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THE PINE WOODS SNAKE, RHADINAEA FLAVILATA
(COPE)

Charles W. Myers



UNIVERSITY OF FLORIDA
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THE PINE WOODS SNAKE, *RHADINAEA FLAVILATA* (COPE)

CHARLES W. MYERS¹

SYNOPSIS: *Rhadinaea flavilata* (Cope, 1871) is a small colubrid snake inhabiting a narrow coastal range in the southeastern United States. Its distribution closely approximates that of the low pine flatwoods, which constitute its principal habitat. A few individuals have been found in other situations, especially in Florida hammocks and on coastal islands. The species is most commonly encountered in pine logs and stumps during March and April; with the approach of warmer weather and drier conditions in May and June, *Rhadinaea* and other small snakes become more difficult to find. *R. flavilata* feeds on small amphibians, lizards, and perhaps snakes; literature records referring to predation on insects are questioned. The pine woods snake kills or incapacitates some of its prey with a venom introduced into wounds made by enlarged rear maxillary teeth. Other snakes are likely its main predators and food competitors. *R. flavilata* lays two to four elongate eggs; the period of egg deposition is speculated to extend from May into August, although it probably is not so extensive in any given season; the natural nest is unknown. There is slight statistical evidence of unbalanced sex ratios in some populations.

Structural variation was observed in many characters, and for discussion is classified as intrapopulational variation (including ontogenetic, sexual, and uncorrelated or "individual" variation) and interpopulational (geographic) variation, the latter being compounded from the former. No geographic races are recognized in this species.

Structurally the pine woods snake is a rather generalized *Rhadinaea*. Its closest living relative is *R. laureata* of the highlands of western Mexico. Fossils show that *R. flavilata*, or a genetic predecessor, had arrived in the southeastern United States at least by the third (Illinoian) glacial stage of the Pleistocene. The lack of marked geographic variation in this species can be explained by the relatively recent (postglacial) dispersal of a homogeneous Floridian stock throughout a relatively uniform pine-flatwoods habitat. Environment, nonselective genetic mechanisms, and natural selection are considered briefly in terms of the evolution of geographic variation. A seemingly primitive color pattern is retained at the northern limits of the range; the southern populations are characterized by loss of pattern and by increased variability (often anomalous) in scutellation. It is inferred that southern populations, being most influenced by a warming post-glacial climate, are evolving faster than northern populations.

¹ The study reported on in this paper was initiated when the author was an undergraduate student at the University of Florida and a research assistant in the Florida State Museum (1958-1960). The paper was completed at the Cooperative Wildlife Research Laboratory, Southern Illinois University, where it was accepted as a thesis in partial fulfillment of the requirements for the Master of Arts degree (1962). The author is currently a visiting scientist at Gorgas Memorial Laboratory, Panama City, Panama, and research associate of the Museum of Natural History, University of Kansas. An earlier contribution to this Bulletin deals with the biology of the ringneck snake in Florida. Manuscript received 1 December 1965.—Ed.

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INTRODUCTION

Rhadinaea flavilata (Cope, 1871) is a small snake of the extensive pine flatwoods on the coastal plain of southeastern United States. As with many small and secretive animals, especially those of limited distribution, knowledge of this species is slight. In this paper I have attempted to provide a more complete account of *R. flavilata* than heretofore available. The principal aim was to determine its structural variation, distribution, affinities, and ecological relationships. On the data assembled is based a hypothetical history of the species' evolution.

