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**VARIATION AMONG THE SOUTHEASTERN  
CROWNED SNAKES, GENUS TANTILLA**

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## VARIATION AMONG THE SOUTHEASTERN CROWNED SNAKES, GENUS *TANTILLA*

SAM ROUNTREE TELFORD, JR.<sup>1</sup>

**SYNOPSIS:** The *coronata* group of crowned snakes in southeastern United States includes three species: *Tantilla coronata* Baird and Girard, 1853, and two species herein described, *T. relicta* and *T. oolitica*. *T. coronata* ranges throughout southeastern United States, but does not enter peninsular Florida south of the Suwannee River; *T. oolitica* is restricted to Dade and Monroe counties in southeastern Florida; *T. relicta* inhabits peninsular Florida.

Variation in characters of pattern, scutellation, body proportions, and habitat support recognition of three subspecies in *T. relicta*: *T. r. neilli* occurs in sandhills and mesic hammocks of northcentral Florida; *T. r. relicta* of central Florida is restricted to scrub habitat where syntopic with *neilli*, but also occurs in sandhills where allopatric in southcentral Florida; *T. r. pamlica* inhabits the narrow strip of coastal dunes and scrub in southeastern Florida. The little evidence of gene flow among subspecies is suggestive of secondary intergradation.

Two named subspecies of *T. coronata*, *wagneri* (Jan) and *mitrifer* Schwartz, are synonymized with *T. coronata*.

The three southeastern species of *Tantilla* probably were derived from a common precursor of the early Pleistocene, diverging during the successive fluctuations of sea level which characterized the glacial-interglacial stages.

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<sup>1</sup> The author completed most of this study while a graduate student at the University of Florida, Gainesville and the University of California, Los Angeles, and presented preliminary conclusions at the annual meetings of the American Society of Ichthyologists and Herpetologists at Austin, Texas, in April 1961. He is currently National Institutes of Health Post-doctoral Fellow in the Department of Parasitology, The Institute for Infectious Diseases, University of Tokyo, Japan. Manuscript received 21 June 1965.—Ed.

## TABLE OF CONTENTS

Introduction .....	262	<i>T. oolitica</i> .....	281
Acknowledgements and		<i>T. coronata</i> .....	285
Abbreviations .....	263	Gross Ecology .....	291
Materials and Methods .....	264	Size and Sexual Maturity .....	294
Taxonomy .....	264	Discussion .....	295
<i>Tantilla relicta</i> .....	270	Summary .....	301
<i>T. r. relicta</i> .....	278	Key to southeastern <i>Tantilla</i> .....	302
<i>T. r. neilli</i> .....	279	Literature cited .....	303
<i>T. r. pamlica</i> .....	280		

## INTRODUCTION

Baird and Girard (1853: 131) described *Tantilla coronata* from a specimen collected in Kemper County, Mississippi. The holotype, United States National Museum 1876, serves also as the type of the genus *Tantilla*, which Baird and Girard defined at the same time. In 1862 Jan described *Homalocranion wagneri* from a specimen collected in "Florida" by a Professor Wagner. Jan and Sordelli (1866: livr. 15, pl. 2, fig. 3) figure what is apparently the type specimen of *H. wagneri*. Garman (1883: 163) treated *H. wagneri* as *Tantilla coronata* var. *wagneri*. Boulenger (1896: 218) referred *H. wagneri* to the synonymy of *Homalocranium coronatum*, adopting the generic designation of Duméril and Bibron (1854). Cope (1900: 1111) mentioned briefly that *H. wagneri* had not been observed by American naturalists, and since the holotype of *wagneri* had an entire anal plate, it could not belong to the genus *Tantilla*, in which the anal is divided. In the same work (1900: 1114), he listed *H. wagneri* as a synonym of *Tantilla coronata*. Until Blanchard's review (1938) of the United States members of the genus, the name *wagneri* was considered a synonym of *T. coronata*. Blanchard resurrected *wagneri* for peninsular Florida *Tantilla*, justifying subspecific relationship to *T. coronata* on grounds of overlap in scale characters. Most workers since 1938 have followed Blanchard's arrangement. Wright and Wright (1957: 733) commented on the polymorphism of Florida specimens, in which all possible variations of banded and non-banded head patterns occur in no proved correlation, and speculated that perhaps there is but one highly variable form of *Tantilla* in southeastern

United States. In the meantime Schwartz (1953) designated montane populations of *Tantilla* in Tennessee and North and South Carolina as *T. coronata mitrifer*.

In 1959 I was impressed by the fact that all *Tantilla* I collected from rosemary scrub habitat (Carr, 1940; Laessle, 1958; Telford, 1959) in southcentral Florida had a prominent light band across the parietal area, separating the black head cap from the black nuchal collar, while all that I collected from sandhills (Laessle, 1958) or mesic hammock (Carr, 1940) habitats in northcentral Florida had a predominantly black head and nuchal collar with no distinct light parietal band. This prompted me to review relationships of southeastern *Tantilla* in the light of additional material accumulated since Blanchard's 1938 review. In the last 5 years I have examined 215 *Tantilla coronata* from sites throughout the range exclusive of peninsular Florida, and 166 specimens from the peninsula, of populations previously called *Tantilla coronata wagneri*.

Useful taxonomic characters in scutellation are restricted to ventrals and subcaudals. Examination of 83 maxillae did not prove particularly fruitful in clarifying the status of the populations. But by comparing structure of the hemipenis with pattern, size, head shape, scutellation, body proportions, and ecology, I am able to interpret the polymorphism of peninsular populations.

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I should like to thank my colleagues F. W. King, D. A. Rossman, C. W. Myers, J. McCrone, A. Arata, H. W. Campbell, M. J. Fouquette, Jr., W. T. Neill, and especially R. H. Mount for many stimulating discussions and much useful advice.

#### MATERIALS AND METHODS

All scale counts were made under a dissecting microscope as follows: ventrals as proposed by Dowling (1951); subcaudals from the tail tip to the vent, excluding the terminal scale; dorsals from the left diagonally across the body at the level of the first ventral; at one head-length posterior to the head; at approximately midbody; and at one head-length anterior to the vent. Head patterns were recorded by shading the appropriate portions of a dorsal and left lateral outline drawing of a *Tantilla* head. Color descriptions of living specimens were based upon Maerz and Paul (1950). All specimens were measured to the nearest half millimeter with a clear plastic ruler. Left maxillae were removed, cleaned gently with a needle, and dried under a light bulb before examination. In every case where extruded hemipenes were not in evidence, sex was determined by examining the reproductive tract. Sexual maturity of males was established on the basis of enlarged, contorted, or turgid vasa deferentia in larger specimens, and by positive sperm smears in the case of smaller individuals. The presence of ovarian follicles of varying size or of oviductal eggs was considered indicative of sexual maturity in females, in contrast to uniformly small follicles in immature individuals.

#### TAXONOMY

The characters found to be of taxonomic importance among the species of *Tantilla* in the southeastern United States are: (1) ventrals, (2) subcaudals, (3) tail to total length ratio, (4) degree of development of the light parietal band, (5) width of the black nuchal collar posterior to the parietal area, and (6) number of basal hooks of the hemipenis. Other characters recorded that either do not vary or do so without demonstrable geographic correlation are the following: (7) number of dorsal scale rows, (8) preoculars, (9) postoculars, (10) temporals, (11) supralabials, (12) infralabials, (13) number of supralabials entering the orbit, (14) number of infralabials contacting the anterior chin shields, (15) condition of the anal plate, (16) contact between the mental and anterior chin shields, (17) number of maxillary teeth, (18) length of retracted hemipenis, (19) degree of pigmentation of the postoculars and ultimate supralabial, (20) lateral extent of the

black nuchal collar, and (21) initial and terminal vertebral scales contacted by the black nuchal collar. Characters 1 to 21 were recorded for all populations.

#### THE PENINSULAR POPULATIONS.

Populations of *Tantilla* from peninsular Florida are presently designated as *Tantilla coronata wagneri* (Jan).

The holotype of *Homalocranon wagneri* was originally located at Munich, according to Jan and Sordelli (1866). Dr. Walter Hellmich indicated (*in litt.*) that it is not there and was perhaps destroyed during World War II. Dr. M. Torchio of the Museo Civico di Storia Naturale, Milan, which had many of Jan's types, has informed me that the Museum was destroyed during World War II and that if the type was there rather than at Munich, it has not survived. In lieu of examining the holotype, it is necessary to rely upon the description, and the fortunate illustration of the presumed type of Jan and Sordelli. I have compared Blanchard's translation of Jan's description with the original and find no discrepancies. Consequently references to the type description refer to Blanchard's translation.

The holotype had "Behind two or three gular scutes . . . 138 ventrals, an entire anal, and 45 double caudals." Disregarding the anal for the moment, when 138 ventrals are plotted against 45 caudals in scatter diagrams as in figure 1, it is obvious that the specimen lies well outside the range of variation of peninsular populations (with the possible exception of the Dade County population), and well within the distribution of *Tantilla coronata*. As sex of the type specimen is not given, it is plotted on scatter diagrams of both sexes. On this basis I conclude that Jan had at hand a specimen of *Tantilla coronata* from a non-peninsular population. Though the type locality is given as "Florida", it should be pointed out that Florida once extended from the Atlantic Ocean to the Mississippi River along the Gulf Coast. Even today those Louisiana parishes east of the Mississippi are called the "Florida parishes." As Jan named the specimen in 1862, it was probably not collected much later than 1859. By that time very few American naturalists had collected in peninsular Florida, and I doubt seriously that Professor Wagner numbered among those who did. *Tantilla coronata* is common in the area between the Appalachicola and Mississippi rivers, and I suspect that Jan's specimen was from this area. Nothing in the type description settles the issue. Presence of a single anal is noteworthy, however, for I found but two specimens among the 381 *Tantilla* I examined that had an undivided anal.

