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GEOGRAPHIC VARIATION IN *RHINEURA FLORIDANA* (REPTILIA: AMPHISBAENIDAE)

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GEOGRAPHIC VARIATION IN *RHINEURA FLORIDANA* (REPTILIA: AMPHISBAENIDAE)

GEORGE R. ZUG[1]

SYNOPSIS: Examination of 11 characters in *Rhineura floridana* reveals no sexual dimorphism and a geographic pattern of variation in only 6 characters: Lateral head scales, supralabials, infralabials, body annuli, caudal annuli having dorsal granular segments, and segments around the midbody. Two populations are identified but not separated nomenclaturally, one on the Lake Wales ridge, the other occupying the remainder of north-central Florida. It is suggested that other Florida scrub or sandhill associated reptiles such as *Ophisaurus compressus, Neoseps reynoldsi, Eumeces egregius, Sceloporus woodi, Stilosoma extenuatum,* and *Tantilla relicta* share a history of isolation and differentiation similar to that proposed for *R. floridana.*

INTRODUCTION

The herpetofauna of peninsular Florida contains a relatively high frequency of endemics that are generally thought to be the result of ecological changes associated with the Pleistocene eustatic sea level fluctuations. Several levels of endemism are recognized: subspecific, specific, and generic (Neill, 1957); these levels are partly correlated with the dispersal abilities of the different faunal elements and the survival of the mainland populations. Of particular interest is the fact that the three monotypic endemic squamate genera (*Neoseps, Rhineura,* and *Stilosoma*) are fossorial and thus would be expected to have relatively low rates of dispersal.

Of the three, *Rhineura* has the largest geographic range and greatest ecological tolerance. *Neoseps reynoldsi* is found only in the marginal areas of rosemary scrub and in the longleaf pine-turkey oak habitat of the central Florida highlands (Telford, 1959; Myers and Telford, 1965). *Stilosoma extenuatum* appears to be restricted to high pine associations in the northern half of peninsular Florida (Highton, 1956). In contrast *R. floridana* occupies the northern two-thirds of the peninsula (Fig. 1) and is found in a variety of mesic and xeric habitats, scrub, sand-hill, flatwood, hammocks, (Neill, 1951).

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[1] The author is a graduate student at the University of Michigan. His current research emphasizes functional anatomy of turtles. Manuscript submitted 3 September 1967.—ED.

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Highton (1956) and Telford (1959) have shown that the distributions and variations of *Stilosoma* and *Neoseps* are positively correlated with marine terraces. Sea level fluctuation must have affected the distribution and variation of other organisms as well. This paper examines the variation of certain morphometric and meristic characters of *R. floridana* to determine its extent, type, and geographic pattern and, if possible, the geologic period of isolation in which it appeared.

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TAXONOMY AND DISTRIBUTION

The Florida worm lizard was described by S. F. Baird in March 1859 as *Lepidosternon floridanum*; the holotype was collected at Micanopy, Alachua County, Florida, by J. B. Barratt. In June 1861 E. D. Cope proposed on the basis of additional material that this amphisbaenid was generically distinct from *Lepidosternon* and erected for it the genus *Rhineura*, in which it has remained ever since.

As shown by museum specimens and literature references, the geographic range of *R. floridana* (Fig. 1) occupies the northern two-thirds of the Florida peninusla except for the area east of the Kissimmee drainage system. Its absence there may represent inadequate collecting, but should be considered real until its presence is confirmed unquestionably. The northernmost locality is Lake City, Columbia County, and the southernmost is the Archbold Biological Station, Highlands County. Burt's (1937) record of a Desoto County specimen is actually from Highlands County, collected before Desoto county was partitioned. A number of records need verification. One specimen (MCZ 4655) reportedly collected in "Georgia" is not improbable, as Lake City is only 30 miles south of the Georgia line, but the record needs confirming. Telford (1959) reports *Rhineura* occurring on the east coast of Florida "as far south as Miami," but unfortunately pro-

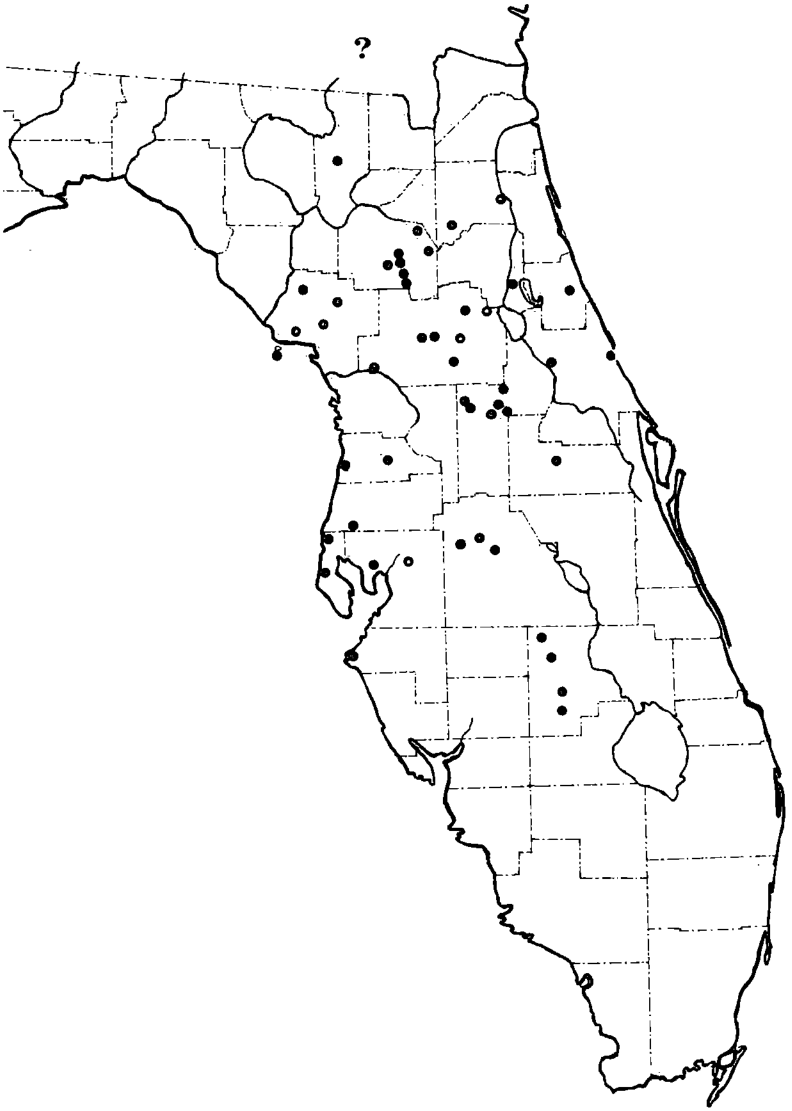


Figure 1. Present distribution of *Rhineura floridana* based on museum specimens (solid circles) and literature records (open circles). The question mark represents an unconfirmed Georgia locality.

vides no positive evidence for the statement. Wilfred Neill (pers. comm., 1963) suggested that *R. floridana* occurs as far south as Immokalee, Collier County, but I have been unable to locate any specimens from this region.