The written history of *Rhadinaea flavilata* is not extensive. Post-surgeon H. C. Yarrow found the type specimen near Fort Macon on Bogue Banks, North Carolina, in November 1871 (Coues and Yarrow, 1878). The novelty was forwarded alive to E. D. Cope, who promptly named it *Dromicus flavilatus*, believing it to have affinities with *D. callilaemus* of Jamaica, and a possible origin in the United States via floating drift in the Gulf Stream (Cope, 1871). Specimens next became available from Florida (Cope, 1877, 1878, 1888), and after an examination of the hemipenis Cope (1894, 1895) decided that *flavilatus* was most closely allied with the species of *Rhadinaea*, a genus he had described in 1863 from the tropical mainland. Boulenger (1894) concurrently placed the species in *Liophis*, a designation no other worker followed, and Boulenger is said (Malnate, 1939) to have realized his error later. Steneger and Barbour (1917) allocated *flavilatus* to *Leimadophis*, and Amaral (1929) placed the remaining species of *Rhadinaea* in *Liophis*. Dunn resurrected the genus *Rhadinaea* in 1932, and since that time the affinities of *Rhadinaea flavilata* have not been questioned. Here ignored are suggestions (Dunn 1944, 1957;

Roze 1958, 1959) that *Urotheca* Bibron, 1843 is the proper generic name for species currently placed in *Rhadinaea* Cope, 1863. I have examined the holotype of *Calamaria dumerilli*, type species of *Urotheca*, and intend to take up this strictly nomenclatorial problem elsewhere.

Rhadinaea flavilata has remained scarce in collections, although Brown (1901) early extended its known range to include the eastern Gulf Coast. Malnate (1939) made the first substantial contribution to a knowledge of this snake; he summarized previous literature, gave original observations on habits and habitats, and analyzed variation on the basis of 55 specimens. E. Ross Allen (1939) found the species abundant at Burbank, Florida, and cited a catch nearly twice as large as Malnate's sample from the entire range. Other interesting contributions were the discoveries that *R. flavilata* possesses a weak venom (Neill, 1954a), and that fossil vertebrae from the Florida Pleistocene can be assigned to it (Auffenberg, 1963; Holman, 1958, 1959). Several other writers cited at appropriate places in the text have supplied additional information.

PROCEDURE OF STUDY. Much of this paper is based on data from museum specimens. My field experience with the pine woods snake is limited to northern Florida. Available for this study were 192 preserved specimens and a small series of skeletons in the following collections: American Museum of Natural History (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); collection of Barry Mansell (BM); Chicago Academy of Sciences (CAS); Carnegie Museum (CM); Chicago Natural History Museum (CNHM); Cornell University, (CU); collection of the writer (CWM); Duke University (DU); Illinois Natural History Survey (INHS); collection of J. Alan Holman (JAH); collection of Joseph Pylka (JP); Louisiana State University Museum of Zoology (LSU); Loyola University, New Orleans (LU); Museum of Comparative Zoology (MCZ); Museum of Vertebrate Zoology (MVZ); collection of Sam R. Telford (SRT); Texas Cooperative Wildlife Museum (TCWM); Tulane University (TU); University of Florida (UF); University of Illinois Museum of Natural History (UIMNH); University of Kansas Museum of Natural History (KU); University of Michigan Museum of Zoology (UMMZ); United States National Museum (USNM); collection of W. E. Brode (WEB); collection of William L. Engels (WLE).

Data on scutellation, color pattern, size, and sex were recorded when possible (some specimens were poorly preserved or mutilated); observations on certain aspects of the internal anatomy were made from selected specimens. All measurements and ratios were based on

preserved specimens. Tooth counts were obtained from the skeletonized specimens; no attempt was made to record detailed osteological descriptions.

The terminology used to describe the hemipenis is that of Dowling and Savage (1960). Ventral plates were counted in the manner suggested by Dowling (1951); neither the anal plate nor terminal caudal spine were included in the ventral or subcaudal counts. The first ventral plate (*vide* Dowling, 1951, fig. 1) was used as the reference point for the first dorsal scale count; this count started with the dorsal scale bordering the posterior corner of the first ventral, and ended at the starting place for the next count (approximately a head's length behind the head). Other dorsal scale counts were made at midbody and immediately anterior to the anal plate.

The temporals of *Rhadinaea flavilata* are defined as those plates lying in vertical rows between the parietals and supralabials. (A row of scales bordering the posterior margins of the parietals and labials has been considered temporals by some authors.)