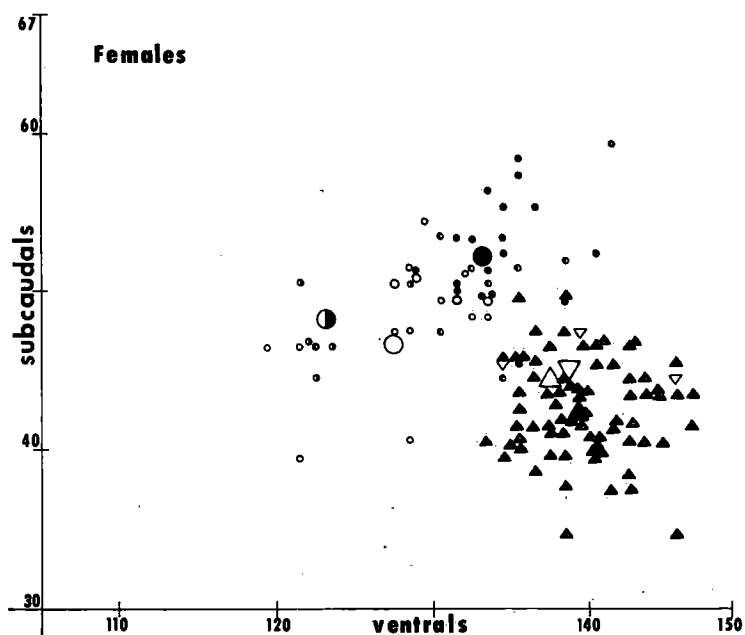
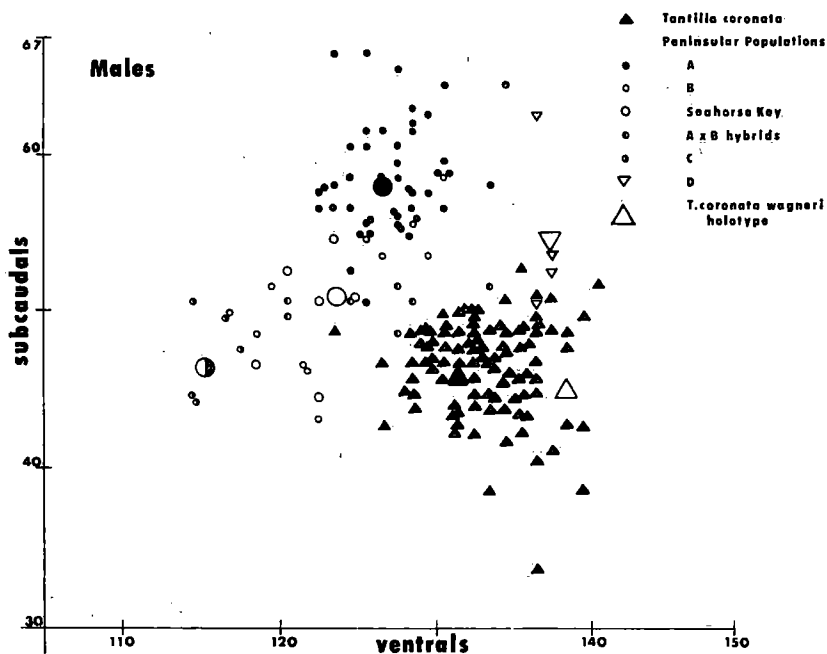


Fig. 1. Scatter diagrams plotting ventrals against subcaudals. Enlarged symbols represent population means, except where otherwise indicated.



The illustration in Jan and Sordelli of *H. wagneri* is that of a typical *Tantilla coronata* with a prominent parietal band. On the basis of the evidence cited, I place the name *Homalocranion wagneri* Jan, 1862 in synonymy of *Tantilla coronata* Baird and Girard, 1853.

While Blanchard was correct in stating that overlap in scale characters between peninsular *Tantilla* and *T. coronata* exists, this overlap is evident only when ventrals or subcaudals are considered separately. If viewed as a combination of characters, as in the scatter diagrams (figure 1), specimens from the peninsula, except for those from Dade and Monroe counties on the extreme southern periphery of the range, show no appreciable overlap with *T. coronata*: 4.1 percent of males and 6.1 percent of females from peninsular populations lie within the distribution of *T. coronata* on the scatter diagrams. Conversely, only 1 percent of males and 2.6 percent of females of *T. coronata* lie within the distribution of peninsular *Tantilla* in figure 1, again with the exception of Dade and Monroe Counties. I interpret this to mean that no intergradation exists between *T. coronata* and peninsular populations of *Tantilla*, which the distribution map (figure 2) substantiates. No specimens of *Tantilla* are available from a broad area between the Appalachicola and Suwannee rivers extending north to Chattahoochee and Irwin Counties, Georgia. Though the hiatus may be real, it may also reflect lack of collecting, for apparently suitable habitat occurs sporadically throughout this area.

The scatter diagrams also reveal substantial scutellation differences between Dade County *Tantilla* and other peninsular populations, and affinity between Dade County *Tantilla* and *T. coronata*. A hiatus of approximately 50 miles exists between the northernmost locality for Dade County specimens at Miami and the southernmost site for *Tantilla* at Boynton Beach, Palm Beach County. There is no evidence of intergradation between these two populations.

Hemipenial characters of all the main populations of southeastern *Tantilla* lend support to the conclusions drawn from characters of scalation. The hemipenis of *Tantilla* (figure 3) is single, bearing a simple sulcus spermaticus, and ornamented with undifferentiated spines. In *Tantilla coronata* the basal half is naked, the distal half spinose, with spine size decreasing toward the apex, which is covered with small spines. There are two basal hooks, a larger postero-lateral hook adjacent to the sulcus in the basal third, and a slightly smaller antero-medial hook in the mesal third of the organ. The hooks are well differentiated from the larger spines, being a good third longer and half wider than the basal spines in the apical half. Although

the spines show minor differences in extent and size, the hemipenes of peninsular populations from the Suwannee River south through Palm Beach County generally resemble that of *T. coronata*—with one important difference: only the large postero-lateral basal hook, adjacent to the sulcus, is present. The antero-medial hook has apparently been lost. Two basal hooks at approximately the same size are present in the Dade County population.

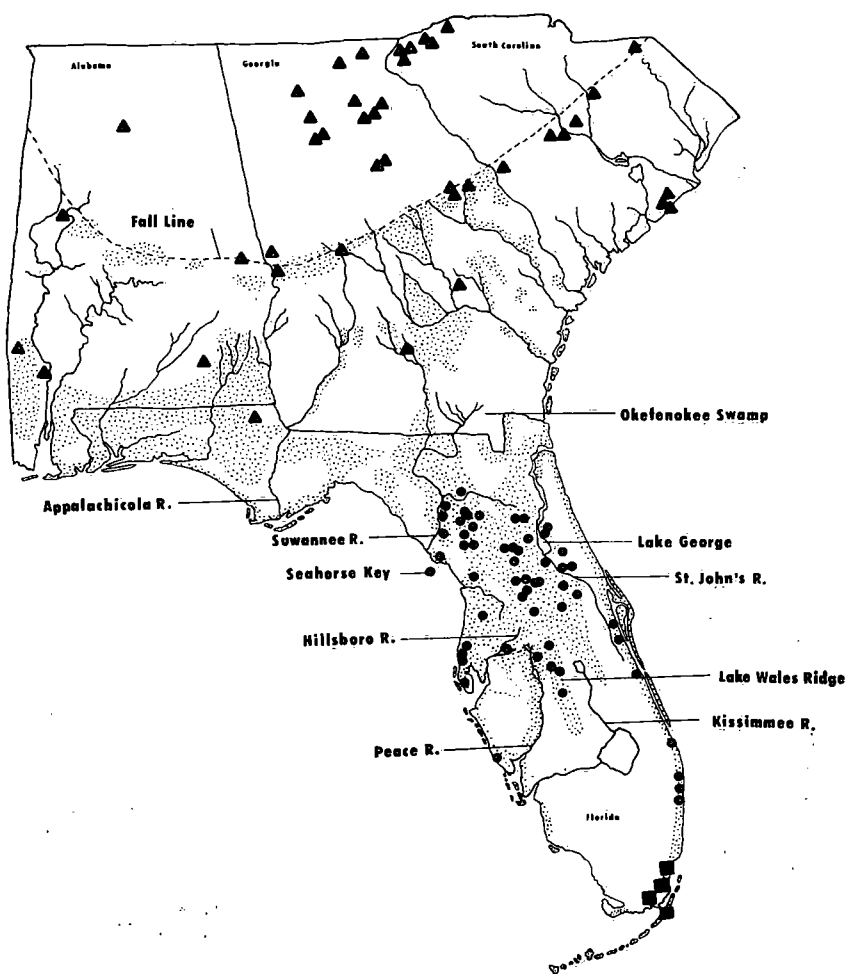


Fig. 2. Distribution of *Tanilla* in relation to availability of scrub and sand-hills habitat in southeastern United States. Triangles *T. coronata*; circles main peninsular population; squares Dade County population.



**a**



**b**



**c**



**d**

Fig. 3. Hemipenes of southeastern *Tantilla*: a, *T. coronata*; b, peninsular population A; c, peninsular population D; d, peninsular population C.

Other differences between these three populations exist, and will be discussed below, along with variation within the divisions. I believe that the characters discussed so far, in conjunction with the real or apparent hiatuses in distribution, justify division of the southeastern *Tantilla* into three distinct species. *Tantilla coronata* extends from Florida north and west of the Suwannee River to Virginia, the Mississippi River, and extreme southern Indiana. A second species extends from the Suwannee River south in Florida to the Peace River on the west coast, and to Broward County along the east coast. The third is restricted to Dade and northern Monroe counties in extreme southern Florida.

In recognition of its probable origin during fluctuations of Pleistocene sea levels, I designate the populations of *Tantilla* within peninsular Florida south of the Suwannee River and north of Dade County and the outlet of the Peace River into the Gulf of Mexico as

*Tantilla relictæ* new species

HOLOTYPE: UF 12421, an adult female collected 26 December 1960 on the south side of Babson Park, Polk County, Florida by Sam R. Telford, Jr.

PARATYPES: Polk County: UF 12429-1&2, 12420, 12419; Palm Beach County: UF 12430-1&2; Alachua County: UF 12406, 7973-1&2, 3586.

DIAGNOSIS: A small *Tantilla*, characterized by the presence of a single basal hook on the hemipenis, postero-lateral in position and adjacent to the sulcus spermaticus in the basal third of the organ. The species is composed of several populations varying somewhat among themselves in details of pattern and scutellation, divisible into three distinct subspecies. Ventrals range between 115 and 142; subcaudals from 39 to 67. Males have fewer ventrals and more subcaudals than females, and are slightly smaller. Although constant within subspecies, head pattern varies from completely black with no light parietal band, to a prominent parietal band separating the black head cap from the black nuchal collar, with extensive unpigmented areas extending forward along outer edges of parietals. Ratio of tail to total length varies between 18.5 and 29.1 percent, males having longer tails on the average. Maxillary teeth 14 to 16, usually 15. Head pointed in outline with countersunk lower jaw; to narrowly rounded with noncountersunk lower jaw, varying somewhat among populations.

DESCRIPTION OF HOLOTYPE: Adult female, 136.5 mm snout-vent

and 34.5 mm tail length. Ventrals 131; subcaudals 50; dorsal scales smooth, in 15 rows throughout; on each side are 1 preocular, 2 postoculars, 1 anterior and 1 posterior temporal, 7 supralabials, and 6 infralabials. Supralabials III and IV enter the orbit; infralabials I to IV contact the anterior chin shields; mental plate in contact with anterior chin shields; posterior chin shields are two-thirds length of anterior; rostral slightly scarred; anal divided. In preservative the head dorsum is black. A light parietal band, about one and one-half dorsal scales in width, extends from the rear fourth of parietals across the distal half of the secondary temporals; the light band is broken by a dark streak extending along the mesal edges of the parietals and the parietal suture to unite with the black first vertebral scale. The black nuchal collar is three and one-half vertebral scales in width and extends laterally on to scale row 2; supralabials I to IV and VI, the loreal region, and superior postocular are black; the distal fourth of inferior postocular, anterior fourth of primary temporal, and dorsal edge of supralabial V lack pigment; the distal half of supralabial VII lacks pigment, the light area merging with the parietal band. The mental, infralabials I to V, and adjacent edges of the anterior chin shields are suffused with black; infralabial VI has dark flecking. The dorsum is light tan, and the venter tannish white. In life, the dorsum was light tan (army brown, 6-A-10) throughout, becoming lighter laterally to pinkish tan (rosestone, 6-C-9). Tail venter pinkish gray (cobwebs, 5-B-7), becoming white along body venter. Parietal band tan (French beige, 13-A-7); head dorsum dark brown (sepia, 8-A-10); nuchal collar black.

#### VARIATION IN TAXONOMIC CHARACTERS.

The correlation and distribution of variation within *Tantilla relicta* show the total sample to be composed of several distinct groups which should be discussed individually. The three most distinct groups of specimens are treated below as subspecies, although no strong evidence is available to establish continuity of gene flow among them. For the moment they are designated populations A, B, and C.