CHARACTER DESCRIPTIONS AND ANALYSES

The characters used in this study are those of scutellation, snout-vent length, and tail length. The scale characters are divided into two

Table 1. COMPARISON OF MALE AND FEMALE *Rhineura floridana*

			Number	Range	Mean X	Standard Deviation	Coefficient of Variance	t value	F value
ANNULI	Body	♂	10	245-256	251.7	3.77	1.5	2.04	1.68
		♀	10	244-254	248.6	2.91	1.2		
	Total Cloacal	♂	10	6-10	7.9	1.20	15.1	1.06	1.44
		♀	10	6-10	8.5	1.43	16.9		
	Caudal	♂	10	16-17	16.7	0.48	2.9	2.48	1.30
		♀	10	16-17	16.2	0.13	0.8		
	Granular	♂	9	12-13	12.4	0.52	4.2	2.42	0
		♀	10	12	12.0	0.00	0		
	Segments around Midbody	♂	10	27-32	29.2	1.31	4.5	1.91	1.10
		♀	10	28-32	30.3	1.25	4.1		
	Total lateral head scales	♂	10	19-29	24.9	3.12	12.5	1.44	1.24
		♀	10	19-29	23.0	2.79	12.1		
	SV/TL	♂	10	13.70-16.14	15.4	0.71	4.6	1.47	1.44
		♀	10	14.00-16.67	15.8	0.85	5.4		

groups, those associated with body annuli and those of the head region. These are described below in detail and their variation analyzed, but only those characters showing geographic variation are discussed fully. In most cases I have followed the procedures and terminology used by Gans and Alexander (1962) for Antillean amphisbaenids except for their head scale terminology, which is unsuitable for *R. floridana*. Instead Smith's (1946) terminology erected specifically for *R. floridana* is the main framework used, though I define the loreals, oculars, and temporals somewhat differently than Smith does.

SEXUAL DIMORPHISM

A sample of 20 *R. floridana* from Gainesville was used to determine the extent of sexual dimorphism. Sex was determined by dissection, and seven characters were compared between the female and male samples (Table 1). The method by which these characters were recorded is discussed below. Comparisons by the t-test shows no significant difference between the means of the sexes in any character at the 0.01 level. The variability of the two sexes is also similar. Thus in these characters *Rhineura* shows no sexual dimorphism.

HEAD SCUTELLATION

The head scales can be divided into four series: dorsal, lateral, labial, and genial. Anteriorly to posteriorly the dorsal series (Fig. 2A) is comprised of a large frontonasal, a small prefrontal, a large pentagonal frontal, and a pair of parietal scales. The frontonasal covers the snout and extends onto the ventral surface; the parietals are usually borded posteriorly by the first body annulus, although in some specimens a wedge of temporal scales extends upward between the parietals and the first body annulus. Variation in the dorsal series includes both the fusion and fragmentation of scales. The fusion may include all members of the series or any fraction thereof. In some instances fusion appears to be a result of injury, for the texture of the scales is different. New scales seem to be formed by the development of a new suture plane in one of the regular members of the dorsal series. As no pattern or regularity could be determined for this variation, no method was devised for recording it.

The lateral series of scales (Fig. 2C) is subdivided into a single anterior nasal, an anterior loreal group, a central ocular group, and a posterior temporal group. This series of scales is extremely variable, making it necessary to delineate boundaries and landmarks. As the anterior most scale of the series is perforated by the external naris,

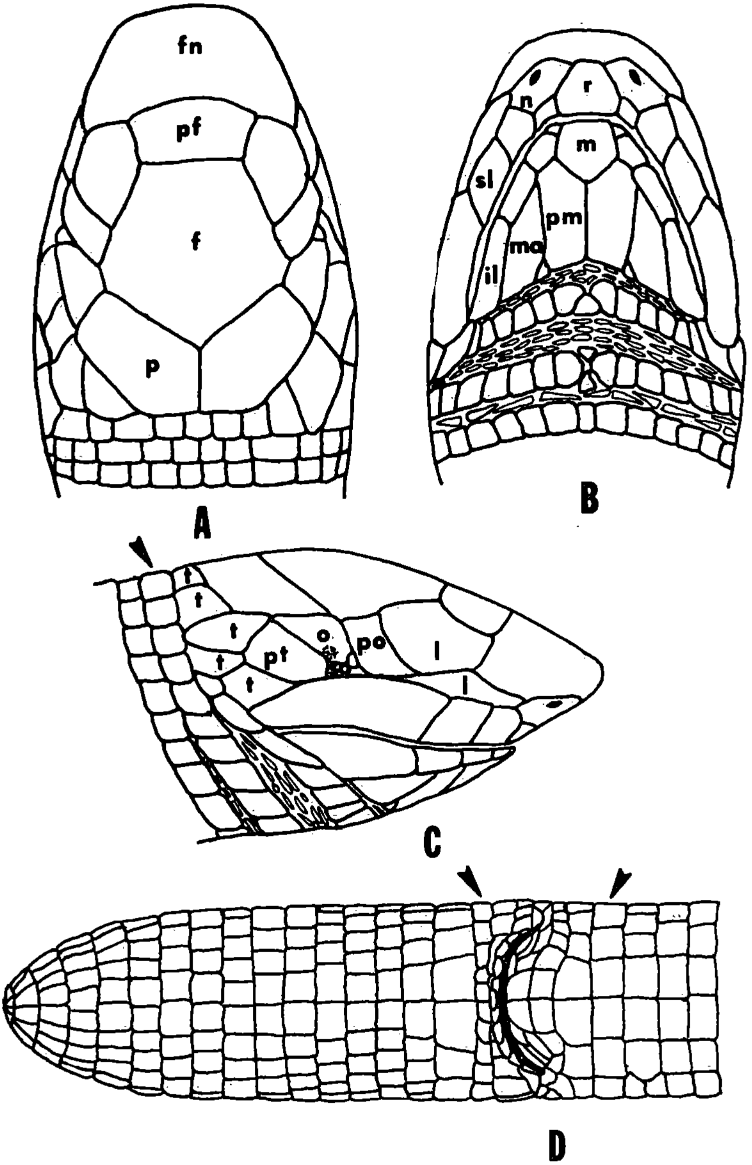


Figure 2. Scutellation of the head and tail of *Rhineura floridana*. A, dorsal view of head; B, ventral view of head; C, lateral view of head; D, ventral view of tail (arrows indicate first caudal annulus and last body annulus). f, frontal; fn, frontonasal; il, infralabial; m, mental; ma, malar; n, nasal; o, ocular; p, parietal; pf, prefrontal; pm, postmental; po, preocular; pt, postocular; r, rostral; sl, supralabial; sc, subocular; t, temporal.

it is referred to as the nasal. Posteriorly the lateral series is bounded by the first body annulus. Establishment of an anterior and a posterior boundary is useful, but does not distinguish the different elements lying between these borders. For this purpose the site of the eye was selected as a landmark; the scale over the eye is considered to be the ocular and the scales immediately surrounding it are referred to the ocular group. The eye has certain limitations as a landmark, as the position of the overlying scales varies and the eye is visible in only a minority of specimens. The eye most often lies beneath the posteroventral corner of a large scale bordering both the parietal and frontal dorsally (Fig. 2C). This scale is designated the ocular, because the eye is most frequently beneath it and the scale maintains a regularity in shape and position. The eyes may also lie beneath the ocular and postocular, the ocular and subocular, the ocular, subocular, and postocular, the postocular, and the subocular. Although its position varies, the use of the eye as a landmark is defensible, for once a terminology has been established arbitrarily and clearly defined, it is possible to assign a scale a definite name with a minimum of doubt. The eye is visible in less than 10 per cent of the specimens examined and only in individuals less than 260 mm. Neill (1951) noted the eye in a 311-mm-specimen and stated that no correlation exists between its development and body length, body scutellation, or geography. Three other authors have commented on the eye of *Rhineura;* Garman (1883) stated that it is present in young individuals, Carr (1949) supported this with observations on hatchling specimens, and Eigenmann (1902) discussed eye anatomy.

