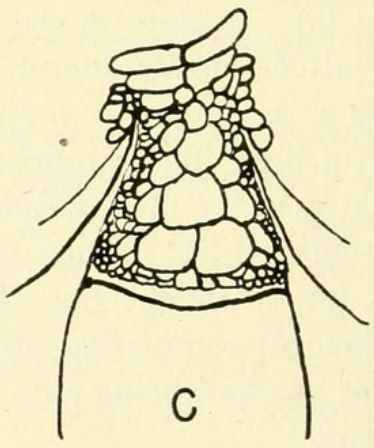
A broad lateral dark zone (A) borders the lateral light line ventrally. It is frequently marked with irregular light spots which tend to be elongate or oval and oriented transversely. Enlargement of these irregular light spots results in a fusion with the lateral light line (or parts thereof) and sometimes with the upper lateral light spots. Specimens in which such a fusion has occurred have irregular transverse light bars on the sides, producing a "tigroid" pattern. The width of the dark interspaces varies considerably, but is, within rather generous extremes, fairly constant for any one form. The narrower the dark bars, the more striking the tigroid effect becomes.

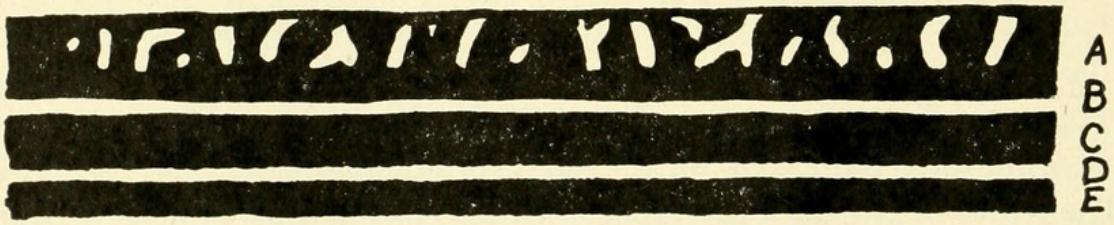
Lamellae. We have counted only the lamellae under the 4th toe, although differences in the lamellar counts of other digits are probably equally significant.

The lamellae on the three basal phalanges of the 4th toe are divided, and differ in number on the two sides. Those on the anterior surface (toward the third toe) are larger and apparently more con-









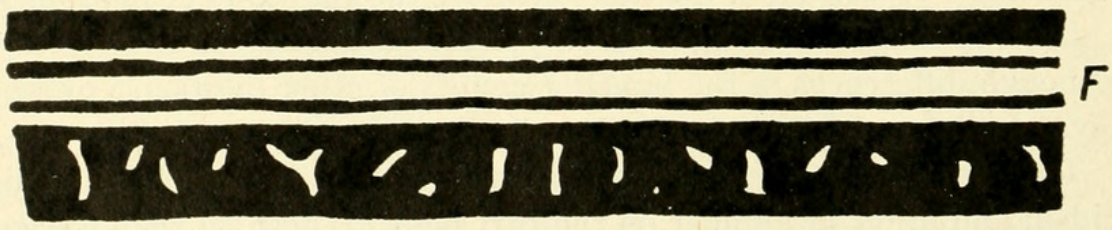


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FIG. 2. A. Preanals of *A. u. podarga*, HMS No. 1597, Huichihuayán, San Luis Potosí.
B. Preanals of *A. u. undulata*, HMS No. 18543, Tehuantepec, Oaxaca.
C. Preanals of *A. u. dextra*, EHT-HMS No. 11682, Acapulco, Guerrero.
D. Diagrammatic scheme of dorsal and lateral pattern of *A. undulata*.
A. Lateral dark line.
B. Lateral light line.
C. Upper lateral dark line.
D. Dorsolateral light line.
E. Dorsolateral dark line.
F. Upper lateral light line.

stant than those in the posterior row. For that reason our counts were made along the preaxial border of the digit.

Fortunately it has been possible to mark an exact basal point from which the counts begin. A relatively large, single tubercle is present at the base of the 1st phalanx, immediately preceding the paired lamellae. Our counts begin with that tubercle as No. 1. Occasionally a single small tubercle precedes it, instead of paired scales; in such cases the count still begins with the larger, proximal tubercle.

The total range of variation in lamellar counts of Mexican *undulata* is from 22 to 36, the minimum occurring in *u. stuarti*, the maximum in *u. hartwegi* and *u. gaigeae*. The maximum range in any one form is 11 (*u. gaigeae*, 26-36), the minimum 7 in forms represented by a reasonable number of counts (*u. sinistra*),* the average 9, excluding doubtfully complete series (*u. stuart* 9, *u. amphigramma* 10, *u. parva* 8, *u. hartwegi* 8).

TABLE 1. Racial Variation in Lamellae and Pores

RACE.	Lamellae.			Pores.		
	Counts.	Range.	Average.	Counts.	Range.	Average.
stuarti	72	22–30	25.5	73	13–18	15.5
podarga	30	28–31	29.4	31	13–18	15.8
amphigramma	187	24–33	27.7	180	14–23	17.0
thomasi	17	25–30	28.4	18	14–20	17.2
parva	97	26–33	29.1	98	13–21	16.4
dextra	20	27–31	28.9	24	15–21	18.2
sinistra	111	26–32	29.6	121	15–22	18.1
undulata	94‡	25–30	27.7	162†	13–20	16.8
hartwegi	97	29–36	31.8	100	16–23	20.5
gaigeae	132	26–36	30.4	138	15–22	18.5

‡ All from Hartweg and Oliver, 1937: 7.

† Of these 94 counts are from Hartweg and Oliver, 1937: 7.

* Unreliable are *u. podarga* (31 counts, range 4), *u. thomasi* (17 counts, range 6), and *u. dextra* (20 counts, range 5).

The lowest average number of lamellae is 25.5 (*u. stuarti*), the highest 31.8 (*u. hartwegi*). For all races the mean average is 29.

Femoral pores. The number of pores has been found useful in the diagnosis of most of the races of *undulata,* separating almost all from at least one close relative. The most useful comparisons have been possible between *u. stuarti, u. hartwegi* and *u. gaigeae.* In other forms average differences may occur, but they do not always reach a minimum of seventy percent reliability desirable for a useful character. In some cases we have found it desirable to compare the total pore counts rather than those on one thigh only.

The total range of variation in Mexican *undulata* pore counts is 11, the actual counts varying between 13 and 23. The minimum number occurs in *u. stuarti, u. parva* and *u. undulata,* the maximum in *u. amphigramma* and *u. hartwegi.* The maximum range of variation in any one form is 10 (*u. amphigramma,* 14 to 23), the minimum 6 (*u. stuarti* and *u. podarga,* 13 to 18), the average 8 (*u. thomasi, u. dextra,* 7; *u. sinistra, u. undulata, u. hartwegi, u. gaigeae,* 8; *u. parva,* 9).

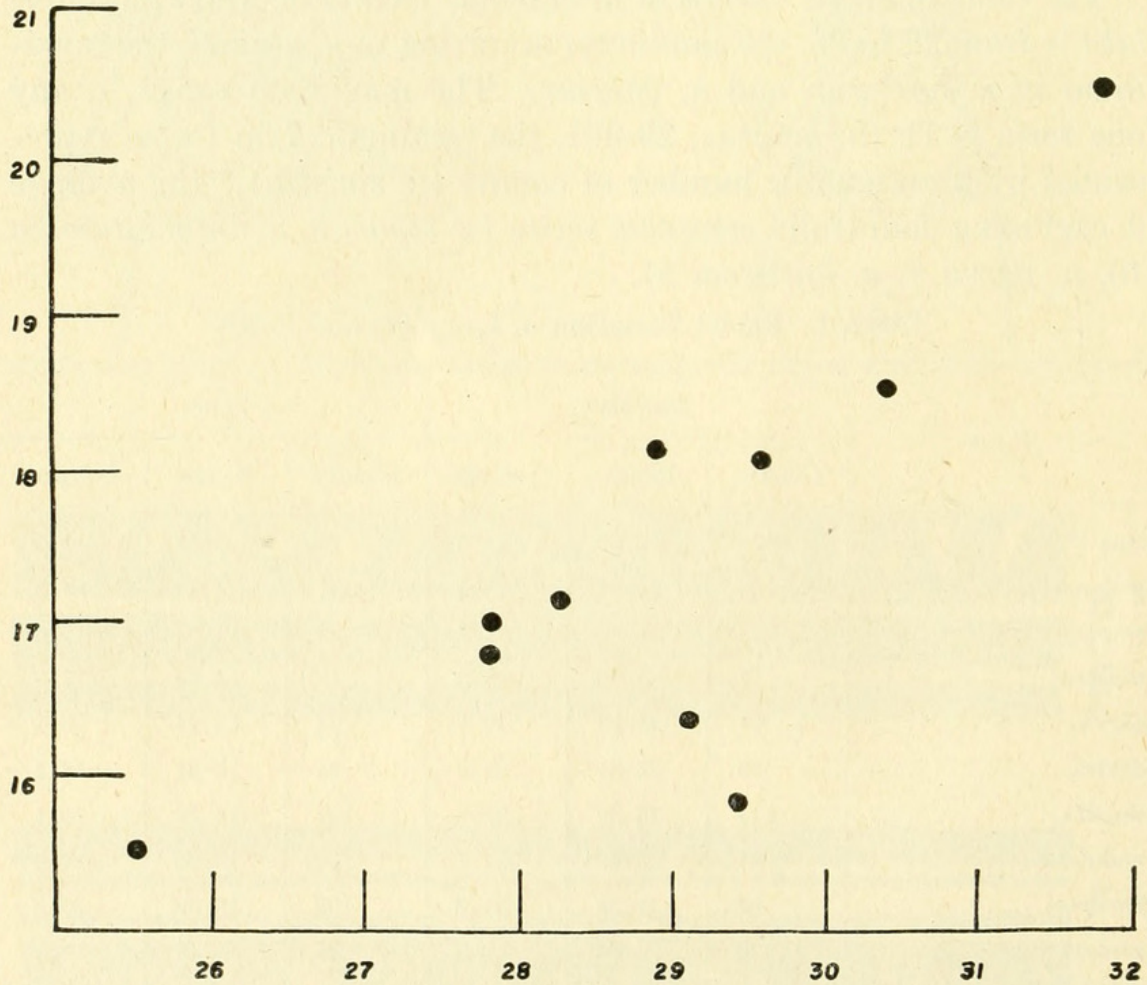

FIG. 3. Correlation in average femoral pore and lamellar counts of the races of *Ameiva undulata.* Based on Table 1. Abbreviations for subspecific names: st, *stuarti;* p, *podarga;* a, *amphigramma;* t, *thomasi;* pa, *parva;* d, *dextra;* s, *sinistra;* u, *undulata;* h, *hartwegi;* g, *gaigeae.*

The lowest average number of pores is 15.5 (*u. stuarti*), the highest 20.5 (*u. hartwegi*). For all races the mean average is 17.4.

There is a direct correlation in variation in number of pores and of lamellae at least racially; we have not attempted to determine whether there is a similar correlation individually. In general, the higher the average number of pores, the higher the average number of lamellae (Fig. 3). *A. u. parva* deviates most conspicuously from this correlation, although it is not far from the expected position. *A. u. podarga* is not represented by sufficient counts to be significant in its apparent divergence. All others are arranged closely about the line of correlation.

It is noteworthy that in average count, in maximum count and in minimum count, *u. stuarti* is the lowest and *u. hartwegi* the highest, in respect both to lamellae and pores. In other respects as well the races are the most widely differentiated of any in the species that occupy adjacent ranges.

Median gulars. We have already mentioned that the abruptness of enlargement of the median gulars is a character readily segregating *u. gaigeae* and *u. hartwegi* (not abruptly enlarged) from all other forms. The character of these scales is of still further use, however, in defining some forms. We recorded variation in two features: number of rows of central gulars, and number of regular and irregular scales.

The number of rows of gulars recorded included only those containing notably enlarged scales. In spite of the arbitrary nature of the count, marked differences definitely do occur. In *u. stuarti,* for example, a relatively large number of gulars (6 to 8) occurs; they are arranged very neatly in a median row which typically is bordered by much smaller gulars not perceptibly increasing in size medially. In most other forms there are fewer median gulars, but they are larger than in *u. stuarti* and somewhat more irregularly arranged. This difference has been used diagnostically in comparing *u. podarga, u. amphigramma* and *u. stuarti* with each other.

The regularity of arrangement of the gulars was measured by counting the number of more or less symmetrical scales (exceeding one) aligned in the midventral line. A minimum of two was recorded since even completely irregular scales might accidentally include one oriented medially.

In considering irregularity (as opposed to regularity) of the gulars some standard is necessary, since the anterior and posterior median gulars tend to be irregular and blend into the adjacent smaller gulars. We therefore selected a maximum of five gulars to be con-

sidered when counting the number of irregular scales. The five observed were the largest and most typical scales of the group. This number was selected of necessity because it was the smallest number of rows of enlarged gulars found in any of the forms compared; a larger number would have necessitated the inclusion, in some cases, of small gulars preceding or succeeding the enlarged series or group.

Lateral gulars. We have observed a marked enlargement of the lateral gulars only in *u. thomasi.* In other races the gulars are very nearly uniform throughout, except of course for the median area, but may be slightly enlarged laterally in the region of the jowls. The greater enlargement in *u. thomasi,* while clearly evident by direct comparison, is not prominent enough to be particularly useful in diagnosis.

Preanals. As stated previously, the preanals are arranged in two strikingly different ways: in a single or a pair of median rows. We have observed no variation of significance in the condition of paired median preanals, but the condition of an azygous row does show some variation of subspecific significance.

There are three races which belong in the group with azygous preanals: *u. undulata, u. dextra,* and *u. sinistra.* In *u. dextra,* however, the last large preanal is usually paired (see Fig. 2C), a condition which may well mean an incomplete transformation from the primitive paired condition. In most *u. sinistra* all are single, and in a very few *u. undulata* are any large scales paired. In other words the latter race approaches the perfect azygous arrangement, and therefore the peak of specialization along this line, more closely than any other. *A. u. sinistra* is intermediate, and *u. dextra* the least specialized.

In taking data on this character we found that there was some difficulty in determining what was to be considered the last preanal. Obviously the very small granules lining the cloaca are not to be counted, but these sometimes merge so gradually with the enlarged preanals that it is not certain just where the line of distinction should be drawn. For that reason it is well nigh impossible to compare homologous scales through large series of specimens of all the three forms involved. Moreover, in *u. undulata* the intermediate preanal-cloacal scales are frequently paired.

A moderately satisfactory solution to this dilemma was found by observing the number of rows of preanals. This was determined by following medially the row of scales in line with the femoral pores,

and from their point of union counting posteriorly the number of rows of enlarged scales. The anterior point for the counts was thus relatively constant in all cases. Posteriorly, again, some doubt was entertained on the terminus of the enlarged scales. Some variation is to be expected and did occur, so that our counts of the number of preanal rows are not to be regarded absolute. It is true, however, that *u. undulata* tends to have more rows of preanals than either *u. dextra* or *u. sinistra*. Observing only the fifth preanal, if one would count five rows or more, we found that the variation introduced by the numerous terminal rows was eliminated in most cases. This procedure was particularly helpful in dealing with *u. undulata*, yielding a high percentage (89%) of single posterior preanals. We would have had a nearly equal dispersal by taking the very last enlarged scales. In *u. dextra* and *u. sinistra* the rows of preanals average fewer than in *u. undulata*, and frequently the last enlarged preanal would be in the fourth row.

Accordingly, we arbitrarily decided that the paired or single condition would be recorded for the preanals of what definitely appeared as the last row of enlarged scales if the number of rows was found to be five or less; if over five, the character of the scales of the fifth row only was recorded.