Population A extends from the Suwannee River south to the Hillsborough River along the west coast of Florida, and in the central portion of the state, west of the St. Johns River to northern Polk County. It is apparently found only in sandhills and mesic hammock habitats.

Population B occurs in disjunct demes from the vicinity of Lake George south along the central ridge to southern Polk County (and presumably Highlands, as well), and in insular type situations along

TABLE 1. VARIATION OF VENTRALS AND SUBCAUDALS AMONG SOUTHEASTERN *Tantilla* POPULATIONS.

		Ventrals				Subcaudals			
		N	range	mean	S <sup>2</sup>	N	range	mean	S <sup>2</sup>
<i>T. coronata</i>									
	males	109	123-140	132.5	10.8	97	34-53	46.7	9.5
	females	86	133-147	140.0	10.2	77	35-50	43.1	9.0
<i>T. oolitica</i>									
	males	6	137-143	138.3	5.4	4	51-63	55.3	28.3
	females	5	135-146	140.2	19.8	3	45-48	46.3	2.5
<i>T. relictæ</i>									
Pop. A	males	50	123-135	127.5	6.9	45	51-67	59.1	10.7
	females	28	129-142	134.2	9.6	20	46-60	53.3	13.1
Pop. B	males	8	117-131	123.6	22.9	8	44-59	50.8	26.1
	females	14	120-134	128.0	19.2	10	40-55	48.1	22.3
Pop. C	males	7	115-118	116.3	2.8	5	45-51	47.8	7.8
	females	10	119-129	123.2	8.0	5	45-51	48.2	7.3
Pop. D	males	8	121-134	126.8	18.7	7	48-52	50.6	2.0
	females	11	123-139	133.2	40.4	8	45-54	50.3	10.1
Seahorse									
	males	6	119-125	122.5	4.6	6	45-55	50.2	13.8
	females	5	128-134	130.6	5.8	4	50-51	50.5	0.3

the west coast from Seahorse Key in Levy County to Charlotte County north of the mouth of the Peace River. In areas of sympatry with population A along the northern ridge, B is restricted to scrub habitat, but in allopatric areas of the southern ridge, it also occurs in sandhills.

Population C is found in coastal dunes and scrub from central Brevard County to southern Palm Beach County. The southernmost record is some 50 miles north of the distinctive Dade County population.

Population D is comprised of 19 specimens that cannot be assigned satisfactorily to either A or B, although they were collected from scattered localities within and on the periphery of the ranges of both A and B. These specimens show an overlap of characters from both A and B and may represent intergrades. They are the principal reason for considering A and B conspecific. The Seahorse Key population of *T. relictus* resembles population B in characters of scutellation and body proportions, but differs somewhat in patterns; it is therefore treated separately in the tables and figures. Variation in ventrals and subcaudals is presented in Table 1.

The Dade County population evidently has the highest number of ventrals among these populations, while the *T. relictus* population closest to it geographically, C, has the lowest. *T. coronatus* has the fewest subcaudals, and the *T. relictus* population geographically closest, A, has the highest number. It is tempting to speculate that these are examples of character displacement.

Variation in proportionate tail length is considerably less than in scale characters. Table 2 presents the ratio of tail length to total length among the various samples, while figure 4 depicts regression lines for this character, calculated by the method of Snedecor (1946: 103).

In correlation with subcaudal number, population A again has the proportionately longest tail, while *T. coronatus* has the shortest.

As the sexes showed no significant differences in color pattern, the data were lumped for analysis. Sorting specimens according to the distribution of pigment in the parietal and temporal regions permitted dividing them into ten different categories (figure 5) ranging from specimens with a completely black head cap which fused with the nuchal collar (category 1) to specimens in which only the anterior, central portion of the parietal was pigmented (category 10). This procedure provided a simple method of quantifying the pattern data (table 3).

TABLE 2. TAIL LENGTH IN SOUTHEASTERN *Tantilla* EXPRESSED AS PERCENT OF TOTAL LENGTH.

	Males				Females			
	N	range	mean	S <sup>2</sup>	N	range	mean	S <sup>2</sup>
<i>T. coronata</i>	94	17.2-23.0	20.6	1.4	77	15.9-21.2	18.2	5.4
<i>T. oolitica</i>	4	20.8-22.4	21.9	0.6	3	19.1-19.6	19.3	0.1
<i>T. relictæ</i>								
Pop. A	45	21.7-28.7	25.0	2.1	20	19.3-29.1	22.3	4.6
Pop. B	7	20.9-23.5	22.2	1.2	10	18.5-23.1	20.9	2.1
Pop. C	5	21.7-24.0	22.7	1.8	5	18.7-23.2	21.1	2.8
Pop. D	7	20.7-23.8	21.9	1.7	8	19.0-22.7	21.2	1.9
Seahorse	6	21.5-25.2	23.0	1.8	4	20.6-21.6	21.2	1.0



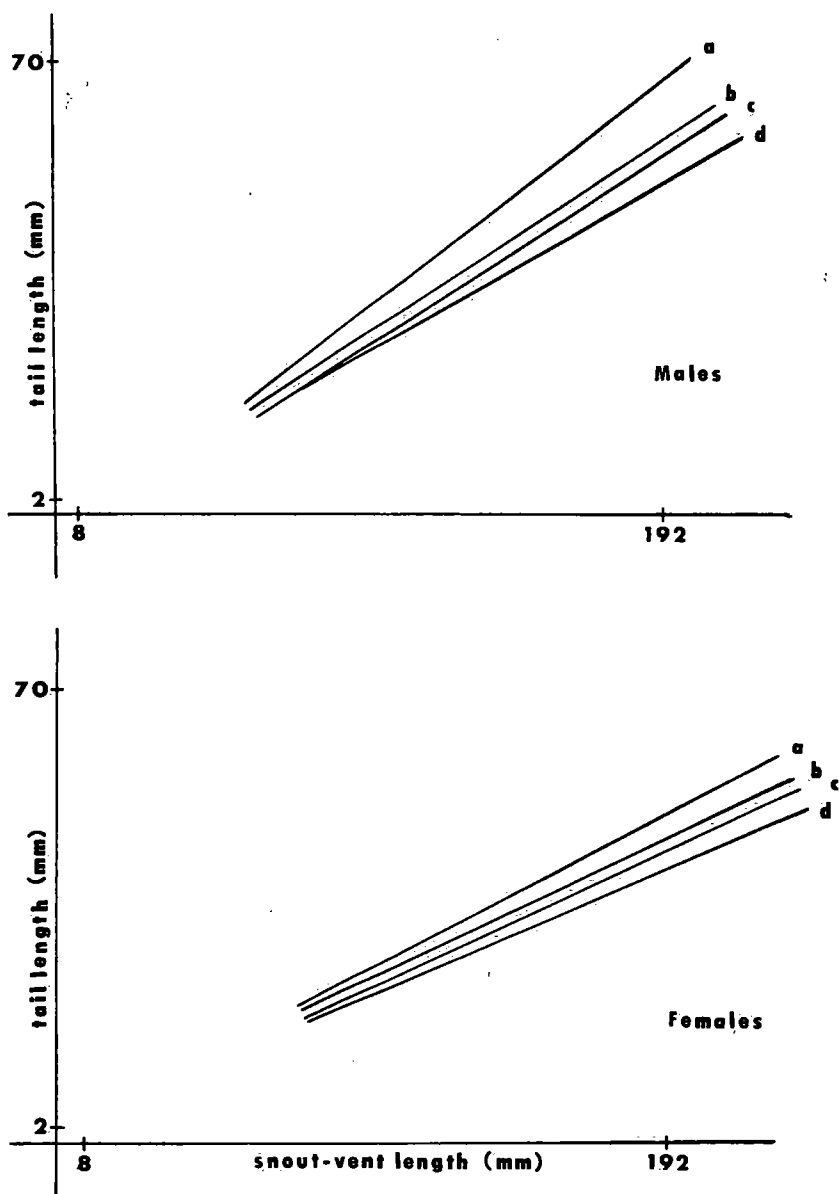


Fig. 4. Regression lines depicting the relationship of tail length to snout-vent length: a, peninsular population A; b, peninsular population B; c, *T. coronata*; d, peninsular population D.

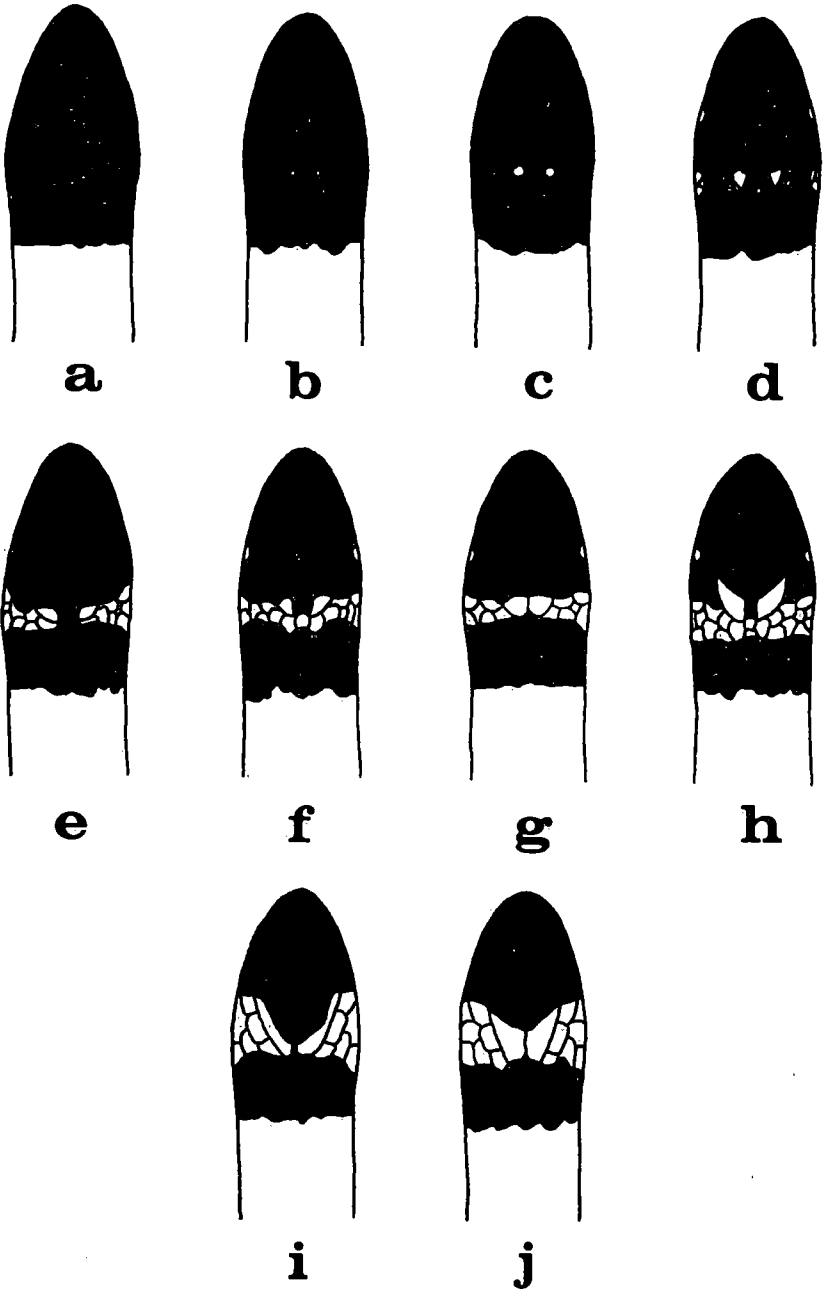


Fig. 5. Variation in parietal pattern among southeastern *Tantilla* populations. Categories a-d are non-banded, e-j banded.