The ocular is bordered dorsally by the parietal and frontal. Usually a pair of suboculars are present between the ocular and the fourth supralabial. A single preocular lies anterior to the ocular and contacts the frontal dorsally and usually contacts the anterodorsal edge of the fourth supralabial ventrally. The anterior scale of the lateral series is the nasal, wedged between the frontonasal and rostral. Between the nasal and the preocular lie the loreals; these are bordered dorsally by the frontal and prefrontal, anterodorsally by the frontonasal, and ventrally by the second, third, and extreme anterodorsal edge of the fourth supralabial. Characteristically there is a large dorsal loreal, and seldom to the loreals contact the ocular. Posteriorly the ocular is in contact with the postocular. The postocular has a broad contact with the fourth supralabial and rarely touches the parietal dorsally. The temporals are enclosed by the first body annulus posteriorly, parietal dorsally, preocular and ocular anteriorly, and posterodorsal edge of fourth supralabial ventrally. Not infrequently one or two temporals extend into or completely through the first body annulus.

The two definite trends observable in the lateral series are reduction and increase in number of scales. The most frequent pattern, that most closely resembling the mean number of scales, is approximated by figure 3B and C. Figure 3A is the reduced pattern; probably best interpreted as the fusion of elements: the ocular and preocular, a loreal and subocular, and the postocular and some temporals. As a result of fusion the preocular and frequently the subocular are absent. Although this reduced pattern is found throughout the range, it occurs in all the specimens from Highlands County and in 54 per cent of the specimens from Polk County.

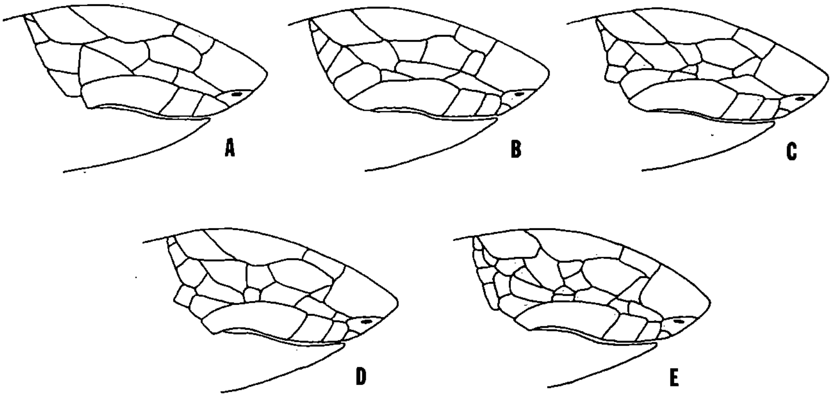


Figure 3. Patterns of variation in the scales of the lateral series of the head. The sequence of A through E illustrates a progressive increase in number; A shows the typical Lake Wales Ridge pattern.

The increase in the number of scales shown in figures 3D and E can be accounted for mainly by the appearance of new suture planes that create more and smaller elements. Another cause of a high total number of lateral head scales is the presence of an additional row of temporals extending upward posterior to the parietals. This row might be interpreted as the dorsal portion of the first body annulus, but if so interpreted the following or second annulus would be incomplete ventrolaterally and ventrally. Specimens with high scale counts occur sporadically throughout the entire geographic range except in Highlands County.

The labial series includes those scales enclosing the mouth and is composed of a supralabial row and an infralabial row (Fig. 2B). The supralabial row has a single anteromedial rostral scale and usually four supralabials extending posteriorly on each side of the mouth. The individual supralabials become progressively larger in size posteriorly; the length of the fourth supralabial almost equals the combined lengths of the first three. In 92% of the samples there are 4 supralabials on each side of the head; other combinations are 3/3, 3/4, and 4/5 (either left or right). The absence of a 5/5 condition is not surprising, as only two specimens have 5 supralabials. In contrast the Highlands County sample all have a 3/3 condition, as do a few specimens from Polk County. Five supralabials result from the division of the first supralabial; three supralabials result from the fusion of the first and second supralabials.

The infralabial row has a large anteromedial mental scale and usually 4 infralabials extending posteriorly on each side. The infralabials are more variable than the supralabials and show the following combinations: 3/3, 3/4, 4/4, 4/5, 5/5, and 6/6. The last combination was present in only one specimen. The frequency of occurrence of the other combinations was 3/3 - 12%, 3/4 - 8%, 4/4 - 59%, 4/5 - 9%, and 5/5 - 12%. Although these combinations occur throughout the range of *Rhineura*, the frequency of some combinations is often higher in certain localities, e.g., 3/3 in 87% of the specimens from Highlands and Polk Counties; 5/5 in 75% of the individuals from Pasco and Pinellas Counties; 4/5 in 31% and 5/5 in 54% of the specimens from Volusia County. Three infralabials result from the fusion of the first infralabial either to the mental or to the second infralabial; five infralabials arise from a division of the fourth infralabial.

The infralabial series usually encloses four scales anteriorly and laterally, the postmentals and malars of the genial series (Fig. 2B). The scales on each side of the midline are the postmentals, and between the postmental and infralabials of each side lies the malar, The variation in the number of genials (Table 2) is not the result of their progressive subdivision into smaller and smaller units, but the development of sutures in their posterior corners. The presence or absence of these small posterior genial scales has no meaningful geographic pattern.

As previously noted, only certain scales or scale series show geographic variation, and the discussion is limited to these characters, which are three in number: the total number of lateral head

Table 2. Scale and proportion variation in *Rhineura floridana*

	Number	Range	Mean X	Stan. Dev. s	Prob. error mean Sx	Coefficient of Variance
HEAD SCALES						
Lt. Loreals	169	1-6	3.2	0.84	0.06	26.19
Rt. Loreals	171	1-6	3.3	0.80	0.06	24.27
Lt. Temporals	170	1-11	4.5	1.86	0.14	41.33
Rt. Temporals	172	1-9	4.4	1.66	0.13	37.73
Lt. Oculars	160	2-7	4.4	1.79	0.14	40.68
Rt. Oculars	169	2-7	4.5	0.94	0.07	20.89
Tot. Lat. Head Scales	159	12.39	24.2	4.89	0.39	20.21
Tot. Supralabials	167	6-9	7.9	0.51	0.04	6.39
Tot. Infralabials	168	6-12	8.0	2.15	0.17	26.74
Total Genials	176	4-13	5.4	1.59	0.12	29.44
BODY SCALATION						
Annuli						
Body	187	226-267	250.2	5.46	0.40	2.18
Lt. Cloacal	189	3-6	4.0	0.72	0.05	18.33
Rt. Cloacal	187	3-6	3.9	0.75	0.05	19.04
Caudal	187	14-19	16.0	0.85	0.06	5.31
Granular	185	8-15	12.4	1.19	0.09	9.64
Segments around Midbody	189	28-37	29.3	2.53	0.18	8.64
SV/TL	179	11.8-20.3	16.41	1.31	0.10	7.98

scales excluding the nasal, total number of supralabials, and total number of infralabials. It might be better to consider only the ocular group of the lateral series, which demonstrates the variation most clearly, but I have used the entire lateral series even though the reduction trend was not always as distinct in the other members.