SUBSPECIFIC SECTIONS

There are four morphological sections in *undulata*, distinguished on the basis of the primary characters previously outlined. Excluding *u. pulchra*, each section occupies a distinct and continuous range, and forms a natural unit. The exceptional form, *u. pulchra*, is most closely related to *u. hartwegi* and *u. gaigeae*, but is morphologically closest to the group containing *u. stuarti*, *u. podarga*, *u. amphigramma* and *u. thomasi*. The natural, subspecific groups or their ancestral stocks have been indicated in Fig. 4 by the Roman numerals I through IV. The forms of these groups may be listed as follows:

I. *A. u. pulchra, u. hartwegi, u. gaigeae* (two rows of preanals; small gulars*).

II. *A. u. parva* (two rows of preanals; large gulars; third supraocular separated).

III. *A. u. stuarti, u. podarga, u. amphigramma, u. thomasi* (two rows of preanals; large gulars; third supraocular not separated).

IV. *A. u. dextra, u. sinistra, u. undulata* (one row of preanals).

* Except *u. pulchra*, with enlarged gulars and other characters as in group III.

Allocation of *u. pulchra* with the subspecific group I, while on morphological grounds it belongs with group III, is prompted by geographic considerations discussed in the following paragraphs.

The distinctness of these four groups in México is rather striking. *A. u. undulata* is the most highly specialized of its group and thus sharply distinguished from *u. parva* and *u. amphigramma*, members of two adjacent sections. *A. u. stuarti* is so widely different from *u. hartwegi* and *u. gaigeae*, the members of an adjacent section, that it might well be considered a member of a different species. We have refrained from considering *u. gaigeae* and *u. hartwegi* collectively as a distinct species chiefly because of the existence of a slight approach of specimens of *u. stuarti* toward *u. hartwegi*. Actual intergrades still are not known, and for that reason the possible specific distinctness of *hartwegi* should be kept in mind. In such an arrangement, however, the problem of relationship to *u. pulchra* becomes acute, for it fits morphologically with some of the other races, although it presumably intergrades with *u. hartwegi*.

Incontrovertible intergrades are known only between sections II and IV, via *u. parva* and *u. undulata*, respectively. None is known between III and either II or IV, or between III and I, although they may occur.

PHYLOGENY

The phylogeny of Mexican races of *Ameiva undulata* is not entirely clear. Forms which differ so slightly as these furnish few clues to their early peregrinations and relationships. Nevertheless certain rather probable steps in the subspeciation of the group seem fairly evident. These steps may be segregated into four groups: those of (1) Lower and Middle Miocene, of (2) Upper Miocene and Lower Pliocene, of (3) Upper Pliocene and Lower Pleistocene, and of (4) Pleistocene and Recent times.

LOWER AND MIDDLE MIOCENE

It is conceivable that in the Lower and Middle Miocene,† when the Isthmus of Tehuantepec was above water, the *undulata* stock was distributed rather widely from southern and probably central (coastal) México through all available territories in Central America (Fig. 4A). Whether this stock was originally dispersed from the north or south is not particularly clear, but because of the indisputable South American center of dispersal of the family we may suppose that the *undulata* stock migrated northward.

† Paleogeography based on Schuchert (1935).

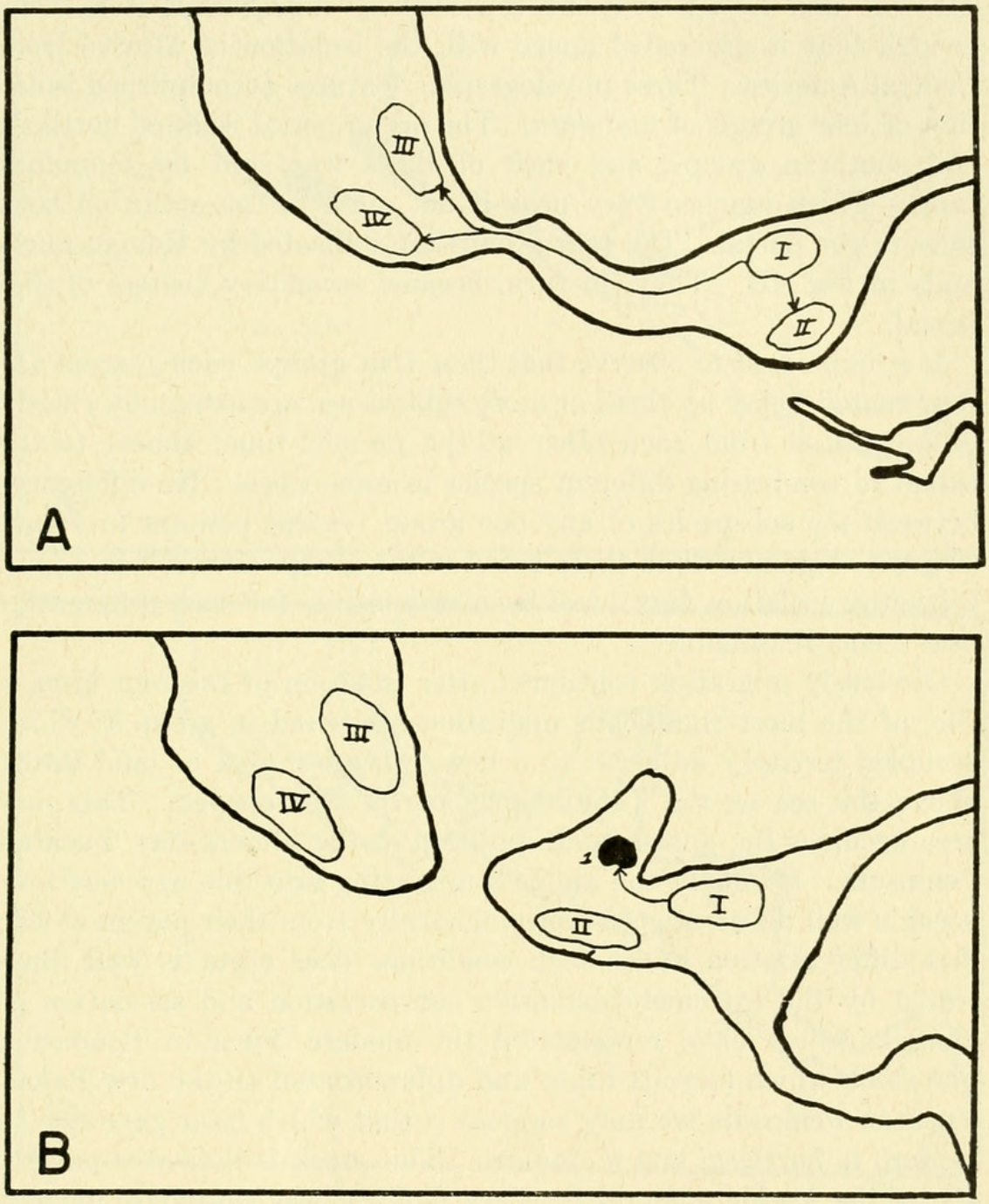

FIG. 4. Paleophylogenetic maps of *A. undulata*.
A. Lower and Middle Miocene.
B. Upper Miocene and Lower Pliocene.
I. *pulchra-hartwegi-gaigeae* parent stock.
II. *parva* parent stock.
III. *podarga-amphigramma-thomasi-stuarti* parent stock.
IV. *undulata-dextra-sinistra* parent stock.
1. *hartwegi-gaigeae* parent stock.

UPPER MIOCENE AND LOWER PLIOCENE

Since in this period these lizards were dispersed over a considerable area, some differentiation may have begun while the Tehuantepec portal (in reference to the oceans) was still closed. Whether it began then or after the opening of the portal in the Upper

Miocene and Lower Pliocene is relatively immaterial; it is clear enough that it proceeded apace with the isolation of México from Central America. Three physiographic features accomplished isolation of four groups of *undulata*. The ocean portal isolated northern and southern groups, and each of these was split by mountain ranges which reached very near if not quite to the ocean on both sides of the portal. The four groups are indicated by Roman numerals in Fig. 4B. They, in turn, became secondary centers of dispersal.

It is important to observe that these four groups, each (except II) represented today by three or more subspecies, are extremely clearly differentiated from each other at the present time, almost to the extent of comprising different species in some cases. No differences between the subspecies of any one group (except perhaps in I) are as great or greater than those between the groups themselves. That a lengthy isolation may have been responsible for such differentiation seems reasonable.

Obviously migration continued after isolation of the four groups. One of the most significant migrations occurred in group I, which occupied territory adjacent to a new, extensive area of land thrust above the sea as the Tehuantepec portal was opened. This new area occupies the approximate position of the present-day Yucatán Peninsula. Probably the animals migrating into this new territory became well differentiated morphologically from their parent stock; that differentiation under such conditions does occur is well illustrated by the extremely extensive subspeciation and speciation of animals which have repopulated the modern Yucatán Peninsula. The stock which migrated into and differentiated on the new Paleo-Yucatán Peninsula we may suppose is that which later gave rise to modern *u. hartwegi* and *u. gaigeae*. This stock is indicated on Fig. 4B by the Arabic numeral 1. Very likely it was similar to modern *u. hartwegi*. The theory of differentiation of the pre-*hartwegi-gaigeae* stock on a Paleo-Yucatán Peninsula accounts satisfactorily for the very extensive differentiation within Group I—a differentiation far greater than has occurred within any other group.

On the northern side of the portal, migration proceeded probably with some differentiation into races. This topic will be discussed later.

UPPER PLIOCENE AND LOWER PLEISTOCENE

In this period the Tehuantepec portal was closed and migration across the Isthmus again became possible. Three important changes took place. It would appear (1) that the migration was effected

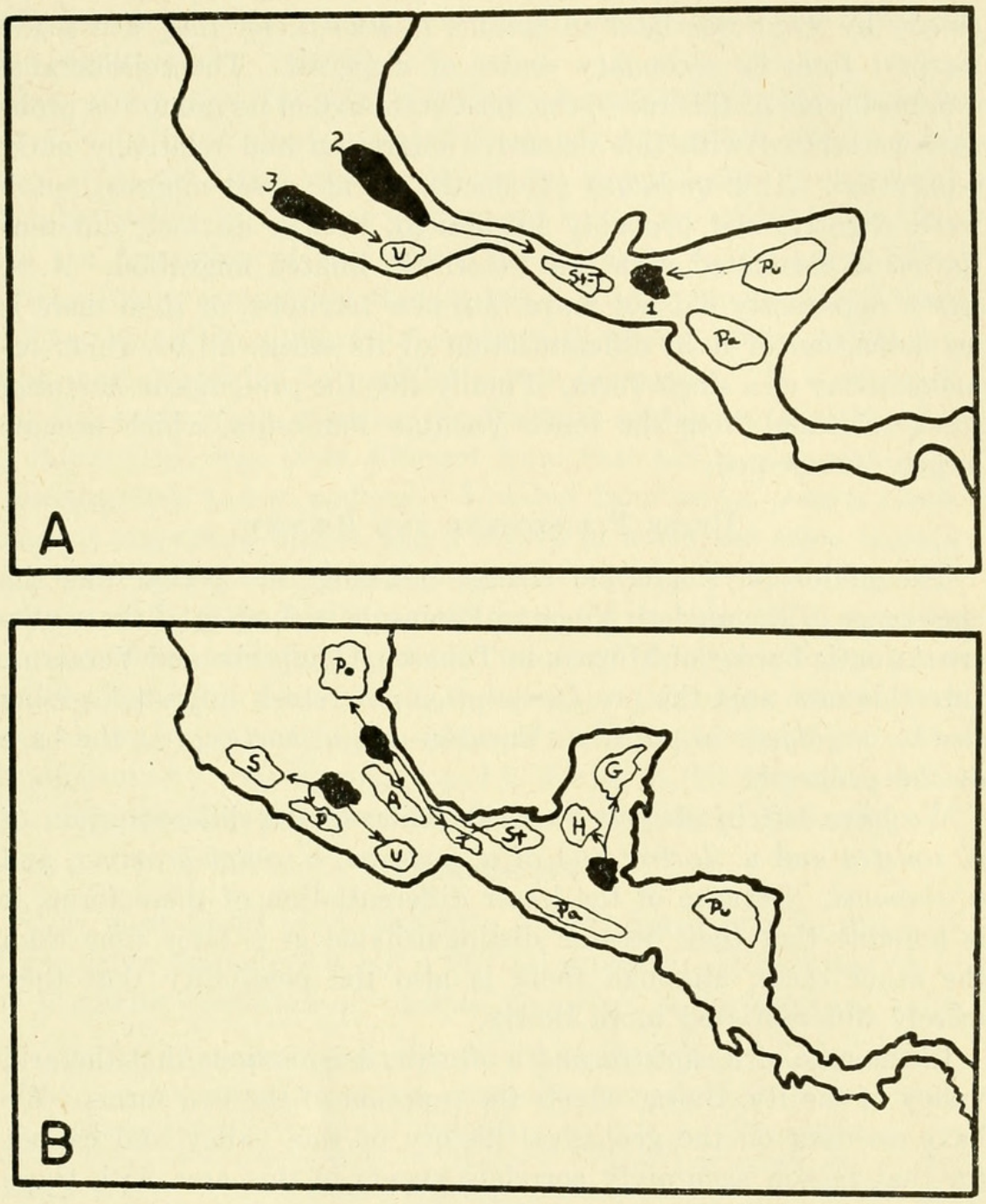

FIG. 5. Paleophylogenetic maps of *A. undulata*.
A. Upper Pliocene and Lower Pleistocene.
B. Upper Pleistocene and Recent.
1. *hartwegi-gaigeae* parent stock.
2. *podarga-amphigramma* parent stock.
3. *dextra-sinistra* parent stock.
A. *amphigramma*
D. *dextra*
G. *gaigeae*
H. *hartwegi*
Pa. *parva*
Po. *podarga*
Pu. *pulchra*
S. *sinistra*
St. *stuarti*
St-T. *stuarti-thomasi* parent stock.
T. *thomasi*
U. *undulata*

chiefly by what was later to become *u. stuarti,* for this race is the farthest from its secondary center of dispersal. The considerable differentiation of this race—the most extensive in its group—is probably correlated with this extensive migration and relatively early separation. *A. u. undulata* (2) on the Pacific coast migrated eastward slightly, and probably its limited, though distinct, differentiation is correlated with that relatively limited migration. *A. u. parva* apparently did not move into new territory, or if so there is no indication of it in differentiation of its stock, all of which remains today as a single form. Finally (3), the pre-*gaigeae-hartwegi* stock retreated from the Paleo-Yucatán Peninsula, which became largely submerged.

UPPER PLEISTOCENE AND RECENT

The major physiographic change marking this period was the emergence of the modern Yucatán Peninsula and much of the southern Atlantic border of México, in Tabasco, Campeche and Veracruz. Into this new area the pre-*hartwegi-gaigeae* stock migrated, giving rise to *u. gaigeae* in northern Yucatán and *u. hartwegi* at the base of the peninsula.

We have left in abeyance consideration of the differentiation of *u. sinistra* and *u. dextra,* and of *u. podarga, u. amphigramma,* and *u. thomasi.* Because of the lesser differentiation of these forms it is possible that they became distinguishable at a later time than the other races, although there is also the possibility that they merely differentiated more slowly.