Numbers on the left and right sides of a slant line (/) show variation in counts made on the left and right sides of the body, respectively (e.g. 9/10 infralabials). Numbers above and below a horizontal line show that a vertical division has occurred in one or more plates

of a vertical row. Thus, the temporal formula $1 + \frac{2}{1}$ means that

the top plate in the second row is divided; the formula $1 + \frac{2}{2}$ shows

that both plates are divided in the second row. The + sign indicates that counts have been made in vertically arranged rows, rather than horizontal ones.

Statistics found useful are range and standard deviation as measures of absolute dispersion, arithmetic mean as a measure of central tendency, standard errors of means and chi-square (χ^2) as clues to the probability of difference between samples, coefficient of divergence (Klauber, 1940, 1943) as a relative measure of difference between characters, and tail length divided by total length as a measure of proportion. Except where sex ratios are tested, chi-square was obtained by use of a 2 x 2 table and a formula that contains a Yates' correction factor for small numbers (Croxtton, 1959, p. 276).

Botanical names used are those given by Small (1933), except for the species of *Pinus*, where the nomenclature is that of Critchfield and Little (1966).

ACKNOWLEDGMENTS. For making available facilities at the Florida State Museum where this study was initiated, and for much encouragement, I am grateful to William J. Riemer. The manuscript was prepared at Southern Illinois University, where it was improved by comments and helpful criticisms given by W. D. Klimstra and Richard E. Blackwelder. The paper also profited from a reading by William E. Duellman, University of Kansas. For field notes and other information I am indebted to Charles M. Bogert, William L. Engels, Sam R. Telford, and Wilfred T. Neill. Isabelle Hunt Conant photographed the pine woods snake in fig. 1 and Robert McFarlane took the photographs in figs. 3, 4, and 10 for me. For typing the manuscript and other favors, I am especially grateful to my wife, Joan W. Myers.

TAXONOMY

Rhadinaea flavilata (Cope, 1871)

- 1871. *Dromicus flavilatus* Cope, Proc. Acad. Nat. Sci. Philadelphia, vol. 23, pp. 222-223.
- 1894. *Liophis flavilatus* (Cope). Boulenger, Cat. Snakes British Mus. (Nat. Hist.), vol. 2, p. 143.
- 1894. *Rhadinaea flavilata* (Cope). Cope, Proc. Acad. Nat. Sci. Philadelphia, vol. 46, p. 428.
- 1901. *Rhadinea flavilata* (Cope). Brown, Proc. Acad. Nat. Sci. Philadelphia, vol. 53, p. 88. [Probably an intended emendation as this generic spelling was used elsewhere by Garman (1884, p. 29) and Brown (1904, p. 467; 1908, p. 123). Several recent authors, apparently following Schmidt's checklist (1953), have used this spelling, but I have been unable to find a valid basis for it.]
- 1917. *Leimadophis flavilatus* (Cope). Stejneger and Barbour, Check List N. Amer. Amphibians and Reptiles, 1st. ed., p. 86.
- 1958. *Urotheca [flavilata* (Cope) included by inference]. Roze, Breviora, Mus. Comp. Zool., no. 88, p. 5. [Followed in this usage by Neill (1963, p. 205; 1964, pp. 287-288).]

HOLOTYPE. ANSP 5583, collected by Dr. H. C. Yarrow, in November, 1871. Now lost (Malnate, 1939; James E. Böhlke, *in litt.*).

TYPE LOCALITY. Approximately 8 miles westward from Fort Macon, on Bogue Banks, Carteret County, North Carolina.

In the original description, Cope (1871) says that the type specimen came from "near Fort Macon, on the coast of North Carolina." Coues and Yarrow (1878) relate that it was found "on Bogue Banks some eight miles south of Fort Macon, near marshy ground." Robertson and Tyson (1950), however, point out that the last is an unlikely locality (being in the Atlantic Ocean), and that Coues and Yarrow probably intended 8 miles west or southwest of Fort Macon.