To demonstrate geographic variation the sample is divided into units encompassing as discrete localities as possible (Table 3). Ideally each sample should be of equal size and from localities of nearly equal size and uniform habitat; unfortunately the fortuitous nature of *Rhineura* collections prevents this. The means for the total number of supralabials, total number of infralabials, and total number of lateral head scales excluding the nasals were determined for each sample; classes for the means of the three characters were established and assigned numerical values, zero representing the class with the lowest mean (Table 4). The assigned values are plotted on maps (Fig. 4),

Table 3. GEOGRAPHIC VARIATION IN *Rhineura floridana*

	Lateral Head Scales		Supralabials		Infralabials		Body Annuli		Granular Annuli		Midbody Segments	
	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean
Sample locality												
Alachua County												
Gainesville (G)	20	23.6	21	8.0	21	8.0	22	250.3	21	12.2	21	29.7
Micanopy (M)	11	29.8	11	8.0	11	7.8	11	249.7	9	12.4	11	29.9
Waldo-Lake Santa Fe (Wa)	3	31.0	3	8.0	3	8.0	3	245.7	3	14.3	3	29.3
Marion County												
Ocala-Silver Springs (Oc)	5	24.4	5	8.0	5	8.0	5	252.6	5	11.4	5	26.6
Eureka (E)	1	25.0	1	8.0	1	7.0	3	253.3	3	11.3	3	29.7
Marion County	34	26.8	34	7.9	34	8.0	34	252.5	34	11.9	34	28.6
Lake County												
Leesburg-Fruitland Park (Le)	4	22.5	5	8.0	5	7.4	5	252.2	5	13.8	5	28.0
Travares-Mt. Dora-Eustis-Umatilla (U)	5	21.6	5	8.0	5	8.0	6	253.0	6	12.8	6	29.0
Orange County												
Orlando (Or)	9	23.8	11	8.0	11	8.4	11	253.7	12	12.9	12	29.6
Hillsborough County												
Tampa area (Tm)	3	25.3	3	8.3	3	9.7	4	251.5	4	13.3	4	30.5
Pasco County (P)	3	24.0	3	8.0	3	10.0	3	252.3	3	13.3	3	33.7
Pinellas County												
Clearwater (C)	2	23.5	2	8.0	2	9.5	2	253.5	2	14.0	2	32.0
Tarpon Springs (Ts)	7	23.4	8	8.0	6	9.5	8	252.1	8	13.3	8	29.5
Volusia County												
Volusia (V)	9	26.1	9	8.0	9	9.6	12	248.7	12	12.8	12	29.3
Polk County												
Winter Haven area (Wh)	6	17.2	7	6.3	7	6.3	8	241.7	8	10.5	8	26.3
Lakeland (L)	3	23.3	4	7.5	4	7.7	5	248.4	5	12.4	5	33.6
Auburndale (A)	3	23.7	3	8.0	3	8.0	4	243.0	4	12.5	4	30.3
Highlands County												
Sebring-Avon Park (S)	1	12.0	1	6.0	1	6.0	2	245.0	2	12.0	2	25.0
Hicoria-Lake Placid (H)	5	12.2	5	6.0	5	6.0	5	242.2	5	10.4	5	24.8

which show a trend towards the reduction of scale number in all three characters at the southern extremity of the range. This area, the Lake Wales Ridge, is the southern spine of the Central Highlands and is a region of high sandy hills largely covered with scrub.

Although the three characters are similar at the southern end of the range, the reduction pattern ends differently in central Polk County. The total lateral head scale mean for the Winter Haven area is intermediate between the extreme low to the south and the areas to the north and west. The supralabial and infralabial means for Winter Haven and Highlands are nearly identical, and may suggest the presence of a continuous population between these two areas. Winter Haven is less than 20 miles from Auburndale and Lakeland, yet the means for the lateral head scales of these latter areas are similar to those of north-central Florida. The situation is the same for the infralabial means of these two areas; however the Lakeland supralabial mean is approximately intermediate between the conditions to the north and the Lake Wales Ridge. As Auburndale is closer to Winter Haven than Lakeland, it would seem more likely for the intermediate condition to be present at Auburndale. A soil map of this region (Fowler, 1927) shows high sand ridges in all three areas, each of which is isolated by low marsh soils. Thus the Lake Wales Ridge

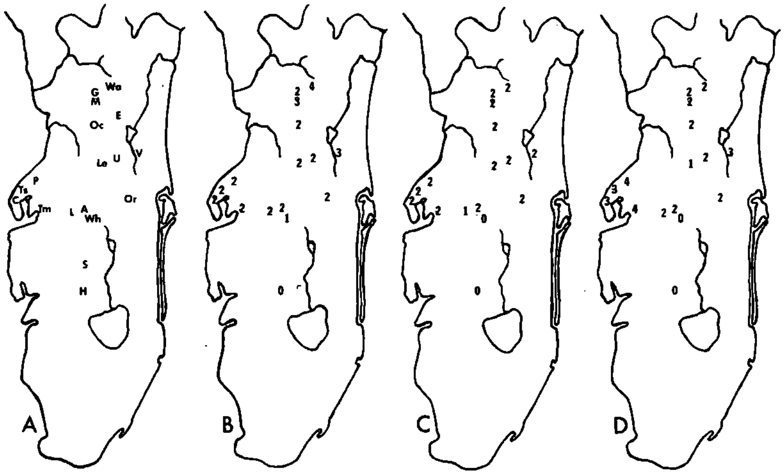


Figure 4. Geographical variation in head scales.[1] A, the sample localities, (see Table 3 for explanation of abbreviations); B, number of lateral head scales; C, number of supralabials; D, number of infralabials.[1]

[1] The integers denote classes of means (Table 4).

population appears to be characterized by a reduction in three scale groups. In north-central Polk County the morphological evidence suggests that gene flow may be occurring between the populations of the Lake Wales Ridge and north-central Florida, though interrupted or reduced by the marshy lowlands between the high sand ridges.

The Lake Wales Ridge samples are not the only ones that fall outside the north-central Florida means. In southwestern Pasco County, eastern Hillsborough County and Pinellas County, the means for the infralabials are appreciably higher than for the rest of the range. This is the only character that shows any differentiation in this region, and it may be explained in two ways: the swamping or elimination of a previously differentiated population, or the beginning of differentiation here. The former hypothesis seems the more reasonable, because *R. floridana* is present in most of the Floridian habitats with the exception of marshes, no barriers isolate this region today.