In the case of *u. sinistra* and *u. dextra,* it is obvious that the arid valley of the Río Balsas effects the isolation of the two forms. We have no data on the geological history of this valley and cannot for that reason accurately correlate events in this area with those at the Isthmus. It is recorded, however, that the entire western coast of México, particularly between the Isthmus and Cape Corrientes, sank extensively after early Pleistocene times. It is possible that this depression extended the aridity of the lower basin of the Río Balsas farther into the interior, where today it penetrates even to within five or 10 miles of the extremely humid Atlantic slopes. This interpretation lends support to the idea of recent segregation of *u. dextra* and *u. sinistra.*

It appears that, like the preceding, *u. podarga* and *u. amphigramma* differentiated *in situ.* There is no prominent physiographic barrier between the areas occupied by the two races. The isolation is, in other words, ecological, and cannot well be considered any-

thing but a relatively recent one—surely as recent as the isolation of *u. dextra* and *u. sinistra.*

The origin of *u. thomasi* is somewhat perplexing. The race appears to be most closely related to *u. amphigramma,* but is separated from the latter race by *u. stuarti* which occurs in the lower Grijalva valley in Chiapas. It cannot well have arrived there before the formation of the portal, for it surely would have differentiated more extensively than it has. It may have arrived there while *u. stuarti* was migrating southward, become more or less isolated, and proceeded to parallel *u. amphigramma.* It is assumed that the early stock crossing the Isthmus southward shortly after its reformation was little different from that which gave rise to *u. amphigramma* and *u. podarga.* Isolated from pre-*u. stuarti* stock, it is not surprising that it might evolve in much the same manner as *u. amphigramma* and *u. podarga* farther north. The differences between all three lie chiefly in pattern, and it is obvious that parallelism in pattern evolution is almost universal in *A. undulata*: practically all, save *u. stuarti* tend to break up the upper lateral dark lines either by forming light spots or a continuous light line. The parallelism of *u. amphigramma* and *u. dextra* in this respect is striking, although the races presumably have no direct relationship.

SPECIALIZATION

Since most forms of *A. undulata* differentiated *in situ,* dispersal of primitive characters is not a critical problem. Determination of the primitive condition of various characters is, however, of value

TABLE 2. Specialized and Primitive Characters in *Ameiva undulata*

CHARACTERS	Primitive	Specialized
Gulars	enlarged, irregular: *u. pulchra, u. podarga*	a. small: *u. hartwegi, u. gaigeae* b. enlarged and very regular: *u. stuarti*
Preanals	2 rows	1 row
Supraocular separation	½–1*	1–2*
Upper lateral dark stripe	unbroken, without light spots: *u. stuarti*	with light spots or stripe
Dorsolateral dark stripe	absent	present: *u. stuarti*
Femoral pores and lamellae	moderate number	a. reduced number: *u. stuarti* b. increased number: *u. hartwegi* and *u. gaigeae*
Dorsal spotting	reduced or none	well developed

* The first integer refers to the length of the row of granules between the last large supraocular and the median head scales; the second integer refers to the number of rows (complete or incomplete) between the last large supraocular and the superciliaries.

in considering the few forms that did arise by migration, and in considering the extent of change in other forms.

The primitive condition of the subspecific characters in *A. undulata* are recorded in Table 2. Our decisions on them are perhaps debatable, but we feel that the evidence available preponderantly favors this arrangement.

According to that evaluation of characters, *u. pulchra* is the most primitive of group I; *u. podarga* of group III; and *u. dextra* of group IV. It is to be expected that *u. pulchra* would be the most primitive of group I, since the rest of the stock moved into an environment probably a little different from that to which the race had become accustomed.

In group III, *A. u. podarga* may have large light spots in the upper lateral dark stripe, but is otherwise primitive and is peripheral.

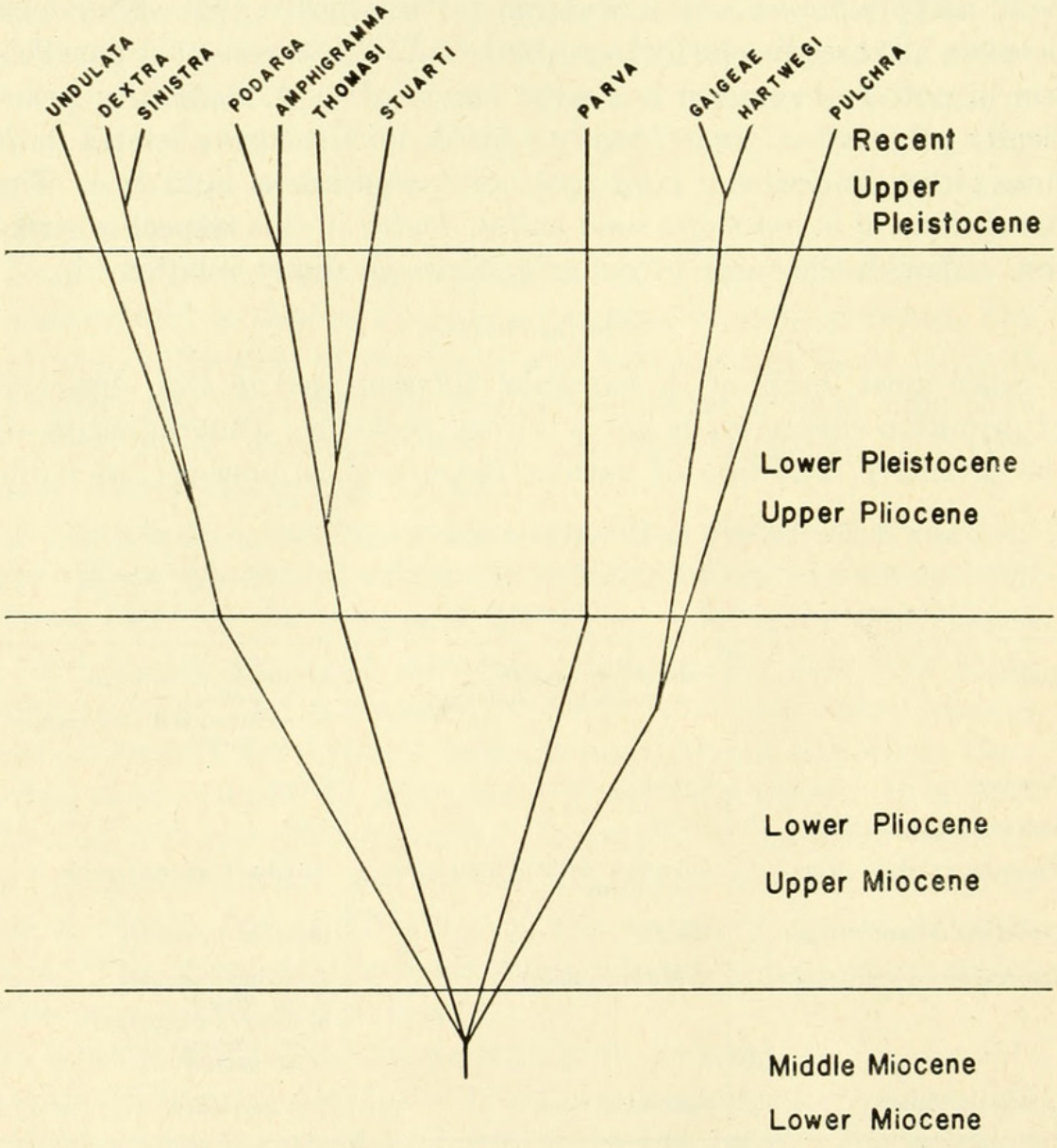

FIG. 6. Proposed phylogeny of the subspecies of *Ameiva undulata*.

With more regular gulars and a distant upper lateral light stripe, *u. amphigramma* is definitely more specialized than *u. podarga*. *A. u. thomasi* is nearly as specialized as *u. amphigramma*, and is a remarkably close parallel in spite of distinct isolation. *A. u. stuarti*, oddly enough, retains the most primitive pattern of the group or even of the species, in some respects, but combines with that a number of strongly specialized characters.

Of all members of group IV, *u. dextra* is clearly the most primitive, having only a partial specialization in preanals and no dorsal spotting, although the pattern in it is extreme in its development (very much like *u. amphigramma*). *A. u. sinistra* is more specialized in preanal arrangement, and *u. undulata* is the most highly specialized.

These relationships, and approximate time of differentiation, are indicated on Figure 6.

DIFFERENTIATION AGENCIES

Two major factors seem to have been involved in the subspeciation of *A. undulata*: isolation (1) *in situ*, due to geographical, physiological, or ecological changes; and isolation by (2) migration into new territory (see Table 3).

Before formation of the Miocene portal obviously a certain degree of differentiation correlated with migration into all available territory may have occurred, at least to such an extent that the 4 groups of *A. undulata* were slightly differentiated.

TABLE 3. Physical Factors Correlated with Subspecific Differentiation in *Ameiva undulata*

RACE OR STOCK	Physical factors
pre-*gaigeae-hartwegi*	migration (from stock of group I)
pulchra	ecological isolation from pre-*gaigeae-hartwegi*
gaigeae	migration (from pre-*gaigeae-hartwegi*)
hartwegi	ecological isolation from *gaigeae*
parva	isolation
stuarti	migration (from stock III)
thomasi	migration (from stock III)
amphigramma	ecological isolation (from stock III)
podarga	ecological isolation (from stock III)
undulata	migration (from stock IV)
sinistra	physiographic isolation (from pre-*dextra-sinistra*)
dextra	physiographic isolation (from pre-*dextra-sinistra*)

After mechanical isolation of the four groups by the portal, differentiation then became a phenomenon accomplished (1) *in situ* (without migration), through formation of barriers here and there and resultant, partial or complete isolation; and in certain instances (2) as the species migrated into new territory also undoubtedly partially isolated, by some factor, from adjacent territory.

Those forms which migrated into new territory differentiated perhaps more extensively than those remaining in the original areas. Unfortunately there are insufficient cases at hand to demonstrate whether the migrants evolved significantly more rapidly. In fact there is little evidence that the speed of differentiation is correlated with anything but time in these lizards; the longer the isolation, the greater the differentiation. There is in all probability little difference in end result between differentiation *via* isolation and differentiation *via* migration, especially since the real factor in the latter case may in reality be isolation. There is this difference, however: that differentiation *via* migration results in a geographic *trend* of specialization, while differentiation *in situ* does not.

CHARACTER DISPERSAL

Peripheral dispersal of primitive characters is commonly recognized in large groups, especially of mammals, but in small groups the phenomenon is not of regular occurrence. We can verify, however, that the peripheral forms of *Ameiva undulata* do appear to be the most primitive of the species; they are *u. podarga,* pre-*dextra-sinistra,* and *u. pulchra.* The reverse situation, however, occurs within the subspecies groups, which demonstrate peripheral specialization. In group I, pre-*gaigeae-hartwegi* is a peripheral specialization of earlier stock; in group III, *u. stuarti* is a peripheral specialization, again from a secondary center of dispersal; and in group IV, *u. undulata* is likewise a peripheral specialization. In each case migration into new territory, as opposed to differentiation *in situ,* has been involved.

Some explanation is in order for the apparently opposite trends of evolution of, on the one hand, the species as a whole, and on the other hand, of its subspecies groups. They appear to be fundamentally different, for migration of the species as a whole to its present peripheral range limits was accomplished with peripheral dispersal of primitive forms, while migration of lesser groups resulted in peripheral specialization.

In this particular case the apparent differences can be explained

as follows. The earliest stock of the species, as it migrated from a center of dispersal, did specialize, and the four subspecies groups at the time of their isolation were in reality specialized as compared with the original stock, none of which persisted unchanged. Reaching the limits of its range, subsequent differentiation was accomplished *in situ* only, with obviously haphazard specialization at various points in the range. Further migration occurred only centrifugally into new territories elevated near the center of the range. Actually these territories can be considered peripheral, inasmuch as they are peripheral in the ranges of the groups themselves. The secondary migration, like the first, was accompanied by peripheral specialization. The peculiar effect of having peripheral primitiveness on the one hand and peripheral specialization on the other is, then, a false illusion. In reality peripheral specialization occurred in all cases.

MIGRATION EFFECTS

Migration has, in these lizards, been the most important factor in specialization of several races. In every case of migration, specialization has followed or occurred at the same time. It can, with some degree of confidence, be suggested that migration always is accompanied by specialization in some respect, at least in these lizards. Peripheral forms may always be expected to be more specialized than their ancestral forms, although they in turn may be more primitive than other derivatives of those ancestors. If these data may be applied to Matthew's theory of peripheral dispersal of primitive groups, it is obvious that Matthew is correct only as one line of derivatives (and migrants) is compared with another line of derivatives (later migrants) of the same ancestors; his theory appears to be incorrect as applied to a single line of derivatives, in which peripheral specialization is the rule. It thus seems that the often-heard, loose statement that this Matthewsian thesis is applicable only to larger categories [each representing a different line] but not the smaller ones [each representing only one line] is, in a general way, correct and reasonable.

NONPRIMITIVE AREAS

Three areas in México are shown by this study to be newly emerged; they are the Atlantic slopes on the eastern side of the Isthmus of Tehuantepec; Pacific slopes on the western side of the Isthmus; and the northern portion of the Yucatán peninsula. All these areas were populated by relatively recent migrants. Those

which evolve at approximately the same rate as *Ameiva undulata* (most reptiles?) have not been able to use these areas as secondary centers of dispersal. Therefore, it is reasonable to postulate that, in those cases in which such animals are represented by one form in any of the three nonprimitive areas, and by one or more closely related species or subspecies in adjacent areas, the form in the nonprimitive area is never the most primitive. This postulate is not to be construed to imply that relatively primitive species cannot occur there; they can and do, but if they are represented in an adjacent area by another close relative, the latter is the more primitive of the two. Likewise this postulate is not to be construed to apply to any migrants which have already set up in those areas secondary centers of dispersal from which other forms have radiated. It is believed that these areas have served as secondary centers for very few, if any, reptiles and amphibians.

AGES OF RACES

Exact ages cannot be given for any race of *A. undulata*, but because of the rather precise correlation in some cases of differentiation with geological events, the geological time estimates can give a clue to the approximate ages of the races, as indicated in Figure 6. *A. u. gaigeae* appears to be the most recent, of Upper Pleistocene date. It is also one of the least well defined of all races. Perhaps equally recent are the differentiations from each other of *u. amphigramma* and *u. podarga*, and of *u. dextra* and *u. sinistra*, but the geological correlation with the Upper Pleistocene is not so well assured as in the case of *u. gaigeae*. *A. u. stuarti* and *u. thomasi* are marked as of no greater age than that of the Upper Pliocene.

ORTHOEVOLUTION

It is pretty clearly demonstrated that the *undulata* stock can be interpreted to have evolved along one particular line with respect to pattern, all forms tending to develop light spots and later a longitudinal light line in the upper lateral dark line. Whether this extensive parallelism was effected by strong survival value of this particular type of pattern, or by a trend of mutation already established before segregation of the four groups, is not readily evident, and we hold no opinion on the basis of evidence afforded by these lizards.

PROBLEMS

Numerous problems in the systematic arrangement of Mexican *Ameiva undulata* await solution. A few are listed below.

1. Of prime interest is the status of the group containing *u. gaigeae* and *u. hartwegi.* If intergrades actually do not occur between *u. stuarti* and either of them, serious consideration should be given to the recognition of a distinct species, *Ameiva hartwegi.* In such case *gaigeae* would undoubtedly be one race of *hartwegi,* but the allocation of *u. pulchra* would remain in doubt until further studies revealed the existence or absence of intergrades between the latter and *hartwegi.* It is assumed that all the territory between these several forms is suitable for their habitation; if this actually is the case the forms must either intergrade or overlap geographically.

2. Of equal interest for future study is the possibility of intergradation between *u. undulata* and *u. amphigramma*— forms which represent two different groups not now proved to intergrade.

3. The status of *u. thomasi* is worthy of further study. It may intergrade either with *u. amphigramma* or, more probably, with *u. stuarti.*

4. Of considerable interest for future work is whether *u. parva* intergrades with *u. amphigramma.* It seems probable.

5. More material is needed to check the validity and variation in *u. dextra* and *u. sinistra.*

6. The range and geographic variation in *u. stuarti* needs further study. At present most of the recorded data are based upon specimens from a single locality.