ETYMOLOGY. The name *Rhadinaea flavilata* is presumably derived from the Greek *rhadinos* (slender or lithe) and the Latin *flavus* (gold colored, or yellow) + *latus* (broad or extensive, full or rich). It seems probable, at least, that the specific epithet was intended to refer to the rich (or extensive) golden-brown coloring of the body. *Latus* is also the past participle of the verb *fero*, and so *flavilata* conceivably could mean "golden borne," but this seems less likely. *Latus* is furthermore a noun meaning side or flank, but it is unlikely that the name is based on this. Cope added the feminine ending "*a*" when he transferred *flavilatus* from *Dromicus* to *Rhadinaea*, and so apparently did not intend a noun in apposition; and had "golden sided" been meant the name should have been "*flavilateralis*."

There seem to be no true vernacular names for this species, as humans living within the range of *R. flavilata* are usually unaware of its existence. The common name in current usage, yellow-lipped snake (A.I.S.H., 1956), is not suitable for most populations; it was apparently coined by Ditmars (1907), who described the upper lip as "bright yellow." The name "brown-headed snake" has been used, but is equally applicable to any of several other small snakes in the eastern United States. "Yarrow's *Dromicus*" is the only other common name that has been used in print. I suggest "pine woods snake" for those in need of an English name. The species is partial to the pine flatwoods, probably even more so than the pine woods treefrog, *Hyla femoralis*.

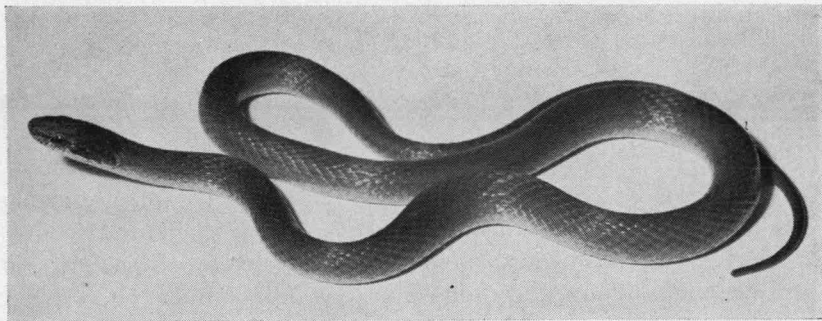


Figure 1. A pine woods snake, *Rhadinaea flavilata*, from Burbank, Marion County, Florida. Isabelle Hunt Conant

DESCRIPTION. A moderately slender snake with head slightly wider than neck. Largest specimen examined 387 mm. Tail/total length ratio 27.0-35.9 percent.

Color above golden brown, lightest on first two scale rows. Mid-dorsal stripe of diffused chromatophores sometimes present on vertebral scale row, with the pigment often confined to apices of the vertebral scales. Diffused lateral stripe usually present on scale rows 1-4, mainly on 2-3 anteriorly and on 3 posteriorly (sometimes not evident until the stratum corneum falls away in preservative). Sometimes a yellowish occipital spot on each side of neck behind head. Top of head usually darker than body and often marked with pale vermiculations. A brown stripe, light-bordered above and dark-bordered below, extends from the snout through the eye and to the angle of the jaws. Labials white to pale yellowish, variably spotted with black, and sometimes with faint splotches of brown. Underside of head and neck white; rest of venter white or pale yellowish green.

Dorsal scales smooth, except for anal ridges on some specimens, and without apical pits; in 17 rows except immediately behind the head, where the count is usually 18 but occasionally 17 or 19. Ventrals 112-139; anal plate divided; subcaudals in 59-83 pairs; tail with terminal spine. Supralabials normally 7, with third and fourth entering orbit and the sixth the largest; occasionally 8, with fourth and fifth entering the orbit and the seventh the largest. Infralabials usually 9, with the first five bordering the genials and the fifth the largest; infralabials sometimes 7, 8, or 10, often with corresponding changes in position of the largest plate and the number bordering the genials. Posterior genials slightly longer than anterior ones; first pair of infralabials meet behind mental. Temporals typically 1 + 2, but these plates, especially in row 2, are frequently divided or fused. One preocular, two postoculars; pseudo-oculars sometimes present as the result of transverse labial divisions. Loreal as high or higher than long, rarely absent. Nasal single, but grooved and may appear divided on casual examination. Rostral about twice as wide as high and barely visible from above. Internasals nearly quadrate; prefrontals nearly as long as wide; supraoculars narrow, longer than wide; frontal about one and one-half to two times longer than wide, pentagonal with apex caudad; parietals elongate; truncate or slightly pointed posteriorly.