Other local differences are illustrated by the maps. Throughout most of the range of *Rhineura* the means of total lateral head scales fall between 20.6 and 25.5, except in Volusia, Micanopy, and Waldo sub-samples. The Micanopy and Waldo means, 29.8 and 31.0, respectively are similar to one another and differ from the remainder of the north-central samples, yet lying between them is the Gainesville sample with an appreciably lower mean of 23.6. Although the Volusia mean (26.1) is higher than that for most of the population, it can hardly be considered divergent. The similarity of the mean number of infralabials for Volusia and the Tampa Bay area may indicate parallelism in this character.

BODY SCUTELLATION

The body and tail of *R. floridana* are encircled by a solid row of annuli, and the only incomplete annuli are those interrupted by the vent. Each annulus is composed of rectangular or square segments or scales. Middorsally the annuli are bisected by a groove, which can always be recognized by the presence of tiny scales wedged between the right and left halves. The segments forming the annuli are very narrow (length>width) dorsally; they become progressively wider ventrad so that laterally they are square (length=width) and ventrally rectangular (length<width). There are some exceptions to this general rule: On the dorsal surface of the posterior two-thirds of the tail the dorsal scales have lost their flattened rectangular shape and become dome-shaped segments surrounded by many small, low, circular scales. The second annulus behind the vent has a pair of greatly

enlarged midventral segments (Fig. 2D). Another group of enlarged ventral segments is present in three annuli of the gular region, the fifth, sixth, and seventh annuli with the sixth frequently the largest. In this case the enlargement is not confined to the midventral pair of segments but extends upward to and including the ventrolateral segments.

Annuli were counted for three divisions, body, cloacal, and caudal, following the procedure of Gans and Alexander (1962). The caudal annuli are those complete annuli posterior of the vent excluding the terminal roseate of segments on the tip of the tail (see Fig. 2D). The cloacal annuli contain both complete and incomplete annuli; posteriorly the cloacal annuli are interrupted by the vent, and anteriorly the complete annuli contain the three pair of enlarged precloacal segments. The body annuli lie between the head and the first cloacal annulus. Determination of the first cloacal and first caudal annulus is not difficult because of the precloacal segments and the completeness of the first caudal annulus. But defining the first body annuli of variant individuals is sometimes a problem. In most specimens the first body annulus is complete and anteriorly borders the parietals, temporals, fourth supralabials and infralabials, and genials. One specimen has a ventral annulus between the first body annulus and the genials. Other specimens have a row of temporals extending dorsally between the first body annulus and the parietals, and usually in this case the first body annulus is constricted posterior to the supralabials, thus giving the appearance of separate dorsal and ventral halves.

It should be noted that each body vertebra is usually encompassed by a pair of annuli, and there appears to be a single annulus for each caudal vertebra. Although X-ray plates show the first three or four annuli enclose the skull and thus, strictly speaking, are not body annuli, I included these cephalic annuli in my counts of body annuli.

Body annuli were counted on the ventrolateral surface of one side, either the left or the right. Restriction to the left or the right was not considered necessary, as it appeared that an intercalation of a half annulus on one side was always followed shortly by the appearance of one on the other side. The caudal annuli were counted in the above manner and the cloacal annuli were counted on both sides. No geographic trend is evident in the cloacal or caudal annuli (Table 2). Only the number of body annuli showed a trend towards reduction at the southern extremity of the range (Fig. 5A).

The caudal annuli bearing dorsal granular segments normally be-

Table 4. NUMERICAL VALUES ASSIGNED TO CLASSES OF GEOGRAPHICALLY VARIABLE CHARACTERS

Character	Classes	Assigned Value
Number of body annuli	240.0-243.9	0
	244.0-247.9	1
	248.0-251.9	2
	252.0-255.9	3
Number of caudal annuli with dorsal granular segments	10.1-10.5	0
	10.6-11.0	1
	11.1-11.5	2
	11.6-12.0	3
	12.1-12.5	4
	12.6-13.0	5
	13.1-13.5	6
	13.6-14.0	7
	14.1-14.5	8
Number of segments around midbody	24.0-25.9	0
	26.0-27.9	1
	28.0-29.9	2
	30.0-31.9	3
	32.0-33.9	4
Total number of lateral head scales	10.5-15.5	0
	15.6-20.5	1
	20.6-25.5	2
	25.6-30.5	3
	>30.5	4
Total number of supralabials	5.5-6.5(3/3)	0
	6.6-7.5(3/4)	1
	7.6-8.5(4/4)	2
	8.6-9.5(4/5)	3
Total number of infralabials	5.6-6.5(3/3)	0
	6.6-7.5(3/4)	1
	7.6-8.5(4/4)	2
	8.6-9.5(4/5)	3
	9.6-10.5(5/5)	4

gin anteriorly as a pair of middorsal granular segments. Posteriorly the number of granular segments rapidly increases so that the dorsal surface of the posterior half of the flattened tail is completely covered. This character also demonstrates a reduction trend on the Lake Wales Ridge (Fig. 5B), but the Sebring mean is higher than the two Marion County means.

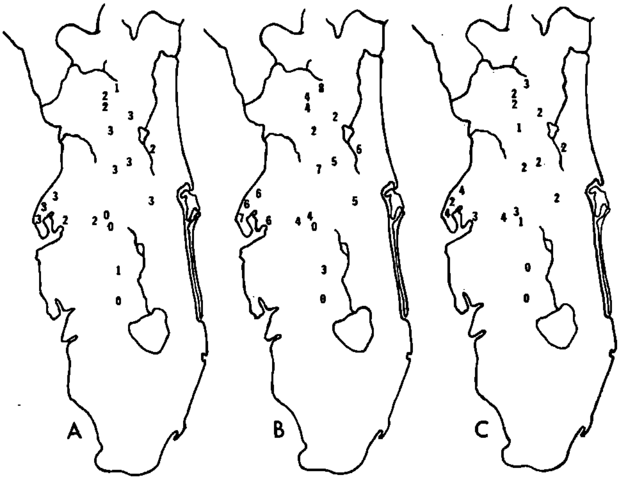


Figure 5. Geographical variation in body scutellation. A, number of body annuli; B, number of caudal annuli bearing dorsal granular segments; C, number of segments around midbody. Sample localities as in Table 3, classes of means from Table 4.

The number of segments around midbody is variable both on the individual lizard and within the population. When the number of segments of consecutive annuli is counted on a single specimen, the following form of variation was seen: 28, 29, 28, 29, 29, 29, 30, 28, 28, 29. As I have counted only a single midbody annulus per specimen, the record count is an approximation and the mean condition may be one and, at the most, two units above or below the recorded count. Even with this individual variation, a reduction trend is evident in the south (Fig. 5C).

Three characters, number of body annuli, number of caudal annuli with dorsal granular segments, and number of segments around midbody, show a distribution pattern similar to that of the head scutellation. The specimens from the Lake Wales Ridge have the lowest number of body annuli, but the Sebring sample is more similar to the

Waldo sample than either is to its nearest geographic sample. Although the similarity of these samples may be due to their small size, it does indicate the existence of continuity between the two populations. In northern Polk County the Auburndale sample is typical of the Lake Wales Ridge samples and the Lakeland sample is intermediate. The remainder of the sample localities with the exception of Micanopy and Volusia have means above 250, although the Micanopy mean is barely below 250. The Volusia mean is similar to the Lakeland mean.