TABLE 3. PARIETAL PATTERN\* IN SOUTHEASTERN *Tantilla* POPULATIONS, EXPRESSED AS PERCENT OF SAMPLE

	Pattern Types											mean
	N	a	b	c	d	e	f	g	h	i	j	
<i>T. coronata</i>	117				3	16	37	23	9	9	3	6.6
<i>T. oolitica</i>	10	80			10	10						1.7
<i>T. relicta</i>												
Pop. A	77	20	27	39	14							2.5
Pop. B	23				14	56	22		4	4		5.4
Pop. C	18					33		6	22	22	17	7.5
Pop. D	19	16		42	32	5			5			3.4
Seahorse	11	9	18	9	36	18		9				3.7

\* See Fig. 5.

Somewhat arbitrarily, the dividing line between banded and non-banded patterns was set between categories 4 and 5, with pattern types 5 and above considered banded. According to this classification population A is clearly 100 percent nonbanded, while 87 percent of B, 100 percent of C, and 96.6 percent of *T. coronata* are banded. The small sample from Dade County (9) are all non-banded; a single specimen from Key Largo has a broken band. Of the 11 snakes in the small Seahorse Key sample, 8 are nonbanded, as are 2 of 4 *T. relicta* from Charlotte County. The series of possibly intergradient *T. relicta*, D, whose body proportions and scutellation characters are perhaps closer to population B, are 89.5 percent non-banded.

Another pattern character of taxonomic use is the width of the black nuchal collar at midline. The data are readily quantified by expressing the width in terms of number of vertebral scales pigmented (table 4).

The banded populations, *T. coronata*, B, and C, have nuchal collars predominantly four scales or less in width, the percentages of the respective samples being 99.5, 91.5, and 67.0. Of the nonbanded populations, A and Dade County, 66 percent of A have collars five scales or more in width, while 4 of the 10 Dade County specimens have collars of this width. Eight of the 11 Seahorse Key *Tantilla relicta* and 52 percent of the possibly intergradient population, D, have collars five scales or more in width. Again, with respect to both pattern components discussed, the greatest contrast is between *T. coronata* and the *T. relicta* population closest to it geographically, population A.

TABLE 4. WIDTH OF NUCHAL COLLAR IN SOUTHEASTERN *Tantilla* POPULATIONS, EXPRESSED AS PERCENT OF EACH SAMPLE

	Width in Vertebral Scales										
	N	1	2	3	4	5	6	7	8	9	mean
<i>T. coronata</i>	183		13	63	23.5		0.5				3.0
<i>T. oolitica</i>	10		10	20	30	20	20				4.2
<i>T. relicta</i>											
Pop. A	76			16	18	46	9	8	3		4.8
Pop. B.	23	4	17	26	44	9					3.4
Pop. C	18		11	39	17	33					3.7
Pop. D	19	11	5	16	16	47		5			4.1
Seahorse	11			18	10	27		27		18	5.8

In summary of variation in the five characters discussed above, it is evident that the three main populations of *T. relicta* are better distinguished among themselves, as well as from *T. coronata* and the Dade County population, by parietal pattern and width of the nuchal collar than by characters of scutellation and body proportion. These latter, however, are useful in some instances, i.e., the longer tail and greater number of subcaudals of population A in comparison to other populations, and the lower number of ventrals in an admittedly inadequate sample of population C.

I believe that sufficient grounds exist to designate populations A, B, and C as subspecies of *Tantilla relicta*, representing geographically and ecologically delimited populations that possess within themselves common and distinctive morphological features.

In accordance with this concept of the subspecies, I designate population B

*Tantilla relicta relicta* new subspecies

HOLOTYPE: UF 12421, an adult female collected 26 December 1960 on the south side of Babson Park, Polk County, Florida by Sam R. Telford, Jr.

PARATYPES: UF 12429-1&2, 12420, 12419, 12418, 12424; USNM 23429, 23430; CNHM 29592, 29595.

DIAGNOSIS: A population of *Tantilla relicta* composed of many more or less isolated demes, restricted in northcentral Florida to scrub habitat, but occurring also in sandhills of southcentral Florida, where syntopic to other subspecies of *T. relicta*. Ventrals range from 117 to 134; subcaudals between 40 and 59. Tail length varies

from 18.5 to 23.5 percent of total length. Parietal pattern is predominantly banded (87 percent). The nuchal collar is usually (43.5 percent) 4 scales wide at midline, but ranges from 1 to 5 (mean, 3.4 scales). The head is pointed in outline, with countersunk lower jaw.

**GEOGRAPHICAL RANGE:** Peninsular Florida from the vicinity of Lake George, Marion County, south along the central ridge to southern Polk County. Presumably this subspecies occurs in Highlands County as well. Disjunct populations occur in coastal scrubs of Charlotte, Sarasota, and Pinellas counties, and on Seahorse Key, Levy County.

**DESCRIPTION OF HOLOTYPE:** The holotype is described above as holotype of *Tantilla relicta* sp. nov.

In recognition of Wilfred T. Neill's contributions to the biography of Florida, I take pleasure in designating the nonbanded population of *Tantilla relicta* in northcentral Florida (A) as

*Tantilla relicta neilli* new subspecies

**HOLOTYPE:** UF 12406, an adult male collected 12 July 1961 on the University of Florida campus, Gainesville, Alachua County, Florida, by John Funk.

**PARATYPES:** UF 7973-1&2, 3586, 12404, 8930, 1047, 9586; CNHM 8558; UMMZ 44967; MCZ 43130.

**DIAGNOSIS:** A population of *Tantilla relicta* relatively continuous in distribution in habitats of sandhills and mesic hammock of northcentral Florida. Ventrals range from 123 to 142; subcaudals between 46 and 67. Tail length varies from 19.3 to 29.1 percent of total length, and is proportionately longer in this subspecies than in any other population of *Tantilla* in southeastern United States. The parietal pattern is nonbanded in all specimens examined, with only 15 percent having unpigmented areas on the parietals larger than a dorsal scale in size. The black nuchal collar, which fuses with the black parietal area, is usually (46 percent) 5 scales wide at midline, but varies from 3 to 8 (mean, 4.8 scales). The head is less sharply pointed in outline than that of *T. relicta relicta*, and the lower jaw is less noticeably countersunk.

**GEOGRAPHICAL RANGE:** Peninsular Florida from the Suwannee River south to the Hillsborough River and northern Polk County, and east to the St. Johns River.

**DESCRIPTION OF HOLOTYPE:** Adult male, 168.0 mm snout-vent and 52.0 mm tail length. Ventrals 131; subcaudals 60; dorsal scales smooth, in 15 rows throughout; on each side are one preocular, two

postoculars, one anterior and one posterior temporal, seven supralabials, and six infralabials. Supralabials III and IV enter the orbit; infralabials I to IV contact anterior chin shields; mental plate separated from anterior chin shields by infralabials I; posterior chin shields are two-thirds length of the anterior; anal plate divided. In preservative the head dorsum is black with no light parietal band; an area the size of one dorsal scale on the posterior tip of the parietals lacks pigment. The black nuchal collar, fused with the black of the parietals, extends onto the anterior tip of vertebral scale IV, and laterally onto scale row 2 of each side. The mental, infralabials I to V, and lateral half of the anterior chin shields are heavily suffused with black; infralabial VI and the gular scales have some black flecking. The entire loreal and postocular regions and supralabials I to VI are black; supralabial VII is black except for a small light area on the rear ventral third. The dorsum is dark tan, venter white. In life the dorsum was dark tan (argus brown, 7-A-12) becoming lighter (Natal brown, 7-A-10) on the sides. The tail venter was yellowish cream (amber white, 11-C-1), and the body venter pinkish gray (greystone, 12-A-2). The head dorsum and gulars were black, with the gulars a slightly lighter shade. The parietal spots were dark tan (Vandyke brown, 7-A-11).

The third population of *T. relicta*, C, inhabits coastal dunes and scrub along a narrow strip of Pamlico terrace in southeastern Florida. In reference to the geological origin of its habitat, I designate this population

*Tantilla relicta pamlica* new subspecies

**HOLOTYPE:** UF 12430-2; an adult female collected 4 February 1960 approximately 1 mile south of Boynton Beach, Palm Beach County, Florida, by Robert H. Mount.

**PARATYPES:** UF 12430-1, 12423; MCZ 19146, 16272, 16273, 12802; UMMZ 55779-1&2, 84193.

**DIAGNOSIS:** A population of *Tantilla relicta* occurring in relatively isolated coastal dunes and scrub of southeastern Florida. Ventrals range from 115 to 129 and are fewer in this subspecies than in any other southeastern *Tantilla* population. Subcaudals range between 45 and 51, and tail length varies from 20.7 to 24.0 percent of total length. The parietal pattern is banded in all specimens examined; over 60 percent show a trend toward total absence of pigment on the parietal, supraocular, and temporal regions, a reduction in pigmentation found in less than 10 percent of *T. r. relicta*. The nuchal collar is usually (40 percent) 3 scales in width, and ranges from 2 to 5 (mean,

3.7 scales). The head is prominently pointed in outline, with countersunk lower jaw. In life the dorsum is reddish brown, a color seldom observed in *T. r. relicta*.

**GEOGRAPHICAL RANGE:** The east coast of Florida from the vicinity of Cape Canaveral south to southern Palm Beach County, and limited to the west by the Kissimmee River valley.

**DESCRIPTION OF HOLOTYPE:** Adult female, 166.0 mm snout-vent length, with an incomplete tail 31.0 mm long. Ventrals 120; subcaudals, incomplete) 30; scales smooth, in 15 rows throughout; on each side are one preocular, two postoculars, one anterior and one posterior temporal, seven supralabials, and six infralabials. Supralabials III and IV enter the orbit; infralabials I to IV contact the anterior chin shields; mental plate is in contact with the anterior chin shields, which are one-third longer than the posterior chin shields; anal plate divided. In preservative the frontal, supraoculars, and anterior two-thirds of the parietals are black; the unpigmented posterior third forms a parietal band, which is narrowed slightly at midline by the black vertebral scale I; the nuchal collar is black and extends onto the anterior edge of vertebral scale V, and laterally on both sides onto scale row 2. The medial anterior corners of the secondary temporal are black, the remainder unpigmented. The loreal region, supralabials I to IV, and superior postocular are black; pigment is lacking from the rostral, three-fourths of the internasals, and nasal half of the prefrontals, anterior edge of the frontal, antero-ventral two-thirds of the primary temporals, distal edge of the inferior postocular, supralabials V to VII, and infralabials V and VI. Infralabials I to IV have a light suffusion or flecking of black. The dorsum is light pinkish tan, and the venter pinkish white. In life the dorsum was light reddish brown (cedarwood, 6-G-10), becoming lighter somewhat (plantation, 6-D-11) in the anal region. Sides were pinkish tan (roseglow, 5-D-9). The tail venter was pinkish gray (cobweb, 5-B-7), becoming lighter (iris mauve 3-B-7) on the body venter. The parietal band was a prominent tan (suntan, 13-B-7), while the head dorsum was dark brown (bracken, 8-C-12), and the nuchal collar black.