7. The color in life has been recorded for only one race, *u. amphigramma.* Detailed notes are much to be desired on live material. Undoubtedly color differences not now evident occur between a number of races. The ventral color, particularly of adult males, may prove to be of diagnostic value.

ACKNOWLEDGMENTS

We wish to express our appreciation for the loan of vital material by Miss Doris Cochran, Mrs. Helen T. Gaige, and Dr. E. H. Taylor; for the assistance of Dr. A. B. Leonard and Mr. Richard Spieler in gathering material together and in the taking of data upon it; for the expert assistance of Mr. Ray Maas who took the photographs; and for financial assistance afforded through the courtesy of Dr. Curt Stern.

KEY TO MEXICAN AMEIVA

1. Outer row of ventrals considerably smaller than the others.....*festiva edwardsii*
   Outer row of ventrals as large as the others..... 2
2. Preanal scales in two rows..... 3
   Preanal scales in one row or with no more than one posterior scale divided..... 9
3. Two rows of granules between third supraocular and superciliaries; third supraoculars generally completely separated from frontoparietals by granules.....*u. parva*
   A single row of granules between third supraoculars and superciliaries; third supraoculars in contact with frontoparietals anteriorly..... 4
4. Median gulars abruptly enlarged..... 6
   Median gulars little enlarged, gradually merging with lateral gulars..... 5
5. Upper lateral vertical light lines from axilla to groin 12 or more .....*u. gaigeae*
   Upper lateral vertical light lines from axilla to groin 11 or less .....*u. hartwegi*
6. Median gulars irregular or no more than 2 regular (87%); lamellae under 4th toe 28 or more; no upper lateral light stripe, although large spots take its place in adult males ..... *u. podarga*
   At least 3 median gulars regular (100% in all except *u. amphigramma*, with 87%); lamellae variable; upper lateral light stripe present or absent..... 7
7. Dorsolateral dark stripes present except in some large adults, in which the upper lateral light spots if present are much narrower than the spaces between them; lamellae on the 4th toe usually (88%) 27 or less.....*u. stuarti*
   No dorsolateral dark stripes; upper lateral light spots as wide as or wider than spaces between, or represented by a continuous upper lateral light stripe; lamellae variable 8
8. Upper lateral light spots or lines not contacting dorsolateral light area or line in adult males, separated by a narrow dark area; lateral gulars not or scarcely enlarged ..... *u. amphigramma*
   Upper lateral light spots merged with dorsolateral light line in adult males; lateral gulars markedly enlarged ..... *u. thomasi*
9. Last preanal scale generally (86%) divided; lateral markings showing little tendency to be arranged vertically; middorsal markings greatly reduced.....*u. dextra*
   Last preanal scale generally entire; lateral markings tending to be arranged vertically; middorsal markings well developed 10
10. Upper lateral light spots in adult males large, wider than intervening dark spaces; generally (95%) 5 or less rows of preanals.....*u. sinistra*
    Upper lateral light spots in adult males small, narrower than intervening dark spaces in all males; frequently (65%) 6 or more rows of preanals.....*u. undulata*

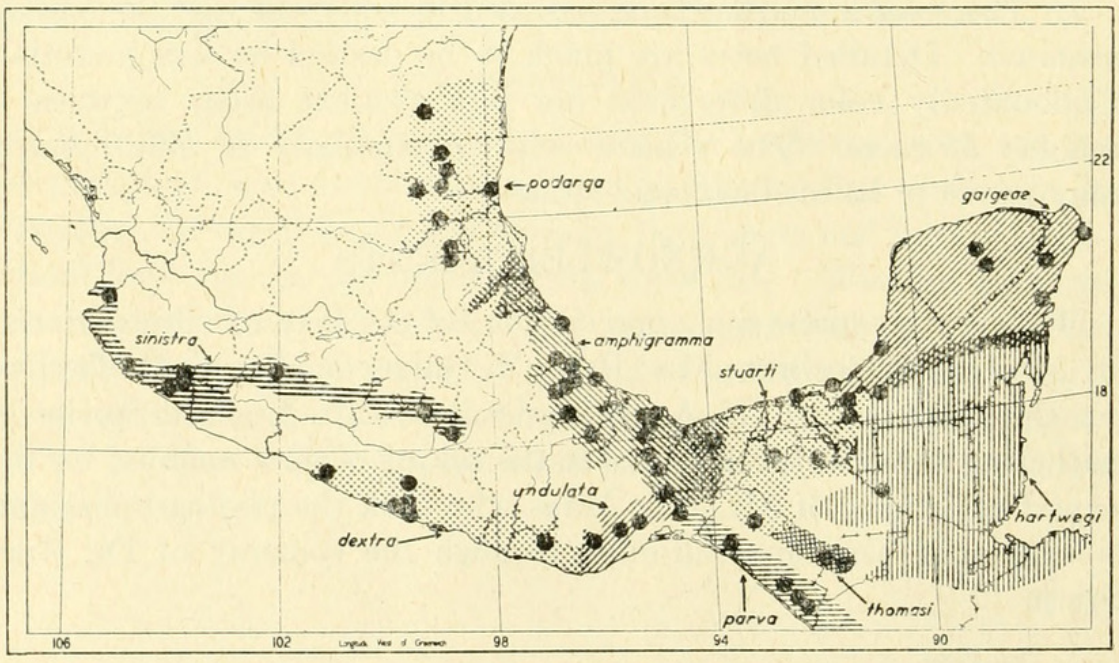

FIG. 7. Distribution of subspecies of *Ameiva undulata* in México.

ACCOUNTS OF SUBSPECIES

The arrangement of these accounts follows, as closely as linear sequence will permit, the apparent phylogenetic relationships of the various forms. As explained elsewhere, we regard the group containing *u. pulchra* as the most primitive of *A. undulata,* even though other members of the group are rather highly specialized. Since *u. pulchra* is not Mexican it is omitted, and the list accordingly begins with *u. hartwegi* and *u. gaigeae* respectively, the latter of which obviously is a derivative of *u. hartwegi* or an ancestor very much like it. *A. u. podarga* is perhaps the least modified of trans-Isthmian forms. In geographic and partly phylogenetic sequence three other forms follow: *u. amphigramma, u. thomasi,* and *u. stuarti.* Whether *u. parva* or the trans-Isthmian Pacific forms should follow is an orbitrary decision; *u. undulata* and *u. parva* are about equally specialized. In deference to the rather remarkable preanal change in the more northerly group, and to the advantage of placing *u. parva* near the other races with paired preanals, we follow with the southern race. It is fairly clear that of the remaining three forms *u. dextra* is the most generalized and *u. undulata* the most specialized.

Ameiva undulata hartwegi Smith

(Pl. 2, Fig. B)

Ameiva undulata hartwegi, Smith, 1940; 55 (type locality Chiapas, México, across the Río Usumacinta from Piedras Negras, Petén, Guatemala; type U. S. Nat. Mus. No. 108600).

When originally diagnosed this form was conceived to be more or less homogeneous, ranging throughout the Yucatán Peninsula and its base, including the Petén area of Guatemala. This interpretation was likewise held by Stuart (1942: 145). Both authors observed chiefly the uniformity of the character of the gular scales throughout this area, Stuart extending its range as far as Honduras. Since the character is so peculiar in the species *Ameiva undulata* it is not surprising lesser geographical variations received little attention. It is well known, however, that a very large percentage of wide-ranging species, whose ranges include the entire Yucatán Peninsula, have differentiated in such a way that a northern Yucatán race is distinguishable. Examination of specimens from northern and southern extremes revealed that differences occur in this form, as well as in many others.

Diagnosis. A. u. hartwegi as at present defined may be diagnosed as follows: gulars small and irregular, preanals in two rows; lam-

ellae on 4th toe 29 or more (100%), generally 31 or more (81.5%) femoral pores on both sides 39 or more (89.8%), upper lateral vertical light lines between axilla and groin 11 or less (98.2%). The last two characters differentiate this race from *u. gaigeae,* comparisons with which are given in Table 7.

Range. Atlantic slopes of México and Guatemala from the vicinity of the southeastern end of Laguna de Términos south and eastward across the base of the Yucatán Peninsula to northwestern Honduras.

TABLE 4. Variation in *A. u. hartwegi*

CHARACTER		Counts	Range	Average
Femoral pores, one side	♂♂	62	17–23	20.9
	♀♀	38	16–22	19.9
Femoral pores, total	♂♂	30	37–45	41.9
	♀♀	19	34–44	39.7
Lamellae on 4th toe		97	29–36	31.8
Upper lateral vertical light lines from axilla to groin		55	8–12	9.6

Locality records. We have examined 78 specimens from the type locality, and from Piedras Negras, Petén, Guatemala. We have taken data on only fifty of this series. We are aware of no other locality records for México.

Discussion. This is the largest of Mexican races of *Ameiva undulata,* reaching a maximum size of 138 mm. snout to vent in males, and 115 mm. in females. Variation in femoral pores, lamellae on fourth toe and upper lateral light lines are given in Table 4.

TABLE 5. Comparisons of *A. u. hartwegi* with *A. u. stuarti*

CHARACTER	*hartwegi*	*stuarti*
Femoral pores	18 or more 98%	17 or less 97.3%
Lamellae on 4th toe	29 or more 100%	28 or less 98.6%
Gulars	small, irregular	large, regular

Comparisons. The only forms in México with which *u. hartwegi* intergrades are *u. gaigeae* and possibly *u. stuarti.* Comparisons with the latter are given in Table 5, with the former in Table 7. The intergrades are discussed with the other species.

Ameiva undulata gaigeae subsp. nov.*

(Fig. 1C; Pl. 2C)

Holotype. An adult male, EHT-HMS No. 11927, from Progreso, Yucatán, collected by Hobart M. Smith, 1935.

Paratypes. Sixty-three, including 6 topotypes (EHT-HMS Nos. 11925-6, 11928-31), fifty-nine (EHT-HMS No. 11985, UMMZ Nos. 68215, 72934-72957, 80847-80860, 80861 (3), 80862 (5), 83289 (3), 80890 (5)) from Chichén Itzá, Yucatán; three (UMMZ No. 78586 [3]) from a locality five miles inland from Vigía, Quintana Roo; and two (UMMZ No. 78587[2]) from Ascención Bay, Yucatán.

Locality records. All specimens available have been included in the type series, except UMMZ Nos. 68216-68224, from Chichén Itzá, all juveniles; UMMZ No. 83535, from Ciudad del Carmen, Campeche; EHT-HMS No. 11942-11945, 13114, from Encarnación, Campeche (intergrades with *u. hartwegi*); and UMMZ No. 83945, from Cobá, Quintana Roo. The U. S. National Museum has specimens (not seen) from La Vega, Mujeres Island, and Tunkas, Yucatán. Gaige (1936:297) reports it from Champotón, Campeche.

Diagnosis. Related to *u. hartwegi,* having small, irregular gulars and preanals in two rows. Differs from that form in having 12 or more (89.5%) lateral vertical light spots between axilla and groin, and in having fewer femoral pores (in males, 19 or less on one side [61%], 40 or less on both sides [77.5%]; in females, 18 or less on one side [76%], 37 or less on both sides [82%]).

Description of type. Head scales typical of *Ameiva undulata.* Frontoparietals very narrowly in contact with second supraocular; 3 supraoculars, followed by a group of 3 enlarged granules; 2 frenoculars; an incomplete secondary row of small scales in addition to the primary between posterior chin shields and infralabials; central gulars irregular, small, one-half or one-third size of largest mesoptychial, about 2 or 3 times as large as adjacent lateral scales; mesoptychials relatively small, no larger than scales in anterior row of abdominals; 32 rows of ventrals; 6 rows of preanals, paired; femoral pores 17-18; lamellae on fourth toe 30-31.

Dorsal ground color dull, bluish slate; middorsum with small, irregular, dark spots posteriorly, none on neck or scapular region; dorsolateral dark stripes and dorsolateral light stripes completely

* Named for Mrs. Helen T. Gaige of the Museum of Zoölogy, University of Michigan, in recognition of her contributions to the knowledge of the Yucatán herpetofauna and to the guidance of many students whose good fortune it has been to be hers. It is a pleasure to associate her name in one genus with that of her closest professional colleagues, Drs. Norman Hartweg, Alexander Ruthven and L. C. Stuart.

absent; upper lateral dark area split into numerous transverse spots, separated from each other by 18 vertical light blue lines from axilla to groin, nearly or quite equal in width to the dark spots; lateral light line indicated by a series of small light spots, one at the ventral end of each of the vertical light lines previously mentioned; sides dimly barred, the lines for the most part tending to coincide with those in the upper lateral zone; hind legs with an ill-defined, open, dark reticulation and with small, scattered, light spots, especially on the shank.

Variation. The males resemble the type very closely, varying chiefly, so far as pattern is concerned, in the amount of spotting on

TABLE 6. Variation in *A. u. gaigeae*

CHARACTER		Counts	Range	Average
Femoral pores, one side	♂♂	80	15–22	19.1
	♀♀	58	15–21	17.6
Femoral pores, both sides	♂♂	40	31–43	38.1
	♀♀	28	31–42	35.3
Lamellae on 4th toe		132	26–36	30.4
Upper lateral vertical light lines from axilla to groin		57	9–18	13 1

the back. The number of vertical light lines in the upper lateral area also varies somewhat as indicated in Table 6. In all the upper lateral spots are clearly defined.

Females, at least in the young and half-grown specimens, possess fairly distinct dorsolateral light lines; the upper lateral dark area is split by dim light lines forming a pattern similar to that of the males, but much less distinct; the lateral light line is more clearly evident than in the males, although it still consists of spots and short lines; the sides below the level of the lateral lines are very feebly marked. On the whole, females are readily distinguishable from males by the emphasis in them of the longitudinal elements of the pattern.

The gulars vary somewhat in size and arrangement, but in very few specimens are any central gulars abruptly enlarged. In occasional specimens there is a tendency toward alignment of the central gulars in a single, median row, but the scales are no larger than in other specimens.

The largest male measures 125 mm. snout to vent; the largest female 107 mm.

Variation in femoral pores, lamellae on the 4th toe, and the number of upper lateral light lines is given in Table 6.

Comparisons. The present race is distinguished from the west coast forms except *u. parva,* by a double row of preanals, and from all others, save *u. hartwegi,* by the small, irregular gulars. It differs from *u. hartwegi* as shown in Table 7.

Intergrades between *u. hartwegi* and *u. gaigeae* are available from Encarnación, Campeche (EHT-HMS 11942-5, 13114). These five specimens are all large females measuring between 95 mm. and 108 mm., snout to vent. The gulars are completely irregular and rela-

TABLE 7. Comparisons of *A. u. gaigeae* and *A. u. hartwegi*

CHARACTER		*gaigeae*	*hartwegi*
Femoral pores, one side	♀ ♀	18 or less 75.9%	19 or more 92.1%
	♂ ♂	19 or less 61.2%	20 or more 90.3%
Femoral pores, both sides	♀ ♀	37 or less 82.1%	38 or more 89.5%
	♂ ♂	40 or less 77.5%	41 or more 73.3%
Upper lateral vertical light lines from axilla to groin		12 or more 89.5%	11 or less 98.2%

tively small; lamellae on the fourth toe vary from 29 to 32 (29, one; 30, four; 31, four; 32, one); femoral pores 15 to 19 (15, one; 16, one; 17, one; 18, three; 19, four); upper lateral light spots between axilla and groin 10 to 14 (10, two; 12, one; 13, one; 14, one).