Two areas in the Central Highlands have low mean numbers of dorsal granular annuli. The Lake Wales Ridge has the lowest means with the exception of the Sebring sample; the next lowest mean is in northeastern Marion County. The Lakeland and Auburndale samples again show a more or less intermediate condition; this is also true of the Gainesville and Micanopy samples. All the other sample means are above 12.5 with the highest mean in northeastern Alachua County.

The lowest number of segments around midbody occur in the samples from the Lake Wales Ridge and Ocala. The highest means are from the Tampa Bay area, north-central Polk County and Waldo. All the other sample means are intermediate between these two conditions.

Thus the characters of body scutellation that exhibit geographic variation show the same pattern as the head scutellation. This further suggests the presence of a distinct population on the Lake Wales Ridge, with northern Polk County as a zone of overlap between this population and that to the north. The distinctiveness of the southern population is somewhat lessened by the means of the Sebring sample and its partial similarity to the northern population. The Tampa Bay area samples show a slight trend towards higher means in the three annuli characters, but hardly sufficient to suggest the presence of a distinct population.

SNOUT-VENT LENGTH AND TAIL LENGHT

Neither of these characters nor their ratio (s-v/t) show any correlation with geographic region. When snout-vent length and tail length are plotted, the regression line is straight with a low slope, which indicates isometric growth and a low rate of tail growth. The smallest specimen examined had a 111mm snout-vent length and a 9mm tail length, the largest specimen 379mm and 26mm. The latter specimen is larger than the one reported by Telford (1955). Carr (1949) reported smaller specimens with yolk sac scars; the 111mm and a 113mm specimen have scars, whereas the scar was absent in a 115mm individual.

DISCUSSION

It is evident from the preceding descriptions of variation that *Rhineura floridana* populations are not geographically uniform, but consist of two differentiated populations, one in north-central Florida, and the other on the Lake Wales Ridge. The characters demonstrating this pattern are the total number of lateral head scales, total number of supralabials, total number of infralabials, number of body annuli, number of dorsal granular annuli of the tail, and number of segments around midbody. As the variation is illustrated by the use of small local samples, it is necessary to consider those specimens not included in the samples and to determine their agreement with the observed trend of reduction in scutellation at the southern extremity of the range. The three specimens from Clay County, Columbia County, and Georgia fall within the range of variation of the Alachua County samples except for the number of body annuli of the Columbia County specimen (242) which is only 2 annuli below the range of the Alachua samples. The holotype from Micanopy and the specimens from Flagler, Putnam, and Levy Counties agree closely with the Alachua and other north-central Florida samples. If the 34 specimens labeled only Marion County were included in the Ocala and Eureka samples, they would change the means and ranges only slightly (see Table 3 and 4).

The Tampa Bay area samples are characterized by the highest mean number of infralabials, high mean numbers of caudal granular annuli, and segments around midbody; the other characters are indentical with the north-central population. The two Hernando County specimens are similar to the Tampa Bay area sample only in a high number of granular annuli (13 and 15). The affinities of two Manatee County specimens appear to be with the Lakeland sample in that the counts are intermediate, and they have a low number of infralabials (3/4, 3/3). The only specimen from Polk County not included in the samples is from Phantom Grove, a locality I have been unable to find; its characteristics indicate that this specimen belongs to the Lake Wales Ridge population: lateral head scales 12, supralabials 6, infralabials 6, body annuli 226, granular annuli 10, and midbody segments 25.

Variations in sample sizes and in size and habitat uniformity of the local areas sampled have doubtless introduced some bias into the analysis, but the data nevertheless indicate strongly the existence of two populations, one in the Lake Wales Ridge, the other in north-central Florida.

The unique characteristic of the Lake Wales Ridge population is the consistent reduction in scutellation. One would not expect a series of unrelated characters all to show the same trend. The number of head scales might be reduced if the head were shortened. There is no evidence for this, as individuals of the same snout-vent length from the two populations have similar facial lengths (length from tip of snout to posterior edge of last supralabial). Alachua County, s-v 192.5, mean, 137-239, range; facial 4.76, 3.8-5.4; Highlands County, s-v 189.5, 115-240; facial 4.85, 3.9-5.4. Thus no correlation between facial or head length and number of head scales is apparent. Nor does there appear to be any reduction in body length that would account for a reduced number of body annuli; although the maximum length of specimens examined from the Lake Wales Ridge was 248 mm, Telford (1955) reported a 356 mm (snout-vent) specimen from Winter Haven.

The Lake Wales Ridge population is distinct, but it is extremely doubtful that it should be recognized taxonomically. The obvious area of overlap between the two populations is between Winter Haven and the Auburndale and Lakeland area; this region is probably a zone of intergradation. Before a name can be applied validly to the Lake Wales Ridge population, I believe that larger samples should be procured from Highlands and Polk Counties to delineate more accurately the statistical parameters, range, and size of the intergradation zone. At this time it seems sufficient to recognize that sea level fluctuation probably isolated this population and that different selective pressures caused divergence. The two populations, still appear to be subject to differential selective pressures, for if these were the same and gene flow were possible between them, one would expect a genetic swamping of the Lake Wales Ridge population. The important question is what has caused a reduction in scutellation? Is the reduction related to difference in soil friability, microclimatic factors, founders principle, or genetic drift?

FOSSIL HISTORY AND PAST DISTRIBUTION

To date seven fossil species of *Rhineura* have been described: *R. coloradoensis* Cope, 1873; *R. hatcheri* Baur, 1893; *R. sternbergi* Walker, 1932; *R. minuta* Gilmore, 1938; and *R. hibbardi*, *R. amblyceps*, and *R. wilsoni*, all Taylor, 1951. These were all recovered from

Oligocene deposits and distinguished on the basis of skull characteristics, except for *R. coloradoensis* which is known only from several dorsal vertebrae. Their combined range is northward from northeastern Colorado through northwestern Nebraska to southwestern South Dakota and east-central Wyoming. *Rhineura coloradoensis* is Early Oligocene; all the others are Middle Oligocene except *R. hatcheri* which extends into the Late Oligocene.

All the species are currently recognized, although their status has changed. Vanzolini (1951) erected the genus *Pseudorhineura* for *minuta*. Gilmore (1938) suggested that *coloradoensis* is conspecific with *hatcheri*, and Brattstrom (1958) implied that *amblyceps* is also conspecific with *hatcheri*. As all the nominate species are temporally and geographically close, some could well be conspecific, but the status of the fossil species must remain questionable until we have more detailed knowledge of the skeletal variation in recent *Rhineura*.