Everted hemipenis a single, clavate organ, extending to between the sixth and ninth subcaudals. Basal part smooth; middle part spinose with greatest enlargement of spines towards surface opposite sulcus spermaticus; distal end capitate and calyculate (calyces papillate apically and spinulate basally). Sulcus spermaticus bifurcate, dividing on the capitate portion of the organ at about the 5th or 6th

subcaudal level and not extending to the apex. The *m. retractor penis magnus* originates at the level of the 21st to 24th subcaudal. Anal sac extending to between the 9th and 14th subcaudals.

Anterior maxillary teeth 14-15, slightly increasing in length from front to rear, followed by a short diastema and two enlarged, ungrooved teeth. Palatine teeth 11-13; pterygoid teeth 19-23; dentary teeth 19-22. The middle, precaudal vertebrae are described by Auffenberg (1963).

DISTRIBUTION

Rhadinaea flavilata occupies a narrow coastal range (fig. 2) from the vicinity of Cape Hatteras, North Carolina (Carteret County), south

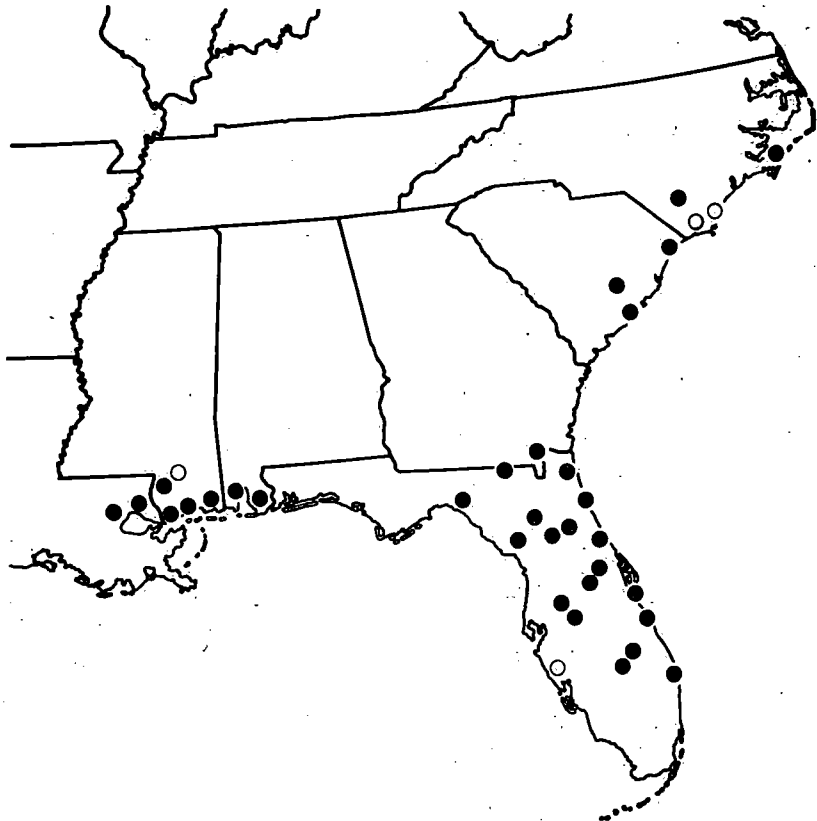


Figure 2. Geographic distribution of *Rhadinaea flavilata*. Only one symbol is plotted per county (or parish) but, with few exceptions, this covers all known localities within the county. Open symbols indicate literature records.

through the northern four-fifths of the Florida peninsula (to Palm Beach County), and west to extreme eastern Louisiana (Livingston Parish).