These specimens cannot be referred to *u. stuarti,* nor do they more than slightly resemble it; in practically every respect they differ from that form. Therefore, we need consider only *u. hartwegi* and *u. gaigeae.* In pattern, one of the chief differential characters, they are intermediate, but perhaps nearer *u. gaigeae;* and in number of femoral pores they are fairly close to *u. gaigeae.* The large size is more typical of *u. hartwegi,* although the difference is slight; one specimen exceeds by 1 mm. the maximum known for typical *u. gaigeae.* For the present we prefer to allocate the population represented with *u. gaigeae.*

Range. Northern half of the Yucatán Peninsula, and southward to the island of Carmen along the extreme eastern coast. Intergrades with *u. hartwegi* occur at least east of Laguna del Carmen, and probably northward through the central part of the peninsula where the high forest meets the coastal scrub. Intergradation with *u. stuarti* probably occurs in areas near the eastern end of Laguna del Carmen.

Ameiva undulata podarga * subsp. nov.

(Figs. 1D, 2A)

Holotype. An adult male, EHT-HMS No. 14471, from 7 miles west of Victoria, Tamaulipas, collected by Hobart M. Smith and David H. Dunkle, 1934.

Paratypes. Fifteen, including 5 (EHT-HMS Nos. 14472-4, USNM Nos. 106141-2) from Hacienda La Clementina, near Forlón, Tamaulipas; 3 (EHT-HMS Nos. 11959-61) from Antiguo Morelos, Tamaulipas; 2 (UMMZ No. 88232 [2]) from Río Guayala, near Magiscatzin; 3 (EHT-HMS Nos. 11677-9) from near Ciudad Maiz, San Luis Potosí; one (EHT-HMS No. 11962) from near Valles, San Luis Potosí; and one (HMS No. 1597) from Huichihuayán, San Luis Potosí.

Diagnosis. Related to *u. amphigramma* and *u. stuarti* having paired preanals, abruptly enlarged gulars, and the last supraocular broadly in contact with median head scales and separated from the superciliaries by a single row of granules. Differs from *u. amphigramma* chiefly in the absence of the upper lateral light stripe and in reduction of spotting, but also in having completely irregular gulars or no more than two regular median scales (84.6%). Differs from *u. stuarti* in having irregular gulars, lamellae on the fourth toe twenty-eight or more (100%), presence of large upper lateral light spots in males, and in the absence of a dark median border on the dorsolateral light stripe.

Description of type. Head scales similar to the type of *u. dextra* except as follows: chin shields separated from posterior infralabials by a single row of small scales; central gulars enlarged, irregular, except for two broad scales in the median line; enlarged mesoptychials in two rows; 32 ventrals from gular fold to preanal region; five rows of preanals, paired; femoral pores 17-18; lamellae on fourth toe 29-29.

Snout to vent, 102 mm.; tail broken; hind leg, 77 mm.; foreleg, 36 mm.; snout to gular fold, 35.5 mm.; snout to anterior margin of ear, 24 mm.

Middorsum slate gray; very few small scattered dark spots on posterior part of back; dorsolateral light line dimly evident on neck, not elsewhere; below the level of the dorsolateral light line a series of large subquadrangular, light spots, separated from each other by narrow, dark brown bars, half as wide as the light spots; sides

* From Greek, swift-footed.

lighter brown, traversed by numerous, narrow vertical, broken or continuous, light streaks which extend from the belly almost or quite to the level of the upper lateral light spots; gular region bluish, belly darker.

TABLE 8. Variation in *A. u. podarga*

CHARACTER		Counts	Range	Average
Femoral pores, one side	♂♂	14	15–18	16.8
	♀♀	17	13–17	15.3
Lamellae on 4th toe		30	28–31	29.4
Rows of gulars		16	5–7	5.7

Variation. Six males are available, all adults except two juveniles, one measuring 48 mm. snout to vent, the other 36 mm. All specimens (save the smallest in which the upper lateral light spots are present but very dim) clearly show markings similar to those of the type, with no tendency whatever of the lateral light spots to fuse, forming a stripe. The spots are, in all, separated by dark bars at least half as wide as the light spots, usually wider. As in the type the middorsum is practically immaculate. The sides are dimly marked in all except the largest male (HMS 1597) which has a distinct, broken lateral light line as well as vertical, lateral light lines; in it also the dorsolateral light lines are distinct, while in the others they are very dim.

Females are very much like the males; the middorsal markings are somewhat better developed; the dorsolateral light stripes are somewhat clearer; the upper lateral light spots are absent in the young, but appear dimly in specimens measuring about 80 mm. or more, and in some specimens closely approach the condition in the males. The lateral light stripe is well developed in the young and is usually retained in the adults, but may disappear (1 specimen). Even to a greater extent than in the males the lateral light markings are reduced in number, size and distinctness.

The largest male measures 116 mm. snout to vent; the largest female 96 mm.

Variation in femoral pores and lamellae are given in Table 8. The central gulars are irregular in arrangement; in six specimens they are completely irregular, no two scales being alike and situated in the median line; in 5 specimens a maximum of two scales are medially situated, and in two specimens all the enlarged central gulars but one (in a total of five) are regularly arranged.

Comparisons. The race of *Ameiva undulata* nearest to *u. podarga* both geographically and, presumably, taxonomically is *u. amphigramma.* There are few differences between the two races except in gulars and pattern. The pattern differences are, however, very striking and include, as the most important, the development of the upper lateral light stripe. In *u. amphigramma* this stripe is, in males, either continuous (the usual condition) or broken into blotches, separated from each other by very narrow dark lines, considerably less than half the width of the blotches. This condition obtains in males of all sizes but increases in distinctness with age. Oddly enough in the females either a continuous or discontinuous upper lateral light stripe similar to that of the males only much dimmer, is developed in adult specimens; unlike the males, however, juvenile females do not show the stripe or spots.

TABLE 9. Comparisons of *A. u. podarga* with *A. u. amphigramma*

CHARACTER		*podarga*	*amphigramma*
Femoral pores, one side..	♂♂	average 16.8	average 17.6
	♀♀	15 or less 64.7%	16 or more 75.0%
Gulars (based on the largest 5 median scales)		irregular or no more than 2 regular 86.7%	regular or no more than 3 irregular 87.3%
Pattern	mottling	reduced	well developed
	upper lateral light stripe	absent or represented by spots less than twice width of intervening spaces	present or represented by spots over twice width of intervening spaces

In *u. podarga* the upper lateral light stripe is never continuous but is represented by large light blotches separated from each other by dark spaces at least half as wide as the light areas. As in *u. amphigramma* this pattern occurs in all males and in adult females with the same limitations.

In *u. amphigramma* the body and legs are rather strongly spotted; the markings are most distinct on the middorsum and, with the exception of adult males, on the legs. In *u. podarga* on the other hand, the back and legs are practically unicolor, and as described for both sexes, the sides have very little spotting.

There is some difference in the average number of femoral pores of these two races as indicated in Table 9, but the character is not of taxonomic value, except perhaps in females. Further data are

required on this point. There is also an apparent difference in the number of rows of sublabials between the posterior infralabials and the chin shields, although again the difference appears to be of little taxonomic value. In *u. podarga* eight specimens have only one row, five have an incomplete secondary row, while one has a short, complete secondary row.

The arrangement of the median gulars is a character of considerable importance in separating *u. podarga* and *u. amphigramma*. In the former 86.7 percent of the specimens have completely irregular or no more than two regular median scales (restricting to five the number of gulars considered); in *u. amphigramma* only 12.7 percent are of that character.

TABLE 10. Comparisons of *A. u. podarga* with *A. u. stuarti*

CHARACTER		*podarga*	*stuarti*
Lamellae on 4th toe.....	.....	28 or more 100%	27 or less 87.5%
Gulars..... (Based on the largest 5 median scales)	arrangement	irregular or no more than 2 regular 86.7%	regular or no more than 3 irregular 100%
Pattern.....	upper lateral light spots	present, broad	absent or narrow
	dorsolateral dark stripe	always absent	present except in some adults
	dorsolateral light stripe	faint or absent	well developed

Comparisons of *u. podarga* with *u. stuarti* are given in Table 10. The differences as cited in the table are self-explanatory.

Range. Aside from the localities represented by the paratypes, we have records of specimens from the following: *San Luis Potosí:* Tamazunchale (EHT-HMS); *Tamaulipas:* Alta Mira (USNM); Victoria (USNM). The range appears to extend along the Atlantic coast from the latitude of Victoria, Tamaulipas, southward into northern Veracruz. The exact area of intergradation with *u. amphigramma* is unknown at present.

Ameiva undulata amphigramma Smith and Laufe

(Pl. 1, Figs. C, D)

Ameiva undulata amphigramma Smith and Laufe, 1945: (type locality San Andrés Tuxtla, Veracruz; type EHT-HMS No. 11983)

Diagnosis. A member of the *undulata* group of *Ameiva*, closely related to *u. stuarti* and *u. podarga;* preanals in two rows; median gulars rather abruptly enlarged, arranged generally in a median row

of 5 to 8 scales. Differs from *u. podarga* in having (1) usually (87%) no more than 2 of the 5 largest gulars divided or irregular, (2) usually (75%) 16 or more femoral pores in females; (3) considerable mottling on the back, and (4) an upper lateral light stripe which is never or rarely broken into light spots less than twice as wide as the dark intervening spaces. Differs from *u. stuarti* to some extent in number of lamellae under the fourth toe (55% with 28 or more), and in having fewer gulars of which more are irregular, but chiefly in pattern: (1) Adult males possess a conspicuous, broad, longitudinal, light, upper lateral stripe which may be broken into large spots not less than twice the width of intervening spaces; this character is discernible although indistinct in adult females, and is generally at least feebly evident in young males; (2) there is no continuous dorsolateral dark stripe, typically, although females may have it broken into spots or reduced in length or width; and (3) the dorsolateral light stripes completely disappear in adult males. Differs from *u. stuarti* and *u. gaigeae*, the only other races with two rows of preanals, chiefly in the possession of the upper lateral light stripe, abruptly enlarged gulars, and a smaller maximum size.

Range. Northern Veracruz (exact area uncertain, perhaps in the vicinity of Laguna Tamiahua, where it intergrades with *u. podarga*, southward at relatively low elevation (below about 4,000 ft.) through most of Veracruz to the Isthmus of Tehuantepec, there intergrading with *u. stuarti;* westward into valleys extending into extreme eastern Oaxaca and probably northeastern Puebla.

Localities. We have now examined a total of 104 specimens of this race. Localities represented by specimens examined include: *Veracruz:* Atoyac, Boca del Río, Cuatotolapam, Lake Catemaco, Jalapa, Orizaba, Potrero Viejo, Puente Nacional, Rodriguez Clara, San Andrés Tuxtla, Tierra Colorada; *Oaxaca:* Cosolapa, Matías Romero. Literature records include Achotal, Hda. del Hobo, Jicaltepec, Mirador, Obispo, Otopa, Perez and Presidio in *Veracruz,* and Agua Fría, *Oaxaca.* The U. S. National Museum has specimens (not seen) from Tuxtepec, *Oaxaca,* San Rafael, *Veracruz,* and La Venta, *Tabasco.*

Discussion. Two additional topotypes (EHT-HMS Nos. 15136-7), from San Andrés Tuxtla, Veracruz, have come to hand since the form was described. One is a juvenile male measuring 54 mm. snout to vent; it shows a dark dorsolateral stripe typical of *u. stuarti* and never present in more northern *u. amphigramma;* the lamellae on the fourth toe, however, number 30-32, as is characteristic of *u. amphigramma.*

The other specimen, an adult male, has large upper lateral spots separated from each other by vertical dark bars generally less than half the width of the light areas; its lamellae on the fourth toe number 29-29. In both these characters it resembles *u. amphigramma*.

TABLE 11. Variation in *A. u. amphigramma*

CHARACTER		Counts	Range	Average
Femoral pores, one side	♂♂	88	14–23	17.6
	♀♀	92	14–20	16.4
Lamellae on 4th toe		187	24–33	27.7
Rows of gulars		95	5–8	5.9

While the type and two paratypes, all adult males, from this same locality have the typical pattern of *u. amphigramma*, they do have fewer lamellae (27-28, 27-?, 27-28) than most *u. amphigramma*, but like most (88%) *u. stuarti*.

These five specimens as a group definitely appear to represent an intergrading population between these two races. The most outstanding feature of *u. amphigramma*, the pattern, is apparently typical of the population.

It is unfortunate that the type locality lies within an area of intergradation, but obviously the intergrades approach the northern race, which we defined and intended to name, much more closely than the southern (*u. stuarti*).

Thirty-three specimens from very near the type locality, at Cuatotalapam (UMMZ 41422-41442, 41444-41454) and Lake Catemaco (UMMZ 41443), Veracruz, agree well with the types in pattern. There are 16 males, of which all but one are of large or moderate size. The smallest (43 mm. snout to vent) shows only faint evidence of a dorsolateral dark band (in the neck region), and has a faint upper lateral light stripe. In the other males, nine have continuous upper lateral light stripes, and five have the stripes broken by a few very narrow dark lines. In one the upper lateral light spots are small and separated from each other by dark spaces as broad as the light spots, or broader. Of the seventeen females, nine show evidence of an upper lateral light stripe; all these are 67 mm. or more in snout-vent length. The other females, which lack any evidence of an upper lateral light stripe, are smaller, 70 mm. or less in snout-vent length. Two show a fairly distinct dorsolateral dark stripe, but no other specimens, male or female, possess them,

even though one female measures only 38 mm. snout to vent. Many females do, however, possess numerous dark spots which may represent the dorsolateral dark stripe, since they border the dorsolateral light stripe medially. This lot of specimens approaches *u. stuarti* in some characters, as in the occasional presence of a dorsolateral dark stripe and in a reduced number of fourth toe lamellae. There is no question whatever, on the other hand, that they represent a population essentially like *u. amphigramma,* and but little diluted by *u. stuarti.* An excellent description of the color in life of this series is given by Ruthven (1912: 320-322), who calls attention to the distinct upper lateral light stripe in males.

The two juvenile paratypes from Matias Romero, Oaxaca, have the low lamellar count (24-24, 27-27) of *u. stuarti,* although in other respects they are typical of *u. amphigramma.* This may indicate an intergradient character for this population.

Four specimens (EHT-HMS 11955-8) from Rodriguez Clara, Veracruz, some 70 kilometers south of the type locality, probably can also be considered as intergrades. The single adult is a female with relatively large upper lateral light spots, which are to be sure narrower than the dark spaces between them, but on the other hand broader than in typical *u. stuarti.* The other three specimens are juveniles with the typical paradorsolateral dark stripes of *u. stuarti.* The lamellae on the fourth toe are intermediate between the expected counts: Two have 29-29, 29-?, as in the northern race, while the others have 26-26, 27-27 as in the southern. In view of the pattern of the female, the intermediate nature of the lamellar counts, and the expected pattern of adult males as based on specimens known from the nearby type locality, we allocate the specimens, tentatively, to *u. amphigramma* although the population represented is undoubtedly an intergrading one.

Forty-four other specimens from central Veracruz at Matacabresto (UMMZ No. 88647), the vicinity of Potrero Viejo (UMMZ Nos. 85407 (5), 85408 (13), 85409 (4), 88648-9, 89325, EHT-HMS No. 19582), and Tierra Colorada (EHT-HMS Nos. 11968-76, 11978-81), have been examined since the original description was written. They are essentially similar to those previously recorded and described from this area.

The largest specimens examined measure 101 mm. in females, 105 mm. in males.