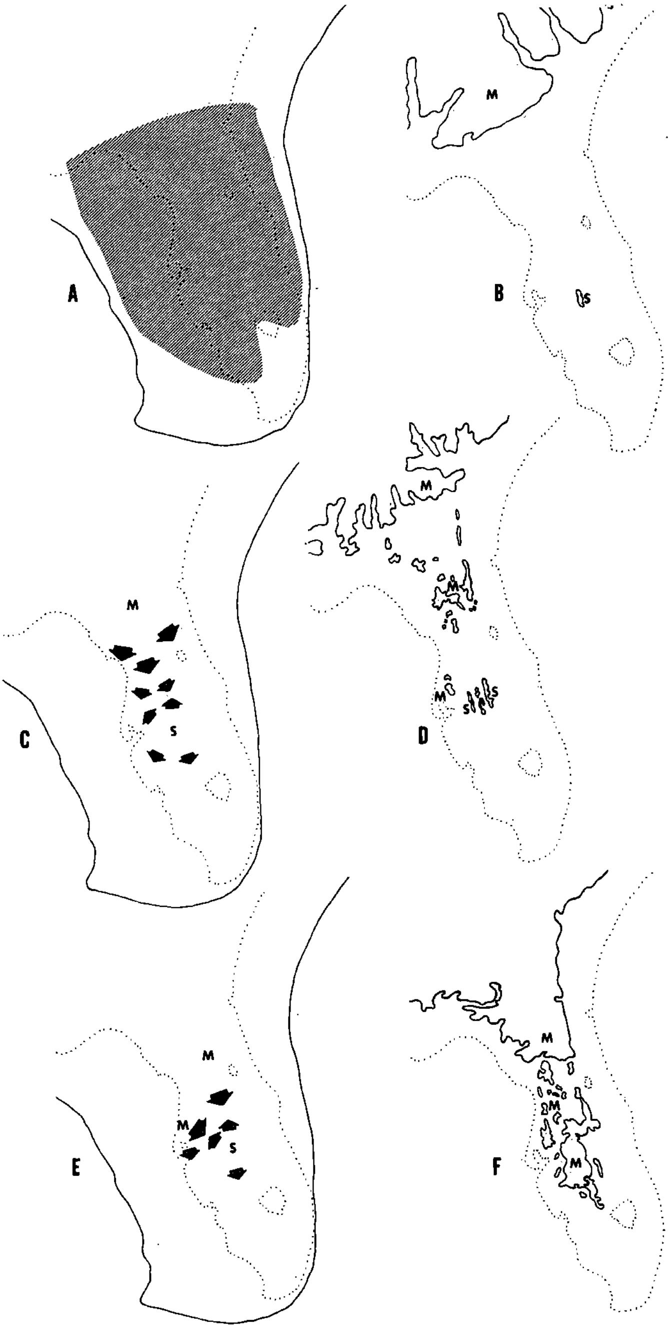
No fossil remains of *Rhineura* have been discovered in any Pliocene or Early Pleistocene sediments. Kluge (pers. comm., 1967) has examined a *Rhineura* skull from a Miocene deposit of the High Plains. Holman (1958, 1959, 1962) reported *R. floridana* remains from Florida Rancholabrean deposits in Arredondo, Alachua County; Williston, Levy County; Reddick, Marion County; Saber-tooth Cave, Citrus County. These localities are all within the present range of *R. floridana* and add no information on Pleistocene dispersal.

Before erecting a hypothetical history for *Rhineura*, it seems advisable to review the geologic and paleoclimatic history of the plains and the Southeast. A gradual cooling trend was evident throughout the entire Tertiary and was climaxed by the Pleistocene glaciation. On the plains the subtropical conditions of the Oligocene slowly shifted to a warm temperate climate in the Pliocene; within this trend other shorter climatic cycles existed, hot-dry and cool-moist periods. The climate of the Southeast and peninsular Florida ranged from tropical in the Oligocene to subtropical in the Late Pliocene. The Pleistocene climate fluctuated markedly; the Southeast was temperate during the glacial epochs and subtropical-tropical in the interglacials, and the plains were subarctic-cool temperate and warm temperature, respectively (Dorf, 1959; Hibbard, 1960). From this climatic data we can conclude that *Rhineura* could have lived in the Southeast since the Oligocene and that it probably remained on the High Plains until the end of the Pliocene.

The plains have been stable since the Oligocene with no uplift or subsidence, and they, particularly the western part, have acted as a depositional site for the erosion of the developing Cordilleras. The history of the Southeast and Florida cannot be as easily summarized because of the various ages assigned to the marine terraces. Cooke (1945) and MacNeill (1950) correlate them with the different Pleistocene interglacial sea levels, whereas Alt and Brooks (1965) suggest that the terraces range from Miocene to Recent in age. Basically the issue rests on the maximum elevation of sea level during the Pleistocene. Cooke (1945) and MacNeill (1950) obviously adhere to a 250-300 feet elevation, Alt and Brooks (1965) to a 25-30 feet elevation. The only point of agreement is that the highest terrace is the oldest and the successively lower terrances are younger or more recent. Cooke (1945) recognized seven terraces (270 ft., Aftonian; 215 and 170 ft., Yarmouth; 100, 70, and 42 ft., Sangamon; 25 ft., Mid-Wisconsin), Alt and Brooks (1965) five terraces (215-250 ft., Upper Miocene; 90-100 ft., Pliocene; 45-55 ft., and 70-80 ft., Upper Pliocene or Lower Pleistocene; 25-30 ft., Pleistocene). As I have no means for dating the terraces on biological evidence and believe in higher sea levels, I am inclined to follow the general land patterns proposed by Cooke or MacNeill. The basic problem with their terraces is their reliance on topographic maps for locating marine terraces (White, 1958). Also, although I am not following the terrace ages of Alt and Brooks, their article convinces me of the existence of five terraces and especially of the highest terrace which has been questioned.

Rhineura probably existed in the High Plains until the Pliocene. If is was not extirpated from the plains by the recurring arid conditions of the Middle and Late Pliocene, it would have certainly been eliminated by the subarctic conditions of the Nebraskan glaciation. Migration of the worm lizard may have occurred in the Miocene. The development of grasslands and savannahs would have made the Gulf Coast Corridor a suitable route, and even if this area contained a more mesic flora, no reason exists why it would not have been passable as *R. floridana* lives today in a humid or moist subhumid environment. It could not have extended into the peninsular at this time, for the Trail-Lake Wales Ridge was probably a sand bar during the Late Miocene.

Penetration of *Rhineura* into the Southeast during the Miocene or even in the Pliocene (Auffenberg and Milstead, 1965) would have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permitted it to extend into the emerging peninsula of the Pliocene. It is likely that by Middle Pliocene the sea level was similar to that of today (Webb and Tessman, 1967), thus the peninsula probably had numerous habitats as today and *Rhineura* could have occupied a number of them. By the end of the Pliocene *Rhineura* should have been well established in Florida.

The Aftonian inundation split *Rhineura* into an insular and a mainland population (Fig. 6). I assume this island was part of what is now the Lake Wales Ridge and was covered mainly with scrub. On the other hand the mainland probably offered a variety of suitable habitats. The initial isolation in the scrub presumably lead the insular population to adapt to the scrub environment, which the mainland population was less likely to do with the several different habitats available.

In the succeeding glacial period, the Kansan, the sea level dropped and both populations probably spread into the recently flooded areas (Fig. 6). If the insular population had become so adapted to a scrub situation that it was unable to occupy other habitats, its expansion would have been drastically limited in relation to that of a more tolerant mainland population. By the end of the glacial period the mainland population probably occupied much of north-central Florida and the insular population the south-central portion. Intergradation of the two populations may have occurred in the region of northern Lake County.