Most localities are less than 100 feet above sea level, although specimens have been found at approximately 180 feet in Gainesville, Florida. At no place has the species been found more than about 70 miles from the coast.

The present-day range of *Rhadinaea flavilata* appears to lie entirely east of the Mississippi River. A Texas record (Netting, 1936), based on a specimen (CM 8937) reputedly from the vicinity of Clifton, in Bosque County, is almost certainly erroneous. *Rhadinaea flavilata* is a coastal form, whereas the Clifton area lies farther inland (by about 175 miles) and at a higher elevation (by over 400 feet) than other known localities for the species. Correlated with this are conspicuous differences in habitat. *Rhadinaea flavilata* is found mainly in low, poorly drained pine woods, whereas Clifton is in a region of cedar-covered ridges and limestone outcroppings. I visited this area in April 1961 with Sam R. Telford and Robert Mount; we collected or observed such animals as the plains narrow-mouthed toad (*Gastrophryne olivacea*), spiny lizard (*Sceloporous olivaceus*), blind snake (*Leptotyphlops dulcis*), ground snake (*Sonora episcopa*), and flat-headed snake (*Tantilla gracilis*). These species occupy habitats more arid than the coastal pine flatwoods, and are members of a faunal unit different from that associated with *R. flavilata*. Grobman (1941, 1944, 1950) advised caution in the acceptance of this and certain other records based on specimens not individually tagged and for which the place of shipment may be given as the collecting locality.

SPECIMENS EXAMINED.—ALABAMA: *Baldwin County*—10 mi. S Foley (CM 9879). *Mobile County*—no other locality data (CU 1739; USNM 51888, 56445-56446); *Mobile* (CAS 12130-12131). FLORIDA: No other locality data (ANSP 10800, 26075; CNHM 38022-38023). *Alachua County*—Air Base (UIMNH 25700); Gainesville (CWM 1855; TCWM 10418; UF 460, 620, 2740, 2977, 7087, 7278, 8021, 8860); near Gainesville (AMNH 36589); approximately 6 mi. NE Gainesville (CWM 1863); 7.1 mi. NNE Gainesville (UF 10023); 7 mi. E Gainesville, ½ mi. W Hatchet Creek (SRT 628); 7 mi. E, 2½ mi. N Gainesville (CWM 1560, 1580-1582, 1800, 1860-1862, 1864); 2 mi. E Paradise (UIMNH 25701-25706). *Brevard County*—Georgiana (USNM 11989, 13642, 13649, 13661, 13708). *Duval County*—Jacksonville (BM [3]); Jacksonville, north section along St. Johns River (UF 3271). *Glades County*—Indian Prairie Canal, 18 mi. SW Okeechobee (town) (UF 8864). *Hamilton County*—15 mi. NNE, 7 mi. W White Springs (town) (KU 68940). *Indian River County*—Sebastian (MCZ 12792; UMMZ 56987). *Levy County*—4 mi. S, 1 mi. W Otter Creek (town) (UF 14904). *Marion County*—no other locality data (CNHM 48287, 95341 [2]); Burbank (CNHM