The extreme southeastern record for the race is one now to be considered dubious. It consists of a single specimen (USNM

TABLE 12. Comparisons of *A. u. amphigramma* with *A. u. stuarti*

CHARACTER		*amphigramma*	*stuarti*
Lamellae on 4th toe.....	.....	28 or more 54.6%	27 or less 87.5%
Pattern.....	dorsolateral dark stripe	absent	well developed
	upper lateral light stripe	present or represented by spots over twice width of intervening spaces	absent or spots very narrow
Gulars.....	No. of rows	6 or less 76.5%	7 or more 56.9%

117350) recorded by Smith (1944) from La Venta, fifteen miles southeast of Tonalá, Tabasco. This specimen, not reëxamined, is said to have 21-21 femoral pores and 30-32 lamellae. Such counts do occur in *u. amphigramma*, but not in *u. stuarti* to our knowledge, in which 18 femoral pores and 30 lamellae are the recorded maximum. We accordingly refer it tentatively to the former race.

Comparisons. Variation and comparisons with *u. stuarti* are given in Tables 11 and 12.

*Ameiva undulata thomasi** subsp. nov.

(Pl. 1, Fig. A)

Holotype. Adult male, EHT-HMS No. 15327, from La Libertad, Chiapas, near Río Cuilco where it crosses the Guatemalan border; collected by Henry D. Thomas.

Paratypes. Eight, including seven topotypes (EHT-HMS Nos. 15323-15326, 15328-15330) and one labeled "Chiapas" and probably from the same locality (EHT-HMS 15374); all collected by Henry D. Thomas.

Diagnosis. A member of the *undulata* group possessing paired preanals, abruptly enlarged gulars, lacking a secondary row of superciliary granules, and with supraoculars broadly contacting the frontoparietals. The adult male pattern differs from that of all other forms of *A. undulata*, in having the upper lateral light spots merged with the dorsolateral light line to form a continuous light band, the dorsal border of which is regular, the ventral irregular and giving rise to the vertical light bars. Possibly differs from *u. stuarti*, the most closely related form, in having more numerous lamellae under the fourth toe (75.5% with more 28 or more). Differs from all other races in that the extreme lateral gulars are enlarged.

* Named for its collector, Henry D. Thomas, who also was a field companion of the senior author in México during the summer of 1936.

Description of type. Scutellation typical except as below: Three supraoculars, the posterior two separated from the superciliaries by a single row of granules; central gulars normal with a regular median row of abruptly enlarged scales; lateral gulars enlarged; largest mesoptychial narrower but longer than largest median gular, approximately the same area; 32 ventrals from gular fold to preanal region; six rows of preanals each consisting of paired scales; femoral pores 20-20; lamellae under fourth toe 29-29.

Snout to vent, 82 mm.; tail regenerated; hind leg, 57 mm.; foreleg, 29 mm.; snout to gular fold, 29 mm.; snout to anterior margin of ear, 21 mm.

Middorsum bluish-gray, flecked with very small, lateral dark spots which tend to form two rows, beginning on rump and disappearing at the level of the shoulders; dorsolateral dark stripe faintly evident, bordered laterally by a broad continuous light line formed by the merging of the dorsolateral light line with the upper lateral light spots between the axilla and groin; anterior to the level of the shoulder the dorsolateral light line continues, normal in width, to the posterodorsal border of the eye; the ventral border of the broad light line is irregular, giving rise to short, light vertical bars which are half as broad as the intervening dark spaces or less; ventrally the vertical light lines meet the lateral light line which is occasionally broken. Ventrum discolored.

Variation. Males show some variation in the dorsolateral light band. In one specimen the pattern is completely typical; in the other two, the upper lateral light spots have merged with the dorsolateral light line, which is very narrowly broken at irregular intervals. In all three the dorsal mottling closely resembles that of the type, and the upper vertical light lines are one-half as broad as the intervening dark spaces or less.

In the five available females, in all but one the lateral light spots are greatly reduced and only faintly evident. In these four specimens, there appears to be no tendency whatever of these spots to merge with the dorsolateral light line which is completely distinct. In the other specimens the upper lateral light spots are well developed anteriorly and medially, laterally fusing with each other but narrowly separated from the dorsolateral line; posteriorly they are reduced as in the other females. In all specimens the dorsolateral dark line is faintly evident and the lateral line is broken into a series of small, rounded or ovoid light spots. In all but one specimen, in which it is well-developed posteriorly, the dorsal mottling resembles that of the males.

TABLE 13. Variation in *A. u. thomasi*

NUMBER	Sex	Femoral pores	Lamellae under 4th toe
15323	♀	16–18	26–?
15324	♀	16–17	27–29
15325	♂	16–17	28–29
15326	♀	14–16	30–30
15327	♂	20–20	29–29
15328	♀	16–18	25–26
15329	♀	16–16	29–29
15330	♂	17–19	29–30
15374	♂	18–19	28–29
Average	♂, ♀	17.2	28.4

The largest male measures 92 mm. snout to vent, the largest female 78 mm.

Variation in femoral pores and lamellar counts are given in Table 13. The central gulars are abruptly enlarged and arranged in a single median row in all the specimens. In only one male one of the median gulars is split. All the specimens possess the enlarged lateral gulars.

Comparisons. The present race is distinguishable from *u. dextra*, *u. sinistra*, and *u. undulata* in its possession of a complete double row of preanal scales; from *u. parva* in lacking an accessory row of granules between the supraoculars and superciliaries; from *u. hartwegi* and *u. gaigeae* in possessing abruptly enlarged median gulars; and from *u. podarga* in possessing regular median gulars. From *u. amphigramma* and *u. stuarti*, its closest relatives, and all other Mexican forms of *Ameiva undulata*, *u. thomasi* differs in having the upper lateral light spots merged with the dorsolateral light lines to form a continuous broad light line. Possibly the present race also differs from *u. stuarti* in having more lamellae under the 4th toe (28 or more 76.5%). Another character of considerable importance separating *u. stuarti* and *u. thomasi* is the nature of the dorsolateral dark stripes. In the former they are well developed, only very faintly evident in the latter. Although in most scutellation characters *u. thomasi* resembles *u. amphigramma*, the difference in the make-up of the broad light line coupled with the geographic isolation of the two forms from each other warrants segregation. Comparisons with *u. stuarti* are given in Table 14.

Range. The race probably occurs in all the dry, hot valleys of the upper tributaries of the Río Grijalva in the interior of Chiapas and of western central Guatemala.

TABLE 14. Comparisons of *A. u. thomasi* with *A. u. stuarti*

CHARACTER		*thomasi*	*stuarti*
Lamellae under 4th toe,		28 or more 76.5%	27 or less 87.5%
Pattern	dorsolateral dark stripes	reduced	well developed
	upper lateral light spots in males	present, fused with dorsolateral light line	absent

Localities. We have seen specimens only from the type locality, but Stuart (1943: 21) records a specimen, referred to *A. u. stuarti*, from Nentón, Guatemala, which undoubtedly belongs to this race. We know of no other localities.

Ameiva undulata stuarti Smith

(Fig. 1B; Pl. 1, Fig. B)

Ameiva undulata stuarti Smith, 1940: 55-56 (type locality Palenque, Chiapas; type U. S. Nat. Mus. No. 108601).

Diagnosis. The salient features of this race include the small size, the paired preanals, the single row of abruptly enlarged, numerous (6-8) median gulars, the reduced number of lamellae on the fourth toe (22-30, average 25.5, 27 or less 87.5%) and of femoral pores (13-18, average 15.5, 17 or less 97.3%), and the presence of well-defined dorsolateral dark stripes (except in some adults). There are no upper lateral light stripes or spots.

Range. Atlantic slopes of México from the middle of the Isthmus of Tehuantepec eastward in the lowlands to the southern borders of Laguna de Términos and to Tenosique, Tabasco; southward up the valley of the Río Grijalva at least as far as Tuxtla Gutiérrez, Chiapas.

Localities. We have examined 107 specimens from Palenque and San Ricardo, Chiapas; Tenosique, Tabasco; Balchacaj and Tres Brazos, Campeche. We have taken data on most of this series. Records for other localities include Frontera and Teapa, Tabasco (USNM).

Discussion. Variation in femoral pores, lamellae on the fourth toe, and in the central gulars is given in Table 15.

TABLE 15. Variation in *A. u. stuarti*

CHARACTER		Counts	Range	Average
Femoral pores, one side		73	13–18	15.5
Lamellae on 4th toe		72	22–30	25.5
Gulars	No. of rows	58	6–8	6.7
	No. of scales regular	58	3–8	6.1

This race possibly intergrades with *u. hartwegi* and *u. gaigeae* toward the west (see Table 5). Intergrades with *u. amphigramma* are discussed with that form (Table 12).

In spite of the close proximity of localities from which *u. hartwegi* and *u. stuarti* are known, we have seen no incontrovertible intergrades between the two. If intergradation does occur, it must be restricted to a very narrow belt. There appears to be a sharp difference in ecological preference, *u. stuarti* preferring the mixed scrub-savanna coastal areas, while *u. hartwegi* prefers the dense, high, inland forests. The specimens from Campeche do approach *u. hartwegi,* since the dorsolateral dark stripes are somewhat variable; otherwise the specimens are typical. Eastward, southeastward, and probably southward also, it meets *u. hartwegi* in the dense inland forests and foothills. Toward the west it meets *u. amphigramma* near the isthmus of Tehuantepec which presumably is occupied by intergrades. The specimens from San Ricardo indicate the extension of the race up to the valley of the Río Grijalva into the lower portion of the Chiapas plateau. No trend whatever toward *u. parva,* which occurs not far from San Ricardo across the Sierra at Tonalá, is evident in these specimens, which include an adult male and female, and a juvenile male. There is no visible approach toward the characters of *u. thomasi,* although intergrades may well occur.

Ameiva undulata parva Barbour and Noble

(Fig. 1A; Pl. 2, Fig. A)

Ameiva undulata parva Barbour and Noble, 1915: 476-477 (type locality Guatemala, here restricted to Mazatenango; type MCZ No. 5831).

Diagnosis. This race, possibly the most ornate of Mexican forms, is characterized by having paired preanals, a median row of about 6 or 7 abruptly enlarged gulars, generally a complete or incomplete accessory row of granules between supraoculars and superciliaries, generally the third supraocular separated from median head scales by its full length; femoral pores rather few, averaging 15.5 in fe-

males, 17.2 in males; lamellae on 4th toe average 29.1; dorsolateral light lines relatively well defined in all specimens, even adult males; upper lateral dark zone broken in adults (both sexes) by vertical light lines which tend to reach the dorsolateral light line and expand somewhat *below* its level at the position of the upper lateral light line (as most other *undulata*); young lined, lacking a dorsolateral dark line. The dorsal spotting is rather variable, but tends to be prominent. The tail is brightly marked below with blue, in adults.

Range. Pacific slopes from the Isthmus of Tehuantepec in Oaxaca, near Niltepec, southeastward to Costa Rica.

Localities. We have examined 377 specimens from the following localities: *Oaxaca:* near Niltepec (EHT-HMS Nos. 27505-27506). *Chiapas:* Tapachula (EHT-HMS Nos. 11917-11924, 15130-15135); Tonalá (HMS Nos. 18728-18787, 18990-19010); La Esperanza (near Acacoyaqua) (HMS Nos. 13485-13516, 13591-13615, 13699-13730, 13877, 13937-13994, 14056-14085, 14098-14099, 14141-14155, 14228-14272, 14407-14413, 14425, 15626, 17424-17425); Cruz de Piedra, Las Nubes, Salto de Agua, Finca Juárez, and Colonia Soconusco, all in the vicinity of La Esperanza (HMS Nos. 14506, 14592-14596, 15276, 15940-15941, 16655-16659, 17398). Data have been taken only on the Niltepec intergrades and twenty-five specimens of each sex from Tapachula (all specimens) and the vicinity of La Esperanza. Tabulated data excludes the intergrades. The only other locality known to us is Huehuetán, *Chiapas,* represented by two specimens in the U. S. National Museum.

Discussion. The secondary row of small scales between the supraoculars and superciliaries, a character which has been accepted as the chief peculiarity of *u. parva,* is subject to some variation. In only six specimens (of 49) are there two complete rows (*i. e.,* to the posterolateral border of the first supraocular); in others the secondary row varies in length from complete absence nearly to the extreme condition of full length. For convenience in tabulation we arbitrarily allocated every specimen to one of five conditions: absence of secondary row (0), secondary row extending to a point at one-half the length of the third supraocular (½), the full length of the third supraocular (1), to a point at one-half the length of the second supraocular (1½), and the full length of the second supraocular (2). Variation in length of the row of small scales between the supraoculars and median head scales, another character which has been considered of considerable significance in *u. parva,* was similarly tabulated. Results of these tabulations as well as

femoral pore and lamellar counts are given in Table 16. They verify the value of the supraocular characters in defining *u. parva.*

TABLE 16. Variation in *A. u. parva*

CHARACTER		Counts	Range	Average
Femoral pores, one side	♂♂	49	15–21	17.2*
	♀♀	49	13–19	15.5
Lamellae on 4th toe		97	26–33	29.1
Granules between supraoculars and superciliaries†		49	0–2†	1
Granules between supraoculars and median head scales†		50	½–2†	1

* Slevin (1942: 460) records the counts of 572 thighs; his range is 11 to 21, two greater than that recorded here. The average, sexes combined, was 16.2, extremely close to our average, 16.35.

† See text for explanation.

The race is of about the same size as most forms of *undulata,* the largest male measuring 109 mm. snout to vent, the largest female 95 mm. It is markedly smaller than *u. undulata* or *u. hartwegi,* and larger than *u. stuarti.*

Two specimens from "between Niltepec and La Gloria," Oaxaca (EHT-HMS 27505-6), while similar to *u. parva* in most respects, resemble *u. undulata* in others and are accordingly, we think, to be considered intergrades. One (No. 27506) is a juvenile female measuring 52 mm. snout to vent. There are four rows of preanals, the last of which consists of paired scales; there are 15-15 femoral pores; the median mesoptychial is enlarged; and the dorsolateral light spots are large and somewhat wider than the dark inner spaces. There is an incomplete second row of granules between the posterior supraoculars and the superciliaries. Likewise the last supraocular is almost completely separated from the median head scales and two or three small scales are intercalated between the other supraoculars and the median head scales. Except for the character of the preanals this specimen resembles *u. parva.*

The other specimen is an adult male measuring 91 mm. snout to vent. There are five rows of preanals, all the median scales of which are paired; there are 18-18 femoral pores; the median mesoptychials are small; the dorsolateral light spots are large and conspicuous, subequal in width to the spaces between; and the dorsal spotting is greatly reduced, nearly absent. There is a very incomplete secondary row of granules consisting of only 3-4 scales, between the supraoculars and the superciliaries; and the last supraocular is broadly in contact with the frontoparietal. The character of

the preanals, the upper lateral spotting, and the additional granules between supraoculars and superciliaries clearly are typical of *u. parva;* while the absence of dorsal spotting, the small median mesoptychials, and very broad contact of the last supraocular with the median head scales are typical of adult males of *u. undulata.*

Both specimens clearly approach *u. parva* more closely than *u. undulata* although certain characters parallel those of the latter race. In considering them as representatives of an intergrading population we emphasize that they are nearly typical *u. parva.* This locality is the nearest to the range of typical *u. undulata* from which specimens of *u. parva* have been taken.

The exact locality is open to some doubt, yet is of considerable importance since Niltepec is on the Pacific slopes at an elevation of about 200 ft.; while La Gloria is on the Atlantic at about 1,500 ft. They are separated from each other in a straight line by the Sierra Madre, which there reaches an elevation of somewhat more than 4,500 ft. We assume in referring these specimens to *u. parva* that they were taken on the Pacific slopes, for *u. stuarti* is to be expected on the Atlantic slopes. We do not believe that these specimens involve *u. stuarti* or *u. amphigrammma* (which at this point are completely isolated by the Sierra Madre from the Pacific coast), since none of the unique characters and few of the general characters are possessed. The brown bands bordering the dorsolateral light stripes medially, which are universally present in *u. stuarti,* are here absent, One specimen has a nearly complete row of median preanals, a condition never occurring in *u stuarti* or any other Atlantic coast form; and the large upper lateral light spots are never found in *u. stuarti.*

Comparisons. This race is unique in the possession of a secondary row of small scales between the supraoculars and superciliaries and in the considerable extent of the row of small scales forward between the third supraocular and median head scales.