The Yarmouth interglacial rise in sea level submerged the area of intergradation and again split the peninsular population. (Fig. 6). A group of southern populations remained on the three parallel island chains. The small size and sandy nature of this area suggest that scrub may have been the only available habitat and that selective pressures on all these populations would have been similar to those on the preceding interglacial population of this region. The northern population was probably restricted to the mainland and

Figure 6. Hypothetical distributions and dispersal of *Rhineura* in Florida during the Pliocene and Pleistocene. Solid line = actual coast line; dotted line = present coast line; diagonal hatching = initial peninsular range of *Rhineura;* M, mainland population; S, insular population; arrows, direction of dispersal. Land forms based on Cooke (1945) and MacNeill (1950). A. Late Pliocene, B. Aftonian Interglacial, C. Nebraskan Glacial, D. Yarmouth Interglacial, E. Kansan Glacial, F. Sangamon Interglacial.

the Marion County islands. The Hernando-Pasco island harbored either intergrades or most likely representatives of the northern mainland population.

A similar regional expansion of *Rhineura* occurred during the Illinoian glacial period. The spread of the combined southern population was probably no greater than in the previous glacial period and may have been less. If this were the case, the northern population would have extended farther south and consequently also have pushed or shifted the area of intergradation southward. With the Yarmouth rise of sea level, a portion of the northern population was probably left on the large Polk County Island and restricted to the scrub ridges of the southern part of the island, thereby preventing a northern expansion of the southern population. On the other hand the adaptation of the southern population to the scrub habitat and the barriers of marshy lowlands in northern Polk County would have prevented a southern expansion of the northern population. Thus the present area of intergradation was probably established at this time. The other islands would have had representatives of the northern population which joined with one another as the land emerged during the Wisconsin glaciation. Thus from the Wisconsin onward the range of *R. floridana* was very similar to its range at the present.

Two main assumptions are made in the postulated history of *Rhineura* to explain the present pattern of geographic variation. First a peninsular population was divided into a mainland and an insular population by the Aftonian rise in sea level. Second the insular population lived in a scrub or scrublike habitat, and adaptation of this population restricted it to this type of habitat.

Similar histories have been postulated for other endemic reptiles in Florida: *Ophisaurus compressus* (McConkey, 1954), *Stilosoma extenuatum* (Highton, 1956), *Neoseps reynoldsi* (Telford, 1959), *Eumeces egregius* (Mount, 1965), and *Tantilla relicta* (Telford, 1966). *Sceloporus woodi* probably shares a similar history (Carr, 1940; Neill, 1957; Telford, 1965). The present ranges of these species and their restriction to scrub, sand hill, and/or xeric hammock associations strongly supports the second of my two basic assumptions, that the initial insular population was isolated in a scrub or scrublike habitat to which it became restricted by adaptation.

The first assumption, that *Rhineura* was divided into an insular and a mainland population by the Aftonian Sea, is somewhat supported by distributional patterns of *O. compressus*, *E. egregius*, *T. relicta*, and *S. woodi*. Increased knowledge of Floridian Pliocene faunas suggests that many reptile species had reached Florida by the Middle Pliocene (Auffenberg, 1963; Auffenberg and Milstead, 1956).

Two sets of facts can be marshalled to support the assumption that the initial separations and isolation occurred during the Aftonian interglacial rise in sea level. The first and best evidence is that three species have differentiated populations (*R. floridana*, *E. e. lividus*, and *T. r. relicta*) on the Lake Wales Ridge. Secondly and a bit circuitous, all the endemic squamate genera except *Stilosoma* are found on the Lake Wales Ridge, and only in *Stilosoma extenuatum* is a different pattern of geographic variation discerned. On these grounds I believe that the ancestors of *N. reynoldsi*, *E. egregius*, *O. compressus*, *S. woodi*, and *T. relicta* were also present on the Polk County island in the Aftonian interglacial sea. Only for *S. extenuatum* is isolation in a later interglacial period required to explain its present subspecific distribution: *S. e. extenuatum* on the Polk County archipelago, *S. e. arenicola* on the Hernando-Pasco island, and *S. e. multistictum* on the Alachua County islands. The succeeding inundation of Florida would probably have reinforced the initial differentiation of the populations of these species, and if their present distributions match the Sangamon marine terraces most closely, it is because this is the area of continuous scrub and sand-hill associations, the only area in which these species can survive.

SPECIMENS EXAMINED

FLORIDA:

Alachua Co., UMMZ 56601-02, 57876; Gainesville, UF 268, 632, 2074, 2193, 2725, 2865, 2902, 3293-94, 5999, 7077, 7997, 8482, 9060, 11134, 14416, 21622; UMMZ 64170, 98747, 100684-5; 3.8 mi S of Gainesville, UFT 1094; 2 mi N of Gainesville, UF 3670; SE of Gainesville, UF 8895; 8.5 mi W of Gainesville, UF 14201; 3 mi SW of Gainesville FMNH 51939-43; west side of Lake Santa Fe, UMMZ 100683; Micanopy, USNM 3202, 4983 (11); Waldo, USNM 13964, 26182.

Clay Co., Gold Head Branch State Park, UF 3666.

Columbia Co., Lake City, USNM 22318.

Flagler Co., Bunnell, UF 12034.

Hernando Co., Bayport, UF 2770; Annutheliga Hammock nr Brooksville, USNM 142478.

Highlands Co., Avon Park, UF 7218; nr Archbold Biological Station, Hicoria, AMNH 65659-60, 66278; Lake Placid, AMNH 64496, FMNH 59193; Sebring, USNM 50960.

Hillsborough Co., USNM 58742-44; Tampa, AMNH 70872.

Lake Co., UMMZ 56533; Eustis, USNM 19993; Fruitland Park, USNM 64013, 69655; nr Lake Joanna, USNM 69656; Leesburg, CM 16808, UMMZ 77490, 97443; Mt. Dora, UF 14636; Tavares, UF 3081, USNM 75238; Umatilla, USNM 80299.

Levy Co., 6 mi S of Bronson, UF 14637; Chiefland, USNM 135472; Seahorse Key UF/SKRC 7,22.

Manatee Co., 5 mi W of Bradenton, CM 26707; Manatee, USNM 8371.

Marion Co., CM 1117-28, FMNH 43385-400, 43402-4, 43407-9; Candler, UMMZ 46938; Dunnellon, UF 11135; Eureka, AMNH 8311-12, UMMZ 48603; Ocala, FMNH 28454-56; Silver Spring, FMNH 35136-37.

Orange Co., MCZ 6808, 6851, 8331; Fairville, CM 23448; Orlando, ANSP 13479-81, FMNH 2016(5), UF 7954, USNM 51075, 83319.

Pasco Co., Argo, ANSP 13478; Odessa, AMNH 64490-91.

Pinellas Co., Clearwater, ANSP uncataloged, USNM 10737; west coast of Tampa Bay, Wieden Mound, FMNH 55493; Tarpon Springs, ANSP 4557, 15237-43.

Polk Co., Auburndale, USNM 59412, 59417, 60501-2; Lakeland, FMNH 3073, 72389-92; Phantom Grove, FMNH 27701; Winter Haven, AMNH 5724-25, 69705, UF 2994; Blue Lake nr Winter Haven, UF 3000; 4 mi NW of Winter Haven, UF 14638, 14639-1 & 2.

Putnam Co., UF Conservation Reserve nr Welaka, UMMZ 100726.

Volusia Co., MCZ 14089-91; Port Orange, MCZ 5125; Volusia, ANSP 13466-76.

GEORGIA:

MCZ 4655.

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