I designate the distinctive species of *Tantilla* restricted to Dade and Monroe counties, Florida, after its association with the dominant geological formation of the area, the Miami oolite, as

*Tantilla oolitica* new species

**HOLOTYPE:** UF 17326, an adult male collected in April 1955 in Miami, Dade County, Florida in a vacant lot on southwest 27th

Avenue near 24th Street. Collector unknown, received through the courtesy of Dennis R. Paulson.

PARATYPES: Dade County, UF 17325, MCZ 37399; CM 20077; UM 55-137, 55-636; Monroe County: UMMZ 103174.

DIAGNOSIS: A species of *Tantilla* resembling *Tantilla coronata* in details of hemipenial structure and scutellation. The hemipenis has both basal hooks, the postero-lateral hook adjacent to the sulcus spermaticus in the basal third, and the antero-medial hook, approximately equal in size to the postero-lateral, in the mesal third of the hemipenis. Ventrals range from 135 to 146; subcaudals between 45 and 63. Males appear to have more subcaudals than females; too few specimens are available to demonstrate a trend in ventrals. Females exceed males in size. Two types of head pattern are evident; all specimens from Dade County exhibit a completely black head and neck with no light parietal band; a single specimen from Key Largo, Monroe County, has a prominent but broken band separating the black head cap from the black nuchal collar. Males have slightly longer tails than females, with tail length ranging (both sexes) from 19.1 to 22.4 percent. Maxillary teeth 14, 15 or 16. Head broadly rounded, with noncountersunk lower jaw.

DESCRIPTION OF HOLOTYPE: Adult male, 166.5 mm snout-vent and 48.0 mm tail length. Ventrals 137; subcaudals 63; dorsal scales smooth, in 15 rows throughout; 1 preocular, 2 postoculars, 1 anterior and 1 posterior temporal, on each side. There are 7 supralabials on the left and 6 on the right, with III and IV entering the orbit on both sides. Infralabials are 5 on the left and 6 on the right; I to III contact the anterior chin shields on the left, and I to IV on the right side. Mental plate contacts the anterior chin shields; posterior chin shields two-thirds length of the anterior. In preservative the head dorsum is black; no light parietal collar, black of the head extending along the neck to the middle of vertebral scale IV and to scale row 2 laterally. Mental and infralabials heavily suffused with black, as is the rear half of infralabial VI at angle of the jaws. Supralabials I to IV and postoculars completely black, as is loreal region. Supralabials V and adjacent portions of VI and primary temporal lack pigment; supralabial VII largely black, lacking pigment in most of rear half. Dorsum is light tan, and venter white. No color notes from life available.

#### THE NON-PENINSULAR POPULATIONS.

Schwartz (1953) based his diagnosis of *Tantilla coronata mitrifer* upon three main points:



- (1) "posterior ventrad extension of the black cap tends not to reach the upper labial border . . ."
- (2) "black collar does not extend farther posteriorly than the fourth scale row in the midline . . ."
- (3) "with more ventral and less subcaudal scutes on the average . . ."

I have examined the holotype from Caesar's Head, Greenville County, South Carolina (CHM 53-92.2), and six paratypes from Roundtop Mountain, Rutherford County, North Carolina (AMNH 66207-66211). Other paratypes were not made available to me. The holotype certainly agrees with the main points of the subspecies diagnosis quoted above, but of the six paratypes I examined, only one agrees with the holotype in character (1) in the other five, the ventrad extension extends well past the upper labial border. This variation appears commonly in other parts of the range; specimens from Indiana, Edmonson County, Kentucky, and Jackson County, Florida, lack a ventrad extension to the black cap. Character (2) also lacks exclusiveness: one of the six paratypes has the black nuchal collar extending on to vertebral scale V, although in the other paratypes and holotype the collar terminates on scale IV. In a series of 37 *T. coronata* from coastal plain Mississippi, 62 percent (23) have the nuchal collar ending on scale IV or anteriorly; in 38 percent (14), it extends onto scale V. Thus, it appears that two of the main characters used by Schwartz are not sufficiently exclusive to be of diagnostic value. This leaves only characters of (3) to be evaluated.

Ventrals and subcaudals of 5 female *T. coronata mitrifer* types were compared with a series of 14 female coastal plain *T. coronata coronata* from Charleston and Berkeley counties, South Carolina, specimens which were examined by Schwartz. Admittedly five specimens is an inadequate sample, but standard tests (the Student T) were performed anyway, with the following results: there is a difference in means of ventrals and subcaudals between coastal plain females (138.3, 42.5) and *T. coronata mitrifer* females (142.8, 39.5). The difference in ventrals is significant at the .05 level; that in subcaudals is not significant at the same level.

Schwartz states that *T. coronata mitrifer* has a darker dorsum than does *T. coronata coronata*. I observed that in the few living *T. coronata* I have seen those specimens from the Upper Piedmont were considerably darker than those from the Coastal Plain. In many preserved specimens this distinction is still remarkably evident, and

specimens from the Blue Ridge and Upper Piedmont constitute a distinct group from those of the Coastal Plain. It seemed reasonable that two distinct populations of *Tantilla coronata* might exist, those of the Coastal Plain and those Schwartz called *T. coronata mitrifer*, but including as well demes occupying the Upper Piedmont. The region of intergradation might logically follow the Fall Line. With this hypothesis in mind, I segregated *Tantilla* from North and South Carolina, eastern Tennessee, Georgia, Alabama, Mississippi, and Louisiana into three groups: Blue Ridge and Upper Piedmont, Lower Piedmont and Fall Line, and Coastal Plain (table 5).

TABLE 5. SCALE CHARACTERISTICS OF *Tantilla coronata* POPULATIONS

	Coastal Plain	Fall Line	Upper Piedmont and Montane
mean ventrals			
males	131.6	134.2	132.0
females	138.1	141.9	142.2
mean subcaudals			
males	46.9	46.5	46.3
females	43.5	44.4	42.6
mean proportionate tail length (%)			
males	20.7	20.5	20.1
females	18.6	18.5	18.3
mean collar width in number of scales			
males	3.1	2.9	2.6
females	3.1	3.1	2.8
distal vertebral scale included in collar (% of sample)			
males 3	1.8	11.1	11.0
4	50.0	55.6	89.0
5	48.2	33.3	
females 3			11.8
4	65.8	57.1	70.6
5	31.6	42.9	17.6
6	2.6		

If one postulates that *T. coronata mitrifer*, in a wider sense geographically than Schwartz defined it, is characterized by more ventrals, fewer subcaudals, a narrower nuchal collar that tends to lie

more anteriorly on the neck, and a shorter tail, in combination with a darker dorsum, in comparison with *T. coronata* from the Coastal Plain, then the data cited tend to support each of these distinctions. And in almost every character, specimens from the proposed region of intergradation are intermediate between *mitrifer* (sensu latu) and *coronata* (sensu strictu). Standard statistical comparison (the Student T test) was made for each of these characters. Differences in mean number of ventrals of both sexes, position of the band (data lumped, as males and females show no significant differences) and collar width in males are significant at the .05 level. Differences in mean number of subcaudals and proportionate tail length in both sexes, and collar width in females are not significant at .05.

On the basis of this analysis, I think a weakly defined population of *Tantilla coronata* exists in montane regions and the Upper Piedmont of North and South Carolina, Georgia, eastern Tennessee, and Alabama, to which the subspecific designation *Tantilla coronata mitrifer* Schwartz might be applied. I consider the variation in scale characters, however, to be insufficient to warrant such distinction. Although a striking contrast in coloration of the dorsum apparently exists, as illustrated by color descriptions below, living material available to me has been too meager to substantiate the value of this character. At this time, I think it is best to relegate the subspecies *T. coronata mitrifer* to the synonymy of *Tantilla coronata* Baird and Girard, and recognize no subspecies of this wide-ranging species.

It is appropriate at this point to define my concept of the species *Tantilla coronata*, as developed from examination of 215 specimens from all areas of its range.

*Tantilla coronata* Baird and Girard, 1853

HOLOTYPE: USNM 1876, collected in Kemper County, Mississippi, by D. C. Lloyd.

DIAGNOSIS: A species of *Tantilla* characterized by the presence of two basal hooks on the hemipenis, one posterolateral in position and adjacent to the sulcus spermaticus in the basal third of the organ, and the other, slightly smaller and anteromedial in position, in the mesal third of the hemipenis. Ventrals range from 123 to 147; subcaudals between 34 and 53. Males have fewer ventrals and more subcaudals than females, and longer tails. Tail to total length ratio varies from 15.9 to 23.0 percent. A prominent light parietal band is present in most (96.6 percent) specimens, separating the black cap of the head from the black nuchal collar. The nuchal collar is usually (76 percent) 3 or fewer scales in width at midline, ranging from

2 to 6 (mean, 3.0). On each side are usually one preocular, two postoculars, one anterior and one posterior temporal, seven supralabials, and six infralabials. Supralabials III and IV enter the orbit; infralabials I to IV contact the anterior chin shields, which may or may not be separated from the mental plate by infralabials I. Posterior chin shields two-thirds length of anterior. Anal plate divided. Maxillary teeth (one side) 14 to 18, usually (55 percent) 16. Dorsum ranges from tan in coastal plain populations to dark brown in montane localities; venter white.

**GEOGRAPHICAL RANGE:** *T. coronata* is found from Florida west of the Suwannee River westward to the Mississippi River and north to southern Indiana and Virginia.

A specimen of *T. coronata* from Coffee County, Alabama (UF 12387) was obtained within a day of its preservation, and the following color notes taken. The dorsum was uniform light brown (army brown, 6-A-10), becoming tan (rose blush, 5-C-9) laterally. The venter ranged from cream (9-D-2) beneath the tail to pinkish white (tulleul-buff, 10-A-2) anteriorly. The nuchal collar was black, preceded by a gray-brown (manon, 6-A-9) parietal band. The black dorsal surface of the head faded to gray (32-A-1) on internasals and prefrontals. This specimen is representative of Coastal Plain populations.

Another specimen (UF 12409) collected in Cobb County, Georgia presents a vivid contrast to the Coastal Plain population. In life the dorsum was dark brown (sepia, 8-A-10) distally, becoming slightly lighter (moose, 8-C-10) at midbody, and light brown (bark, 8-C-11) on the anterior third of the body. The sides of the body were dark tan (bracken, 8-C-12). The pinkish gray (rosedust, 6-B-2) tail venter became gradually lighter to pinkish white (folkstone, 13-A-3) on the anterior third. The parietal band was cream (vanilla, 10-C-3), and the nuchal collar and dorsal surface of the head were black. Identical coloration was present in a series of three *T. coronata* (UF 12402) from 2 miles south of Millry, Washington County, Alabama, well within the Coastal Plain. In scalation and pattern, these specimens clearly belong to Coastal Plain *T. coronata*. As the Black Warrior River system flows from the Piedmont to the Gulf of Mexico through this region, it may well be that some gene flow from Upper Piedmont populations, which extend south as far as Tuscaloosa, follows this drainage system well into the Coastal Plain.