*Ameiva undulata dextra** subsp. nov.

(Fig. 2C)

Holotype. Adult male, EHT-HMS No. 11966, near Rincón, Guerrero, collected by Edward H. Taylor and Hobart M. Smith, 1932.

Paratypes. Thirteen, including three topotypes (EHT-HMS Nos. 11964-5, 11967); one from Organos, Guerrero (EHT-HMS No.

* In reference to the occurrence of this form on the right (southern) watershed of the Río Balsas.

11963); one from El Treinta, Guerrero (EHT-HMS No. 11683); three from Acapulco, Guerrero (EHT-HMS Nos. 11680-2); and five from 8 kilometers east of Coyuca, Guerrero (HMS 5234-8). All those in the EHT-HMS collection were secured by the same collectors and at the same time as the type; those in the U. S. National Museum (HMS) were collected February 7, 1939, by Hobart M. and Rozella Smith.

Diagnosis. Related to *u. undulata* and *u. sinistra,* having essentially a single median row of preanals, and a median row of enlarged gulars. Differs from *u. undulata* in pore counts and in preanal rows: in males femoral pores generally 19 or more on one side (73%), 38 or more on both sides (86%); in females femoral pores usually 17 or more on one side (62.5%), 34 or more on both sides (50%); 5 rows of preanals or less (100%). Differs from *u. undulata* and *u. sinistra* in having the last preanal divided generally (85.8%) and in pattern; lateral markings showing little tendency to be arranged vertically; upper lateral light spots in males tending to form a continuous broad band; and back little mottled.

Description of type. Head scales typical; frontonasal separated from both rostral and frontal, broadly in contact laterally with postseminasal; four supraoculars, anterior in contact with frontal and narrowly with loreal, posterior very small; one row of small scales between three posterior supraoculars and superciliaries; third supraocular very broadly in contact with frontoparietal, latter very narrowly in contact with second supraocular; only three small scales extending forward from posterior corner of supraorbital disc adjacent to the parietal and interparietal, completely separating the last supraocular from these scales; interparietal single, half as large as parietals; two rows of large flat scales posterior to parietals; three suboculars; one frenocular; one preocular; five supralabials to below middle of eye, two following; five infralabials; one undivided postmental; five chinshields on either side, separated from posterior three infralabials by two rows of smaller scales; central gulars enlarged, very irregular;† enlarged mesoptychials larger than median gulars, extending laterally nearly to level of arm insertion.

Dorsals subgranular, subconical, slightly mucronate; ventrals in eight longitudinal rows, thirty from gular fold to preanal region; five rows of preanals, each of the anterior four with an enlarged median scale, posterior row consisting of enlarged paired scales;

† This is an anomaly; in others the gulars are enlarged and in a regular median row.

largest preanal slightly smaller than largest mesoptychial; femoral pores 20-21; lamellae under fourth toe 28-29.

Two rows of radials, anterior smaller; two rows of humerals, posterior smaller; one row of postbrachials; three rows of tibials, posterior much the smallest, anterior somewhat the largest.

Snout to vent, 84 mm.; tail, 205 mm.; hind leg, 62 mm.; foreleg, 32 mm.; snout to gular fold, 30 mm.; snout to anterior margin of ear, 22 mm.

Ground color dull yellowish-brown; dorsolateral light stripe very faintly evident, broken over most of its length into small spots; a narrow, irregularly serrate-edged, dark brown band bordering this laterally; lateral to this a broader, light blue, upper lateral stripe beginning on shoulder and disappearing at base of tail, with irregular edges, bordered laterally by a dark brown area similar to that which borders it medially; lateral ground color merging with the lateral dark border of the upper lateral light stripe; numerous small, light bluish spots on sides, tending more or less to be arranged in vertical series; middorsum uniform; no distinct markings on head; limbs with irregular, very feeble light spots above. Venter discolored.

TABLE 17. Variation in *A. u. dextra*

CHARACTER		Counts	Range	Average
Femoral pores, one side	♂	15	15–21	19.1
	♀	9	15–19	16.6
Femoral pores, total	♂	7	31–42*	38.6
	♀	4	30–35	32.5
Lamellae on 4th toe	♂	14	27–31	29.1
	♀	6	28–31	28.3
Row of preanals		13	4-5	4.4

* One aberrant specimen of the 7 available has a total count of 31 (15-16); all others have 38 or more.

Variation. Four adult males including the type are available; in two of these the upper lateral light stripes are continuous, while in the other two they are broken into large, more or less rectangular, or irregular spots separated from each other by short vertical dark brown streaks of varying width. The other four males, varying in snout-vent length from 48 to 60 mm., are similar to the adults except that the lateral pattern is not so clearly evident; the youngest is so discolored that no pattern can be discerned. One shows a developing continuous upper lateral light stripe similar to that of the type; in the other two that stripe is broken and there is a tendency

in one to form fairly distinct vertical bars on the sides. Thus in three of the seven males in which this character is evident the upper lateral light stripe is continuous. The dorsolateral light stripes are very poorly defined, even in the smaller specimen.

Females possess a pattern essentially the same as that of the males, with the following differences. The dorsolateral light stripes are well defined throughout life, although more distinct in the shoulder region; their median borders are ill-defined, the lateral border sharply delimited. There is a distinct upper lateral dark zone between the dorsolateral and lateral light lines. In two specimens vertical bars are dimly evident in this zone, while in the others no markings are evident. The lateral light line is broken into a series of small, rounded or elongate light spots. The sides below this may either be uniform brownish or provided with small light blue spots arranged irregularly or tending to form vertical series.

The largest male measures 113 mm. snout to vent, the largest female 80 mm.

The median scales in the posterior row of preanals are paired in twelve specimens (excluding the type), single in two. In two specimens the median gulars are irregular, in one all except two are subdivided, while in all others there is a single regular median row. Variation in femoral pore, preanal and lamellar counts is indicated in Table 17.

TABLE 18. Comparisons of *A. u. dextra* and *A. u. undulata*

CHARACTERS		*dextra*	*undulata*
Femoral pores... ♂♂	one side only	19 or more 73%	18 or less 81%
	total	38 or more 86%	37 or less 90%
♀♀	one side only	17 or more 62.5%	16 or less 76.7%
	total	34 or more 50%	33 or less 84.5%
Preanals.....	number of rows	5 or less 100%	6 or more 65%
	5th (or last if less than 5)	divided 85.8%	entire 89.2%
Pattern.....	lateral vertical bands	poorly developed, particularly in females	well developed, young and adult males and females
	middorsal markings	greatly reduced or absent	well developed
	continuous upper lateral light band in males	present in 43% (3 out of 7 specimens), represented by large, narrowly separated light blotches in the remainder (57%)	never present or represented by light spots as large as intervening dark spaces 100%

Comparisons. The present race is easily distinguishable from all the Atlantic coast forms of *Ameiva undulata,* as well as *u. parva,* by the essentially single row of preanals (in spite of the subdivision of the posterior scale), which character links it with *u. undulata* and and *u. sinistra.* Comparisons with the former are given in Table 18, and with the latter in Table 20.

Discussion. Four unique characters, within the group with a median row of preanals, define *u. dextra*: the divided posterior preanal, the absence of middorsal markings, the reduction of the lateral bars, and the presence of a continuous upper lateral light stripe. In all these respects *u. undulata* and *u. sinistra* are alike. The last possibly is not of sufficiently frequent occurrence to be a reliable indicator in itself, since less than fifty percent of known *u. dextra* males possess the stripe; yet in conjunction with the other characters it is of considerable importance since it is unknown in either of the adjacent races, and in fact is known elsewhere in *Ameiva undulata* only in *u. amphigramma.* In the latter race the stripe is of regular occurrence. Whether the partial parallelism of these two races in this character is coincidental or indicative of close relationship is not certain; we believe the former. In *u. undulata* the broad upper lateral band is usually not evident at all, even as isolated spots, while in *u. sinistra* large light spots are present in its position. Longitudinal extension of the spots would result in creation of a line typical of *u. dextra.* In the latter all adult males which lack the continuous line do at least have the large spots in its position.

It is unfortunate that so few *u. dextra* have been available. We believe that a larger series will reveal a more appreciable difference from *u. undulata,* particularly of females in femoral pore counts, than is apparent now (*cf.* Table 18). The number of rows of preanals is markedly different in the two races, but the extent of overlap is considerable; further data on *u. dextra* are required.

The nature of the dorsal and lateral markings is evaluated with some difficulty since there is no sharp distinction, and, moreover, an actual overlap of extremes in the two races. Vertical bars are, nevertheless, a conspicuous feature of *u. undulata,* even in the young, which usually (i. e., in most races of *undulata*) have no transverse markings. The usual condition obtains in *u. dextra,* few specimens showing marked transverse bars. The distinction between the two races in this character is most clearly evident in females; there is little postnatal ontogenetic change in specimens of this sex in *u. dextra.*

The dorsal spotting is not extensive in any specimen of *u. dextra,* although it is prominent in most *u. undulata,* with the exception of adult males.

Range. Southern slopes of the Sierra Madre del Sur of Guerrero and perhaps extreme western Oaxaca, below about 4,000 ft. above sea level. In addition to the types records are available of specimens from Juquila, *Oaxaca,* Chilpancingo (USNM), Cocoyul (Gadow), and Los Cajones (Gadow), *Guerrero.*

*Ameiva undulata sinistra** subsp. nov.

Holotype. Adult male, EHT-HMS No. 11908, from Manzanillo, Colima, collected by Hobart M. Smith, 1935.

Paratypes. Sixty, including 8 from Quesería, Colima (EHT-HMS Nos. 11906-7, 11946-8, 14499, 15121; UMMZ No. 80109); 20 from Hacienda Paso del Río, Colima (EHT-HMS Nos. 11909-16, 11949-51, 14500, 15122-9; UMMZ Nos. 80110, 80111 [3], 80112 [5], 80115 [3], 80120); Salvador (UMMZ No. 80116); Pascuales (UMMZ Nos. 80113 [3], 80114); and Periquillo (UMMZ Nos. 80117 [11], 80118 [2], 80119).

Diagnosis. Related to *u. dextra* and *u. undulata,* having a single row of median preanals (posterior sometimes divided, 37.7%), and a single median row of enlarged gulars. Differs from *u. dextra* in usually having all the median preanals entire (or at least the fifth is entire if there are more than five preanals), and in pattern: lateral vertical bars present in males, taking the form of a tigroid pattern (dark bars relatively widely separated); well developed middorsal markings; and no continuous upper lateral light band in males (although there is a tendency to form large light spots). Differs from *u. undulata* in pore counts, preanals and in pattern: in males femoral pores generally 19 or more on one side (54.4%), thirty-seven or more on both sides (63%); in females femoral pores usually seventeen or more on one side (81.2%), thirty-four or more on both sides (72.8%); five rows of preanals or less (95%); and in the presence of large upper lateral light spots in adult males.

Description of type. Similar to the type of *u. dextra* except as follows: Three supraoculars; interparietal asymmetrically split longitudinally; central gular scales normal with a median row of enlarged scales; largest mesoptychial subequal in size to median gulars; thirty-two ventrals from gular fold to preanal region; four

* In reference to the occurrence of this form on the left (northern) watershed of the Río Balsas.

rows of preanals, each of the anterior two rows consisting of a pair of scales, third row with one very large scale, larger than any mesoptychial or gular, fourth row with three scales, the central one twice as large as the others and approximately three-fifths the size of the preceding scale; femoral pores 18-19; lamellae under fourth toe 30-30.

Snout to vent, 90 mm.; tail 228 mm.; hind leg, 71 mm.; foreleg, 34 mm.; snout to gular fold, 33 mm.; snout to anterior margin of ear, 23.5 mm.

Middorsum bluish gray-brown, varied by small dark brown spots, largest posteriorly, beginning on rump and becoming gradually smaller anteriorly and disappearing at the level of the shoulders; these spots tend to form two rows; dorsolateral light stripe very dimly evident, bordered laterally by a continuous narrow dark brown band which varies in intensity in pigmentation; lateral to this is a longitudinal series of large, subquadrangular, bluish-white spots, each connected ventrally with one or more wavy, vertical, light blue lines which extend to the sides of the belly; the upper lateral light spots are separated from each other by dark bars one-half or one-third as wide as the light spots; these dark bars expand in width on the sides of the body.

Variation. Males show little variation in pattern. The smallest available (72 mm. snout to vent) possesses the typical adult pattern. The most conspicuous variation is in the size of the upper lateral light spots; in four specimens they are not or scarcely wider than the intervening dark spots, while in all the other twenty-four specimens the light spots are enlarged much as in the type.

TABLE 19. Variation in *A. u. sinistra*

CHARACTERS		Counts	Range	Average
Femoral pores, one side	♂♂	57	17–22	18.8
	♀♀	64	15–22*	17.5
Femoral pores, total	♂♂	27	34–43	37.7
	♀♀	33	31–42	35.1
Lamellae on 4th toe	♂♂	57	27–32	29.7
	♀♀	54	26–32	29.4
Rows of preanals		61	3–6	4.6

* Only one aberrant specimen has 22 pores on one side. All other specimens have 20 or less.

In females the dorsal mottling is somewhat better developed than in males; the dorsolateral light lines are somewhat more distinct; the upper lateral light spots are not or poorly developed; and the

lateral light line, which is not or scarcely evident in males, is strongly indicated by a series of elongate spots; below this irregular, narrow, wavy, vertical light streaks may or may not be present.

The largest male measures 109 mm. snout to vent, the largest female 95 mm.

Variation in femoral pores, preanal and lamellar counts is given in Table 19. The central gulars are irregular in three specimens, but in all others they are arranged in a single, regular median row in which no more than one scale is divided, if any.

Comparisons. Like *u. undulata* and *u. dextra* the present race is distinguishable from all other forms of *Ameiva undulata* by the presence of a single median row of preanals. Comparisons with *u. undulata* and *u. dextra* are presented in the accompanying tables (Tables 20 and 21). The pattern characters which distinguish *u. sinistra* from *u. dextra* and *u. undulata* are perhaps the most important; in comparison with the former, the tigroid pattern of males is very distinctive, and equally striking in comparison with *u. undulata* are the large upper lateral light spots. Obviously the three races are very close, but since there are some very significant differences (which by themselves would not meet the minimum require-

TABLE 20. Comparisons of *A. u. sinistra* with *A. u. dextra*

CHARACTERS		*sinistra*	*dextra*
Preanals	5th (or last if less than 5)	entire 62.3%	divided 85.8%
Pattern	lateral vertical bands	well developed in adult males	poorly developed, particularly in ♀ ♀
	middorsal markings	well developed	greatly reduced or absent
	continuous upper lateral light band in ♂ ♂	never present	present in 43% (3 out of 7 specimens)

ment of seventy percent recognition) in scutellation, in addition to those in pattern, we feel that the sum total of peculiarities characterize a population recognizably as well as genetically distinct. *A. u. sinistra* is physiographically isolated from other forms of *undulata,* being separated by the arid Balsas Basin from *u. dextra* and *u. undulata,* and by the plateau from other forms of the Atlantic coast. The isolation makes reasonable the divergence of *u. sinistra* and *u. dextra,* which probably would not remain even as feebly distinct as they are at present if no barrier existed between them.