*Tantilla coronata* extends up the eastern Mississippi Valley through western Tennessee and Kentucky to southern Indiana. The Indiana series does not differ appreciably from Coastal Plain Mississippi speci-

TABLE 6. SUMMARY OF VARIATION IN CHARACTERS LACKING TAXONOMIC SIGNIFICANCE

Character	Normal condition	Variations (No. cases)	% of each population varying from normal						
			A	B	C	D	E	F	G
preoculars	1-1	2-1 (1)							
		1-2 (1)	1.0	4.4				5.3	
		0-0 (2)							
postoculars	2-2	2-0 (1)							
		2-1 (2)	1.0	4.4	2.6	16.6	9.1	5.3	
		1-2 (4)							
		1-1 (3)							
supralabials	7-7	7-6 (7)							
		7-4 (1)	1.5	8.2	3.8		9.1		27.2
		6-6 (4)							
supralabials in orbit	III,IV-III,IV	III,IV-II,III II,III-II,III	(1) (3)	1.0					9.1
infralabials	6-6	7-7 (1)							
		7-6 (2)							
		6-7 (5)							
		6-5 (7)	6.2	8.7	2.6		9.1		36.4
		5-6 (2)							
		6-4 (1)							
		5-5 (3)							

TABLE 6. SUMMARY OF VARIATION IN CHARACTERS LACKING TAXONOMIC SIGNIFICANCE (continued)

Character	Normal condition	Variations (No. cases)	% of each population varying from normal						
			A	B	C	D	E	F	G
infralabials contacting anterior chin shields	I-IV,I-IV	I-IV,I-III (9)							
		I-III,I-IV (5)							
		I-V,I-IV (1)							
		I-IV,I-V (4)	6.7	8.7	2.6	5.6	18.2	5.3	45.5
		I-IV,I-II (1)							
		I-III,I-III (4)							
		I,II,IV,V;I-IV (1)							
		I-III,V;I-V (1)							
temporals	1&1,1&1	1&1&1,1&1&1 (7)							
		1&1&1,1&1 (7)							
		1&1,1&1&1 (7)	6.2	4.4	9.0	11.1			.91
		1&1,0 (1)							
		1&1,1&2 (1)							
dorsal scale rows	15-15-15-15	17-15-15-15 (1)							
		16-15-15-15 (2)							
		14-15-15-15 (2)							
		15-14-15-15 (1)	3.1		2.6			5.0	9.1
		14-14-15-15 (1)							
		15-16-15-15 (1)							
		15-13-15-15 (1)							
		15-15-15-13 (1)							
anal plate	divided	single (2)	0.5		1.3				

A. *T. coronata*  
 B. *T. relictata relictata*  
 C. *T. relictata neilli*

D. *T. relictata pamlica*  
 E. Seahorse *T. relictata*  
 F. *relictata* x *neilli* intergrades

G. *T. oolitica*

mens. A single specimen was available from southern Virginia, and resembles those from coastal North Carolina. I have seen only two *T. coronata* from Florida, both from the vicinity of Marianna, Jackson County, which lies west of the Appalachianicola River, and these resemble the Alabama and Mississippi specimens. Although no specimens are in existence from the region between the Appalachianicola and Suwannee rivers, south of Chattahoochee County, Georgia, *T. coronata* may be there. It does not cross the Suwannee River into peninsular Florida.

#### VARIATION IN CHARACTERS OF NO TAXONOMIC SIGNIFICANCE.

Most of the variation found in characters that lack taxonomic significance is presented in Table 6. Temporals and infralabials were found to be the most variable scales, and less than 10 percent of these varied from the usual condition in each population sampled, except in the *T. relicta* sample from Seahorse Key and the *T. oolitica* sample. Both samples numbered only 11 specimens each, and while small sample size probably influenced disproportionately the percentage of specimens varying from the norm, the facts that both populations are insular in nature and probably small in numbers may also be of moment. In the 11 *T. oolitica* specimens, 4 of the 8 showing scale aberrations were aberrant in multiple characters. Most cases of multiple aberrations observed in all samples were correlations between variations in labial number and the number of supralabials entering the orbit or infralabials contacting the anterior chin shields. Table 7 presents the percentages of each sample that vary from the normal scutellation listed in Table 6.

TABLE 7. PERCENTAGES OF ABERRANT SPECIMENS IN  
SOUTHEASTERN *Tantilla* POPULATIONS

	N	% aberrant in at least one character	% with multiple aberrations
<i>T. coronata</i>	195	15.4	43.4
<i>relicta</i> x <i>neilli</i> intergrades	19	15.8	1/3
<i>T. relicta neilli</i>	78	19.3	26.6
<i>T. relicta pamplica</i>	18	27.8	1/5
<i>T. relicta relicta</i>	23	30.2	2/7
Seahorse <i>T. relicta</i>	11	36.4	1/4
<i>T. oolitica</i>	11	73.0	4/8
all peninsular populations	165	25.4	31.0

The peninsular populations clearly show a trend toward more aberrant individuals than does *T. coronata*. I attribute this to the distribution of peninsular *Tantilla* in discontinuous demes, with gene flow severely restricted by habitat barriers. The slightly lower percentage of aberrant individuals of *T. relictæ neilli* may reflect greater continuity of gene flow within the sandhills and mesic hammock habitats, in contrast to the insular nature of the occurrence of scrub. No significant differences were found between the sexes.

Through an oversight on my part, one character, not listed above, was not recorded for all specimens examined. This is the contact of the mental plate with the anterior chin shields, and its corollary condition, separation from them by infralabials I. In view of the importance attributed to this character in some descriptions of *Tantilla* species, 53 specimens available to me at the time the oversight was discovered were checked to determine whether or not the character might be taxonomically useful. Table 8 tabulates the results.

Clearly, either condition may be encountered within the same population, and from this small sample, equal frequency is indicated. No correlations with sex were found. Descriptions of *Tantilla* species that stress this character should be re-evaluated.

TABLE 8. CONTACT OF MENTAL AND ANTERIOR CHIN SHIELDS  
IN SOUTHEASTERN *Tantilla* POPULATIONS

	N	Contact	No contact
<i>T. coronata</i>	22	15	7
<i>T. oolitica</i>	3	1	2
<i>T. relictæ relictæ</i>	6	3	3
<i>T. relictæ neilli</i>	10	5	5
<i>T. relictæ pamlica</i>	2	2	
<i>relictæ</i> x <i>neilli</i> intergrades	2	2	
Seahorse <i>T. relictæ</i>	8	2	6
Total	53	30	23

Maxillary dentition of several *Tantilla* species was described by Smith (1940: 61). In the group to which *T. coronata* belongs the two abruptly enlarged, grooved rear teeth are not in line with the anterior smaller teeth and are separated from them by a diastema. The 83 maxillae, I have examined in this study, 49 from *T. coronata*, 3 from *T. oolitica*, and 31 from *T. relictæ*, all have a similar morphology. The diastema varies from one to two tooth spaces in width,



and the enlarged teeth are approximately three times the size of the preceding teeth. The smaller teeth decrease slightly in size as they approach the diastema, and are strongly recurved. Table 9 presents data on the total maxillary counts (enlarged plus smaller teeth) recorded.

TABLE 9. NUMBER OF MAXILLARY TEETH (LEFT SIDE) IN SOUTHEASTERN *Tantilla* POPULATIONS

	Number of Teeth					Mean
	14	15	16	17	18	
<i>T. coronata</i>	6	16	26		1	15.3
<i>T. oolitica</i>	1	1	1			15.0
<i>T. relicta relicta</i>	2	6	5			15.2
<i>T. relicta neilli</i>	3	6	4			15.7
<i>T. relicta pamlica</i>	2	3				14.2
<i>T. relicta</i> , all subspecies	7	15	9			15.4

Although *T. coronata* tends to have one more maxillary tooth (55 percent have 16 or more) than does *T. relicta* (71 percent have 15 or less), there is no significant difference in mean tooth count.

Two few data were recorded concerning the position of the retracted hemipenis to evaluate this character properly, but the little information available suggests that it may be of little taxonomic use in this species group. The retracted hemipenis was found to extend to subcaudals 9 to 11 in *T. coronata*, 10 to 12 in *T. relicta*, and 8 in the single *T. oolitica* in which it was measured. The postero-lateral basal hook is located at subcaudals 3 or 4 in *T. coronata*, 4 or 5 in *T. relicta*, and 3 in *T. oolitica*. The antero-medial basal hook, absent in *T. relicta*, is located at subcaudal 5 in both *T. coronata* and *T. oolitica*. Terminal spination begins at the level of subcaudals 5 to 7 in *T. coronata*, 7 or 8 in *T. relicta*, and 5 in *T. oolitica*.

#### GROSS ECOLOGY

*Tantilla r. relicta* is restricted, in areas of syntopy with *T. r. neilli*, to scrub habitat on St. Lucie fine sand. In areas of allopatry, *T. r. relicta* may inhabit sandhills, as at the type locality, Babson Park, or coastal dunes and scrub. *T. r. neilli* is found only in sandhills and dryer mesic hammock areas. *T. r. relicta* appears completely fossorial, while *T. r. neilli*, although semifossorial, may be found occasionally beneath logs, debris or rocks. Both subspecies inhabit the mounds

of loose sand thrust up by *Geomys pinetis*, the pocket gopher. The distribution of both subspecies is confined to areas of dry soil in Florida, as is that of *T. r. pamlica* in the coastal dunes and scrub (figure 2). *Tantilla coronata*, however, seems to have broader habitat tolerances, being found in sandhills, hardwood forests, and pine woods. I have been informed (J. Dobie, personal communication) that it is frequently collected from rotten stumps in seasonally flooded pine flatwoods of Mississippi and Louisiana. Collecting notes on 22 museum specimens include the following situations: rotten stump, in rotten pine log, in pine straw, under log in sandhills (3), under rocks (9), and in spider web! Habitat notes on these specimens include pine woods, pine-hardwood upland, edge of hardwoods, edge of river, and second growth of thin, oak-forested hillside. Neill (1951: 49) mentions collecting *T. coronata* by "digging into piles of decaying bark scrap, by uprooting rotten stumps, or by overturning large rocks and boulders on the wooded hillsides," and finding the eggs in debris from a rotting longleaf pine in this locality. Neill and Boyles (1957) discuss the eggs of a female collected "in leaf litter on a rocky exposure along the Black Warrior River" in Tuscaloosa County, Ala-

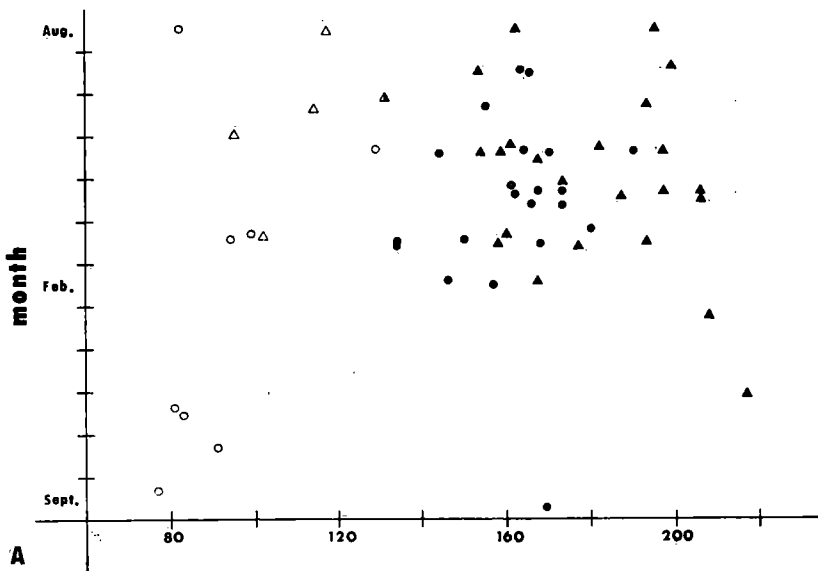
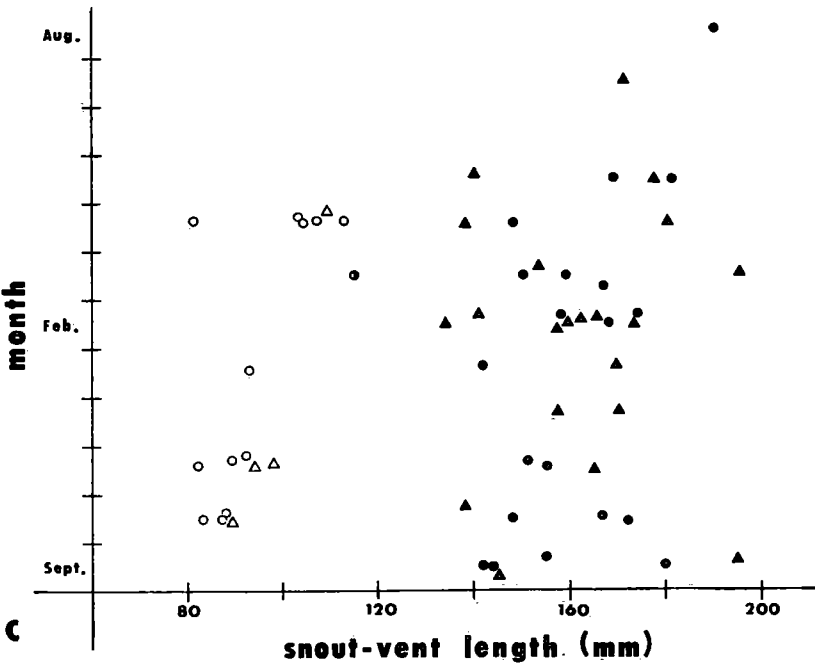
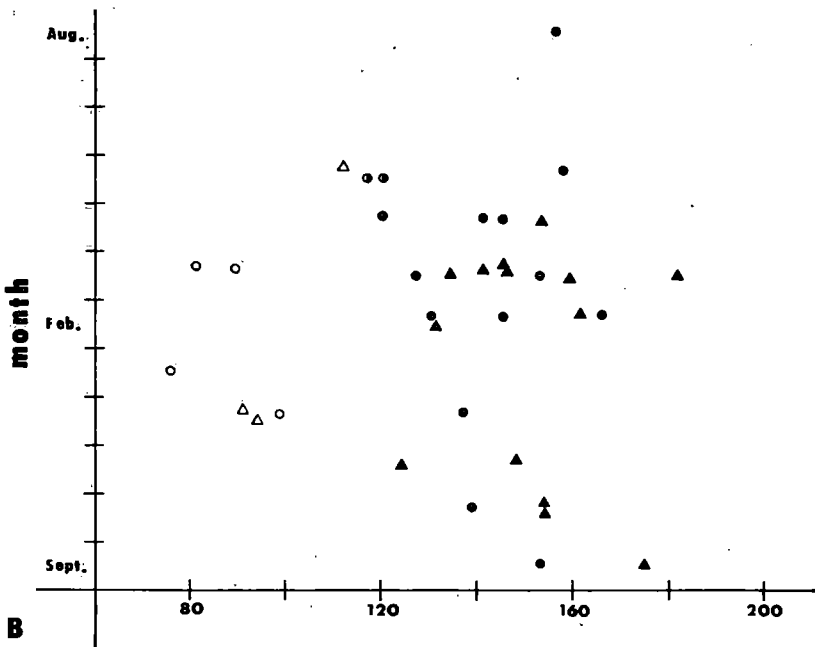


Fig. 6. Scatter diagrams plotting snout-vent length against month of collection: A, *T. coronata*; B, *T. relictta relictta*; C, *T. relictta neilli*. Solid symbols are mature individuals; hollow, immature; divided, apparently pubescent. Circles represent males, triangles, females.



bama. Hardy (1952:188) reported five specimens from Roundtop Mountain, Rutherford County, North Carolina, as "taken in a cleared field beneath rocks." Schwartz (1953:156) collected the holotype of *T. coronata mitrifer* "beneath a flat rock, about 18 inches in diameter" on a slope wooded with *Pinus echinata* and *Ilex opaca*. One of his paratypes was "caught on a wooded hillslope beneath a flat rock," two others "under one rock in a pine-oak woods," and five were dug out of the ground from depths of 2 to 12 inches on a steep, rocky hillside. It seems rather clear from these accounts that while *T. coronata* may burrow as most small snakes probably do, it is characteristically secretive and is usually associated with forests containing pines.

The only habitat data available in the literature on *Tantilla oolitica* are those of Duellman and Schwartz (1958:306), who state: "In southern Florida *Tantilla* has been collected only on the eastern rim and on Key Largo. Individuals have been found beneath rocks and boards in sandy soil in the pine woods, in hammocks, and in edificarian situations. The specimen from Key Largo was dislodged from a rotten stump." From their color notes they appear not to have confused *T. relictta pamlica* from coastal scrubs in southeastern Florida with *T. oolitica*. A specimen not available to Duellman and Schwartz was collected beneath a log in a pasture southwest of Miami, and the holotype was found beneath a board on a vacant lot in Miami. Dennis R. Paulson (personal communication) states the holotype and two others were "collected under logs and trash in an empty lot with much shrubby growth and a few *Pinus elliotii*. The area was undoubtedly pine woods before clearing, with oolitic limestone overlain by some sand. The Martin Co. record is probably more characteristic of central Florida habitat—the specimen was under the dead, fanned out on the ground, leaves of a *Serenoa repens* partially buried under St. Lucie Fine sand, in typical *Pinus clausa* and *Ceratiola* habita." The Martin County specimen referred to is a *Tantilla relictta pamlica*, and the passage quoted well describes the habitat difference between the two species in southeastern Florida.

#### SIZE AND SEXUAL MATURITY

Upon plotting snout-vent length and maturity against month of collection (figure 6), some differences between *T. coronata*, *T. r. neilli*, and *T. r. relictta* become apparent. *T. coronata* and *T. oolitica* are the largest species, and *T. relictta* the smallest. Within *T. relictta*, the nominate subspecies is intermediate, and *neilli* the largest, with

*T. relictæ pamlica* smallest in size, to judge from the small sample of the latter available. Table 10 presents size statistics of the main populations of southeastern *Tantilla*.

TABLE 10. SNOUT-VENT LENGTH (IN MM) OF SOUTHEASTERN  
*Tantilla* POPULATIONS

	Smallest Juvenile	Smallest Mature Male	Mature Female	Largest Male	Largest Female
<i>T. coronata</i>	78	134	153	190	217
<i>T. oolitica</i>	92	147	165	171	246
<i>T. relictæ relictæ</i>	77	120	124	166	187
<i>T. relictæ neilli</i>	80	142	134	190	194
<i>T. relictæ pamlica</i>	99	129	146	160	176

*T. coronata* apparently becomes mature at about 130 mm, *T. r. neilli* and *T. r. relictæ* at 120 mm. The samples of *T. oolitica* and *T. r. pamlica* are too small to permit such analysis. Males mature at slightly shorter lengths than do females. I discern four size groups in *T. coronata*: juveniles less than 105 mm; immature, young and young adult individuals from 110 to 150 mm; adults from 150 to 180 mm; and very large specimens over 180 mm. In both the *T. relictæ* populations considered, only three size groups may exist: juveniles and young individuals below 120 mm in both; in *neilli* adults from 120 to 170 mm and very large specimens over 170 mm; and in the nominate subspecies adults from 120 to 155 mm and large individuals over 155 mm. It seems from these approximations that all three species become mature during their second growth season, but do not necessarily breed until the following year. Force (1935: 651) found that the *Tantilla gracilis* population in Oklahoma (where the active season is shorter than in the southeast) is composed of three age groups, that males mature at the same age as females but at a shorter length, and that maturity probably is reached in the third growth season at about 2½ years of age.

## DISCUSSION

### HEAD PATTERNS.

With respect to the populations of *Tantilla relictæ*, an intriguing question recurred frequently during this study: What is the relationship of pattern to habitat in this species? The banded populations, *T. r. relictæ* and *T. r. pamlica* characteristically inhabit scrub, a plant

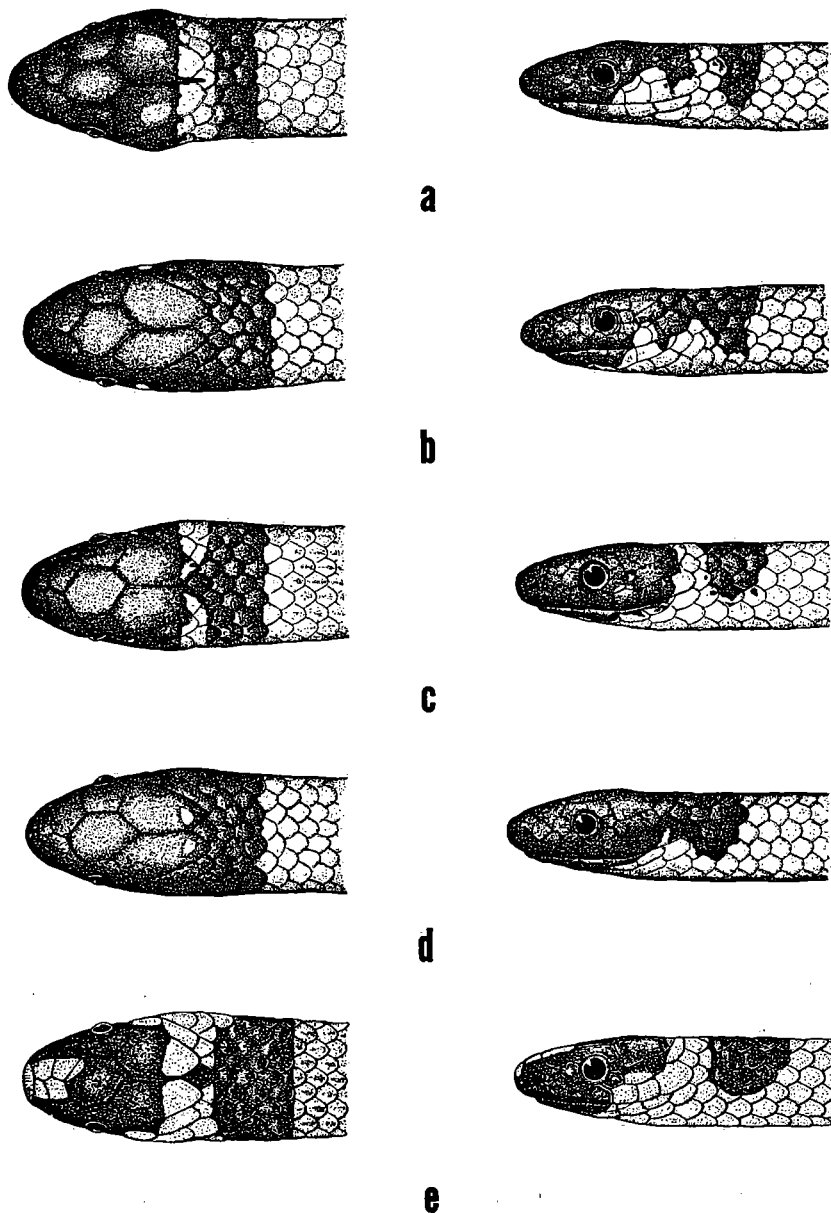


Fig. 7. a, Coastal Plain *T. coronata* (UF 12387, Coffee Co., Ala.); b, *T. oolitica* holotype (UF 17326, Dade Co., Fla.); c, *T. relictata relictata* holotype (UF 12421, Polk Co., Fla.); d, *T. relictata neilli* holotype (UF 12406, Alachua Co., Fla.); e, *T. relictata pamlica* holotype (UF 12430-2, Palm Beach Co., Fla.).

association that grows on white St. Lucie Fine sand, and which is a seral stage in dune succession (Laessle, 1958). The nonbanded *T. r. neilli* is found in both sandhills and mesic hammock, but is more common in the former, and possibly occurs only in those mesic hammocks bordering sandhills areas. In areas of syntopy, *relicta* and *neilli* seem completely segregated ecologically from each other by this habitat preference, yet in the southern ridge section of Florida where *neilli* does not occur, *relicta* is found in both scrub and sandhills.