Range. Pacific coastal drainage from the arid Balsas Basin at

TABLE 21. Comparisons of *A. u. sinistra* with *A. u. undulata*

CHARACTER		*sinistra*	*undulata*
Femoral pores... ♂♂	one side only	19 or more 54.4%	18 or less 81%
	total	37 or more 63.0%	36 or less 75%
♀♀	one side only	17 or more 81.2%	16 or less 76.2%
	total	34 or more 72.8%	33 or less 84.5%
Preanals.....	number of rows	5 or less 95.0%	6 or more 65%
Pattern.....	upper lateral light spots in adult males	large, wider than intervening spaces 83.3%	small, narrower than intervening spaces in all males 100%

the border of Guerrero and Michoacán northwestward at least to Jalisco, and perhaps farther; the northern drainage of the Río Balsas, at lower elevations and in humid localities, from Michoacán to Puebla. It is completely isolated from *u. dextra,* its closest relative both geographically and taxonomically, by the extremely arid valley of Río Balsas. Aside from the 61 in the type series, specimens have been recorded from Tenacatita and Tenacatita Bay, *Jalisco;* Colima, *Colima;* Uruapan, *Michoacán;* and Chiautla, *Puebla.* The U. S. National Museum has specimens (not examined) from Ixtapa, *Jalisco,* and Puente de Ixtla, *Morelos.* All of the specimens from the southern part of the range of *u. sinistra* are of special interest; their allocation with this race is tentative.

Ameiva undulata undulata (Wiegmann)

(Fig. 2B)

Cnemidophorus undulatus Wiegmann, 1834: 27 (type locality, México by inference; restricted to Tehuantepec by Smith 1940: 56).

Diagnosis. A member of the *undulata* group of *Ameiva,* with usually one row of preanals (89%), a median row of abruptly enlarged gulars, one row of granules between supraoculars and superciliaries, third supraocular generally at least partly in contact with median head scales. Most closely similar to *u. dextra* and *u. sinistra,* differing from them in the following: reduced number of femoral pores, greater number of rows of preanals, lack of division of the last preanal (from *u. dextra* only), presence of tigroid lateral marks, presence of well-developed middorsal markings (from *u. dextra* only), and reduction of the size of the upper lateral light spots.

Range. The Pacific slopes of the Isthmus of Tehuantepec in Oaxaca, as far west as Puerto Angel and eastward about to Niltepec.

Localities. A series of thirty-seven specimens has been examined from the following localities, all in Oaxaca: El Limón (USNM No. 18383); Palmar (USNM Nos. 18543-6, 185438); Tres Cruces (USNM Nos. 12052-7, 12392-5, 12499-12508, 16278-87, 18541-2). In addition, two intergrades with *u. dextra* are available as follows: one (EHT-HMS No. 27516) is from San Felipe Lachillo, Oaxaca; and the other (EHT-HMS No. 27523) is from Finca Mirador, between San Felipe Lachillo and San Juan Guivini, Oaxaca. Records for localities other than those cited above are as follows: Cafetal Concordia (USNM), Juchitán (USNM), Puerto Angel (USNM), Totontepec (USNM), Tehuantepec (USNM), and Ranchería La Manga (UMMZ), all in *Oaxaca.* Of particular importance are those from Cafetal Concordia and Puerto Angel, which probably are intergrades with *u. dextra,* as indicated by the existence of intergrades nearby at San Felipe Lachillo; they may well approach *u. dextra* more closely than *u. undulata,* however, and be referable to the former race.

Coloration. The salient features of the pattern in males are as follows: young with numerous middorsal dark spots decreasing in size and number anteriorly; in adults these spots disappear completely or nearly so; dorsolateral light stripes not evident except feebly in juveniles; upper lateral dark stripe broken by narrow vertical light streaks narrower than, or not more than subequal to the dark spaces between; even in the youngest specimens the dark band is as described for the adults; sides with irregular light markings or with narrow vertical light lines which frequently are fused with the light streaks in the upper lateral zone, forming a rather bold, barred pattern of alternating broad dark bands and narrow light streaks. Throats suffused with orange.

There appears to be less sexual dimorphism in this race than in any other in México in dorsal pattern. The middorsal spotting is more prominent in the females and does not disappear in the adults.

TABLE 22. Variation in *A. u. undulata*

CHARACTERS		Counts	Range	Average
Femoral pores, one side	♂♂	42	14–20	17.4
	♀♀	26	13–18	15.5
Femoral pores, total	♂♂	20	29–29	35.
	♀♀	13	27–35	31.
Rows of preanals		37	4–7	5.8

The sides, however, are marked much as in the males, although perhaps more dimly. In females the throat is not marked with orange.

Scutellation. There is a strong tendency for the gulars to be arranged in a single median row. The median preanals are arranged in a single row, with the exception of the posterior scale which is frequently divided (52%). Hartweg and Oliver (1937:7) record that there is a single row of median, enlarged, preanal scales . . . in . . 91.5 percent of their specimens (47). The discrepancy between their percentage and ours can be attributed to the difficulty of determining which is the last row of preanals. Preceding the anus is one row of small scales varying greatly in size, sometimes nearly equalling the other preanals. They vary more in disposition than the others, as indicated by our counts. To eliminate the variation caused by consideration of the small posterior row we have arbitrarily selected the 5th row from the abdominals as the critical one, disregarding the form of the following rows. Thus the fifth (or the last if less than five) median preanal is entire in 33 out of our 37 specimens (89.2%).

Our largest male slightly exceeds Hartweg and Oliver's (1937:7) figure, measuring 116 mm. snout to vent. Their maximum measurement for females (95 mm.) remains the record.

Variation in the number of femoral pores and preanal rows is presented in Table 22.

Intergradation. The specimens from near San Felipe Lachillo combine certain characters of *u. undulata* and *u. dextra.* They resemble *u. dextra* in number of femoral pores (20-21 male, 16-18 female). The female (No. EHT-HMS 27523) has only four rows of preanals, and in the male the posterior two preanals are paired. However, they resemble *u. undulata* since in the female the preanals are undivided, and in the male there are six rows. The pattern also resembles that of *u. undulata;* the sides in both are strongly barred with wide, dark bands, and the middorsal area is strongly spotted. We regard these specimens as approaching *u. undulata* more closely than *u. dextra.*

Ameiva festiva edwardsii Bocourt

Ameiva edwardsii Bocourt, 1873: 1-2 (type locality Izabal and Santa-María de Panzos near Río Polochic, Guatemala; cotypes in Mus. Hist. Nat. Paris).

Diagnosis. Most closely related to *f. festiva* but differing from that race in having the most posterior sublabial scale divided into three scales which form a rough triangle. Differs from *A. undulata* in having the outer row of ventrals considerable smaller than the

others; in possessing fewer enlarged median gulars; in having one extremely enlarged median preanal; and in possessing two rows of distal tibials.

Range. Atlantic foothills from southern México (Tabasco) through Honduras, in heavy forests.

Locality records. We have examined 49 specimens from the following localities: Piedras Negras, Petén, Guatemala; Palenque, Chiapas, and from Chiapas just across the border from Piedras Negras. The only other locality record for this race in México is Ixtacomitán, Chiapas (Dugès, 1894).

Discussion. The original diagnostic characters proposed by Bocourt (1873) were proven by Stuart (1943) to be fallible. However, Stuart was able to diagnose the race on the character of the posterior sublabial.

Of the 42 USNM specimens we have examined, in only one is the posterior sublabial entire (one side). In five specimens it is divided into four scales, and in another five it is divided into two. Variation in femoral pores and lamellae under the fourth toe is given in Table 23.

TABLE 23. Variation in *A. festiva edwardsii*

CHARACTER		Counts	Range	Average
Lamellae under 4th toe		69	23–33	29.4
Femoral pores	♀ ♀	40	19–23	20.25
	♂ ♂	34	19–22	20.6

The species differs so remarkably from *undulata* that the relationship cannot be close. There are several rows of small scales between the posterior part of the frontoparietals and the supraoculars; the gulars are extremely large; there is but one row of enlarged mesoptychials; the distal preantebrachials are in one row; there is but one row of prebrachials; there are but two rows of large tibials; the femorals are large and fewer; the preanals extremely large and not grading into the much smaller adjacent scales; the ventrals in the lateral row are small; the postantebrachials are smaller; and there are various other peculiarities, less easily described.

There is surprisingly little dimorphism in dorsal and lateral pattern. In both sexes the juveniles are dark brown with a conspicuous, broad, light blue middorsal stripe extending from the rostral to the rump, where it fades. The edges of the stripe from the shoulder

region posteriorly are wavy. A fine dorsolateral light stripe extends from the head in line with the superciliaries to the tail; it is discontinuous usually, broken into numerous short lines. A discontinuous lateral light line extends from the upper postocular region above the tympanum to the upper edge of the groin. In the shoulder and axillary regions a number of vertical light blue bars extend from the level of the forelimb to the lateral light stripe.

This pattern remains constant throughout life except for the middorsal light band, which gradually becomes fainter until it disappears in specimens measuring about 95 mm. snout to vent. The dark color originally occupying all the area between the dorsolateral light lines and the middorsal stripe decreases in extent and forms a row of dark spots on either side, each spot marking the approximate position of an indentation into the middorsal stripe. The spots remain as long as the middorsal stripe is evident, but finally disappear. The ground color between the dorsolateral light stripes is then light brown. The color remains dark between the dorsolateral and lateral light lines, but the sides below the latter become lighter, like the middorsum.

Males are bluish below and no doubt in life are strikingly different from females in the entire ventral color, but the preserved material examined is so discolored that no accurate description of differences in ventral color can be given.

Males appear to have wider heads and more slender bodies than females.

SUMMARY

1. Ten forms of *Ameiva undulata*, six of which are new, and one form of *Ameiva festiva* occur in Mexico:

a. *Ameiva undulata hartwegi* Smith
b. *Ameiva undulata gaigeae subsp. nov.*
c. *Ameiva undulata podarga subsp. nov.*
d. *Ameiva undulata amphigramma* Smith and Laufe
e. *Ameiva undulata stuarti* Smith
f. *Ameiva undulata thomasi subsp. nov.*
g. *Ameiva undulata parva* Barbour and Noble
h. *Ameiva undulata dextra subsp. nov.*
i. *Ameiva undulata sinistra subsp. nov.*
j. *Ameiva undulata undulata* (Wiegmann)
k. *Ameiva festiva edwardsii* Bocourt

2. Characters of primary importance in differentiating subspecies in *Ameiva undulata* are: (1) size and arrangement of the median gular scales, (2) arrangement of the preanals, and (3) separation of the third supraocular from the median head scales and, by two rows of granules, from the superciliary scales.

3. Characters of secondary importance are: (1) pattern, (2) number of lamellae under the 4th toes, (3) number of femoral pores, (4) the arrangement of the gulars, (5) the size of the lateral gulars, and (6) the arrangement of the preanals.

4. A tentative phylogeny of the four subspecific sections of *Ameiva undulata* is suggested.

5. The Matthew concept of peripheral dispersal of primitive forms is upheld insofar as it may be applied to a comparison of the end products of several lines of derivatives from common ancestors, but it is not applicable to evolution in single lines of derivatives, in which peripheral specialization is the rule.

6. Differentiation of all races of *Ameiva undulata* appears to have been accompanied by isolation, either *in situ* or by migration. The rate of differentiation appears to be the same in either case and is correlated chiefly with time.

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PLATE I

A. *A. u. thomasi,* EHT-HMS No. 13330. La Libertad. Chiapas.
B. *A. u. stuarti,* HMS No. 8798, Tenosique, Tabasco.
C. *A. u. amphigramma,* male, EHT-HMS No. 11983, Tierra Colorada, Veracruz.
D. *A. u. amphigramma,* female, EHT-HMS No. 11971, Tierra Colorada, Veracruz.

PLATE I

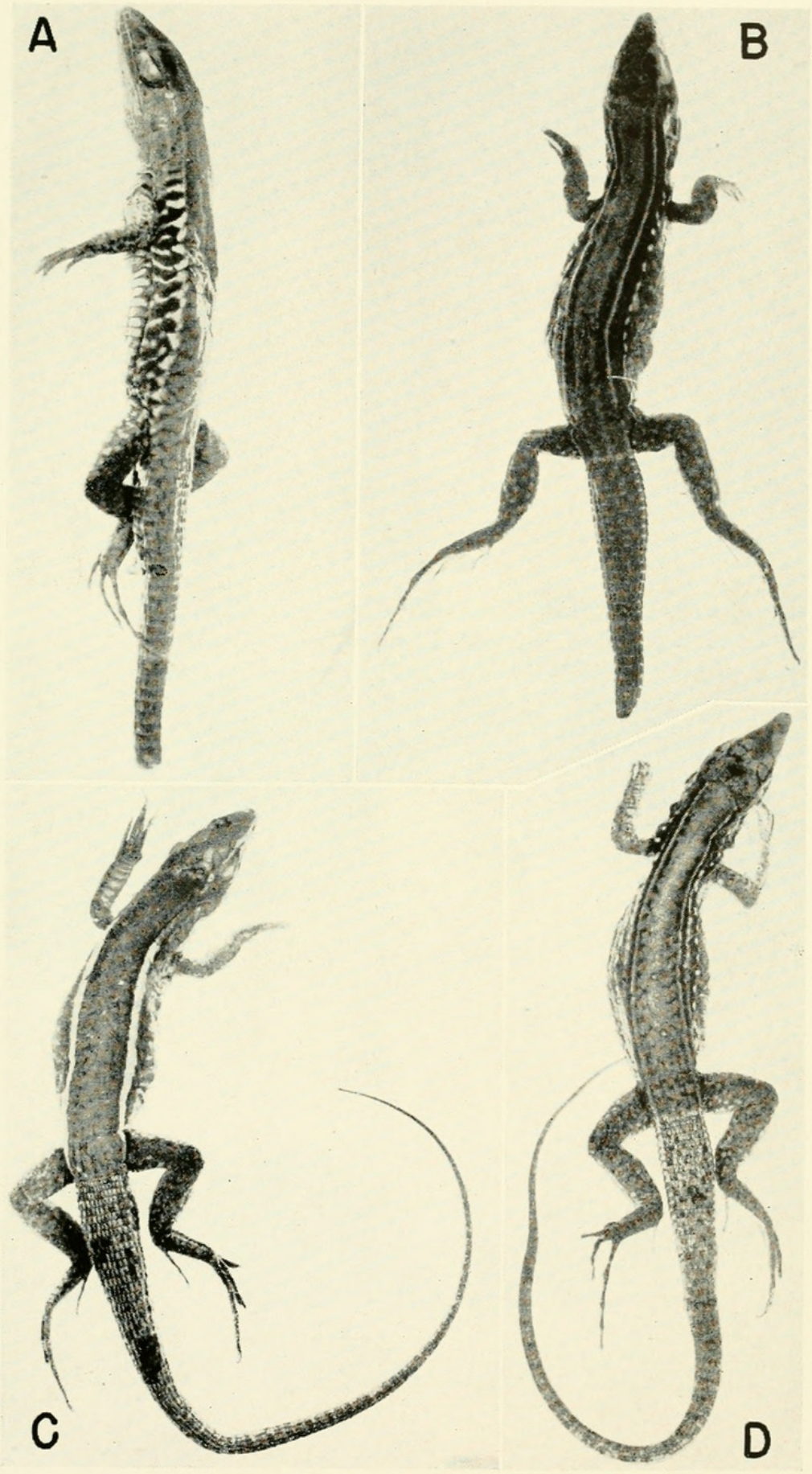

PLATE II

A. *A. u. parva,* EHT-HMS No. 11921, Tapachula, Chiapas.
B. *A. u. hartwegi,* HMS No. 7801, Piedras Negras, Guatemala.
C. *A. u. gaigeae,* EHT-HMS No. 11927, Progreso, Yucatán.

PLATE II