I suggest as a purely speculative hypothesis that perhaps selection acts against uniform head patterns on white sand substrates. *T. relicta* is a "submerged basker." It lies, in captivity at least, just beneath the sand, with the head at the surface. A banded head pattern would tend to break up head outline on the white sand and render a basking *Tantilla* less obvious to avian predators, to whom these diminutive snakes should pose no greater problem to ingest

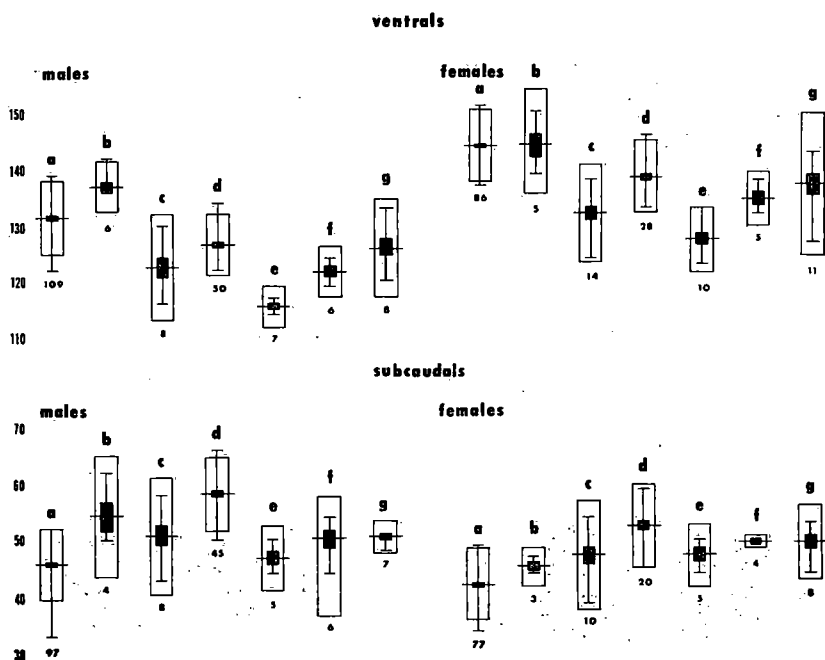


Fig. 8. Variation in ventrals and subcaudals: a, *T. coronata*; b, *T. oolitica*; c, *T. relicta relicta*; d, *T. relicta neilli*; e, *T. relicta pamlica*; f, *T. relicta* from Seahorse Key; g, series possibly intergradient between *relicta* and *neilli*. Vertical line is range; horizontal line, mean; hollow bar, two standard deviations of the mean; solid bar, twice the standard error. Sample size is indicated beneath each histogram.

than a large earthworm. The only known instance of avian predation on *Tantilla* was one D. Jenni (personal communication) found in a cattle egret (*Bubulcus ibis*). I suspect that many of the birds inhabiting scrub, sandhills, and hammock prey upon *Tantilla*. Submerged basking is perhaps less dangerous for small snakes in sandhills and hammock, both habitats with abundant vegetation on the ground. The scrub, however, a fire-climax association, typically has wide areas of open sand bearing little or no vegetation. The ability to bask with less likelihood of detection from above would thus make scrub more habitable for banded *Tantilla*, and reduce the likelihood of competition by a possibly more effective, blackheaded competitor. The predominantly nonbanded condition of disjunct populations of *T. relicta* in Charlotte County and on Seahorse Key is conceivably correlated with the overgrown, mature scrubs found there. Perhaps as the banded pattern becomes less advantageous a simple Mendelian dominant pattern reduces the frequency of banded phenotypes in these populations. This may also account for the presence of nonbanded *T. relicta* in the mature scrubs east of the St. Johns River.

#### INTERGRADATION.

Most of the specimens treated above as possible intergrades between *T. r. relicta* and *T. r. neilli* are not truly intermediate between *neilli* and *relicta*, but show some similarities to both. For instance, head pattern and ventrals seem closer to *neilli*, while subcaudals and tail length closely approximate *relicta*. Most of these specimens are from Putnam, Volusia, and Seminole counties, east and south of Lake George. Others are from scattered areas in Marion, Lake, Levy, Citrus, and Pinellas counties. I suspect that *relicta* and *neilli* do not intergrade along a continuous front, but that some gene flow occurs through secondary intergradation, in the sense of Mayr (1963). These two long-isolated populations have probably come into contact since the closing of the Suwannee Straits and intergradation may be occurring only in those areas of longest contact, notably in the area around Lake George. A single specimen is available from Eau Gallie, Brevard County, which may represent a similar hybrid between the central populations and *T. r. pamlica*. In characters of scutellation it resembles *pamlica*, but its pattern is nonbanded. Intensive collecting in Volusia County from the St. Johns to the Atlantic Ocean and south to Cape Canaveral will probably provide a less speculative interpretation of these *Tantilla* populations. For the time being it is reasonable to consider them intergrades.



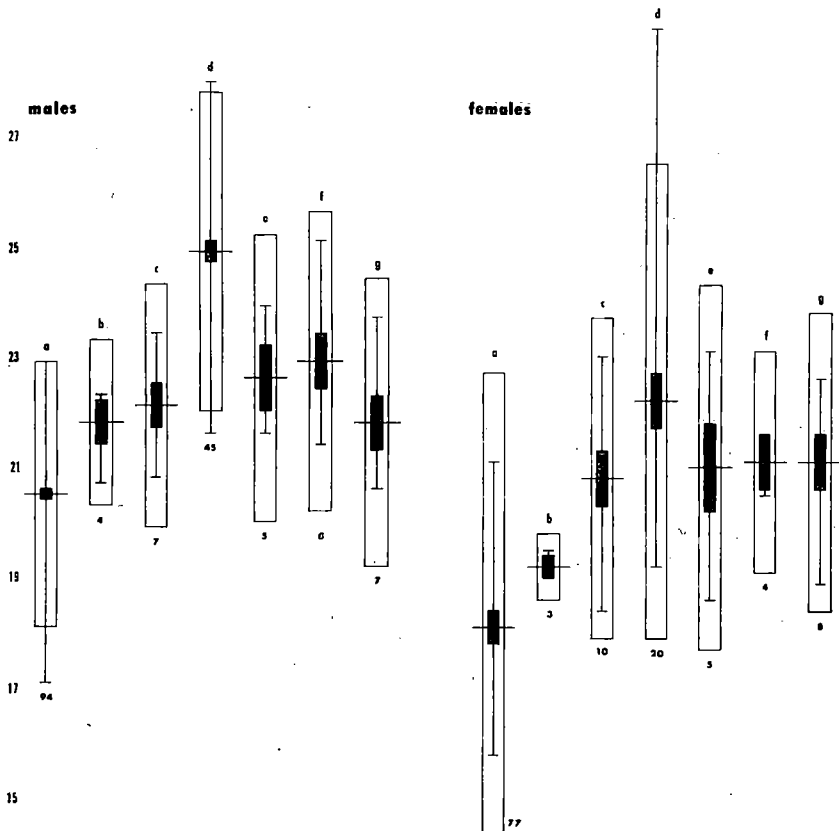


Fig. 9. Variation in proportionate tail length, expressed as per cent of total length. Symbols as in Fig. 8.

#### PLEISTOCENE INFLUENCES UPON SPECIATION.

Probably the most significant influence upon present distribution of the Floridian herpetofauna was that of fluctuating Pleistocene physiography. Correlations of ranges of such Florida endemics as *Ophisaurus compressus* (McConkey, 1954), *Stilosoma extenuatum* (Highton, 1956), *Neoseps reynoldsi* (Telford, 1959), and *Eumeces egregius* (McConkey, 1956; Mount, 1961) have been made with marine terrace levels, and the present study shows that the same isolating phenomena probably contributed to divergence within the Florida *Tantilla coronata* complex.

Pertinent geological factors in the history of the peninsula have been presented by Cooke (1939), Laessle (1958), Puri and Vernon

Highton, R.

1956. Systematics and variation of the endemic Florida snake genus *Stilosoma*. Bull. Florida State Mus., Biol. Sci., 1 (2): 73-96.

Jan, G.

1862. Enumerazione sistematica delle specie d'ofidi del gruppo Calamaridae. Archiv. Zool., Anat., Fisiol., 2 (1): 1-76.

Jan, G., and F. Sordelli

1866. Iconographie générale des Ophidiens. Paris. Tome premier, livr. 15. (1961 reprint, J. Cramer, Weinheim).

Laessle, A. M.

1958. The origin and successional relationship of sandhill vegetation and sand-pine scrub. Ecol. Monogr., 28: 361-387.

Maerz, A., and M. R. Paul

1950. A dictionary of color. McGraw-Hill, New York. 207 p.

Mayr, E.

1963. Animal species and evolution. Belknap Press of Harvard Univ. Press, 797 p.

McConkey, E. H.

1954. A systematic study of the North American lizards of the genus *Ophisaurus*. Amer. Midl. Nat., 51 (1): 133-171.

McConkey, E. H.

1957. The subspecies of *Eumeces egregius*, a lizard of the southeastern United States. Bull. Florida State Mus., Biol. Sci., 2 (2): 13-23.

Neill, W. T.

1951. Notes on the natural history of certain North American snakes. Publ. Res. Div., Ross Allen's Reptile Instit., 1 (5): 47-60.

Neill, W. T., and J. M. Boyles

1957. The eggs of the crowned snake, *Tantilla coronata*. Herpetologica, 13: 77-78

Puri, H. S., and R. O. Vernon

1960. Notes of the surficial geology of central peninsular Florida. IN: Late Cenozoic stratigraphy and sedimentation of central Florida, p. 24, Southeastern Geological Society Guidebook, Tallahassee.

Schwartz, A.

1953. A new subspecies of crowned snake (*Tantilla coronata*) from the southern Appalachian mountains. Herpetologica, 9: 153-157.

Smith, H. M.

1940. Descriptions of new lizards and snakes from Mexico and Guatemala. Proc. Biol. Soc. Washington, 53: 55-64.

Snedecor, G. W.

1946. Statistical methods. Iowa State College Press, Ames, 4th edit., 485 p.

Telford, S. R., Jr.

1959. A study of the sand skink, *Neoseps reynoldsi* Stejneger. Copeia, 1959 (2): 110-119.

Wright, A. H., and A. A. Wright

1957. Handbook of snakes of the United States and Canada. Ithaca, Comstock Publ. Assoc. Vol. II, p. 565-1105.

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Amer. Inst. Biol. Sci., Washington. 92 p.

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