48288-48296; MVZ 53907; TCWM 10416-10417; UF 2714, 2750 [2], 7504; Burbank, 7 mi. N Silver Springs (CNHM 48297-48306); 4 mi. NE Burbank (UF 10026); Ft. McCoy (UF 10028); near Silver Springs (CM 9636-9646); 10 mi. from Silver Springs (CU 2211 [2]). *Okeechobee County*—Opal, NE of Okeechobee (AMNH 63891-63892); near Opal, N of Okeechobee (AMNH 50491); S of Okeechobee (AMNH 63364, 63436-63438). *Orange County*—Orlando (MCZ 6978). *Palm Beach County*—Palm Beach (UMMZ 85110). *Polk County*—5 mi. N Lakeland (JAH [skeleton only]); ½ mi. SE Pasco-Polk County line, on U.S. Highway 98 (JP 58-20); Winter Haven, Lake Shipp (SRT 49); 7 mi. SW Winter Haven, Lake Hancock (SRT 119, 1136). *Putnam County*—Univ. Florida Conservation Reserve, Welaka Mud Springs (CM 21439). *St. Johns County*—Anastasia Island, near St. Augustine (AMNH 63362-63363, 63434-63435); Anastasia Island, 5 mi. SE St. Augustine (CU 4980). *Seminole County*—4 mi. E Sanford (UF 10024). *Taylor County*—7½ mi. 315° from Perry (UF 14903). *Volusia County*—Daytona Beach (UF 10030); 3 mi. N DeLand (UF 10029); 7 mi. E DeLand (UF 10027). “Warren” [Walton ?] *County*—no other locality data (ANSP 11730). *GEORGIA: Charlton County*—Okefenokee Swamp, Chesser’s Island (CM 19869). *LOUISIANA: Livingston Parish*—5 mi. NW Springfield (LSU 7433-7435). *St. Tammany Parish*—Bayou Lacombe (TU 11849); Covington (TU 3237-3238); Mandeville (TU 3235); Oaklawn (TU 3239); Pearl River (town) (TU 369, 3889); 5 mi. W Slidell (TU 7031, 14991, 15044, 15073); Sun (CAS 12132); 0.3 mi. N Talisheek (TU 16098). *MISSISSIPPI: No other locality data* (USNM 56443-56444). *Jackson, Hancock, Harrison, and Pearl River counties.* [The tags on the following specimens were attached by slip-knots and came loose during shipment.]—(WEB 31a-31b, 37, 52, 68, 78, 87, 91, 109, 111-113, 115). *Hancock County*—Bay St. Louis (ANSP 12061-12062; LU 456 [2]; USNM 24452-24454); 10 mi. W Bay St. Louis (TU 13770 [2]); 4 mi. NE Logtown (TU 14264); Pearlinton (LU 295 [3]); 7.5 mi. NNW Pearlinton, just W of Westonia (TU 17618); 5 mi. N, 3 mi. W Pearlinton (TU 17351-17352); 4 mi. W Waveland on U. S. Highway 90 (UF 10025 [2]). *Harrison County*—Biloxi (CNHM 21533; CU 1867 [2]; UMMZ 76827; USNM 125546); near Biloxi (AMNH 46745; CM 5240); 3 mi. N Biloxi (CNHM 12000); 6 mi. N Biloxi (INHS 6336); 13 mi. NW Biloxi on State Highway 55 (TU 17353); Gulfport, AAF (UMMZ 93998); 4 mi. N d’Iberville (UIMNH 29110). *NORTH CAROLINA: Bladen County*—North River, Camden Pt., Councils [“Council” on recent maps] (CU 1342). *Carteret County*—6 mi. E Beaufort, on Highway 70 (DU [1]); Harkers Island (WLE 1142-1143); 24 mi. SW Morehead City, 3 mi. from Swansboro (DU [1]); Shackleford Banks [an island] (WLE 778); South end of Shackleford Banks (UIMNH 5233). *SOUTH CAROLINA: Berkeley County*—Alvin (CM 21791); 2.1 mi. N, 0.3 mi. E Cainhoy (UMMZ 109235); 7 mi. W Moncks Corner (CM 25190-25191); 8 mi. W Moncks Corner (CM 28892-28893). *Charleston County*—Mt. Pleasant (CNHM 4076). *Horry County*—St. Park [presumably Myrtle Beach State Park] (UMMZ 94166). *TEXAS: Bosque County*—Clifton (CM 8937). [Locality data not acceptable; see text.]

LITERATURE RECORDS. Specimens were not available from the following counties, indicated on the distribution map (fig. 2) by unshaded symbols. *FLORIDA: Sarasota County* (Allen, 1939). *MISSISSIPPI: Forest County* (Cliburn, 1959). *NORTH CAROLINA: Brunswick County*—near Shallotte (White, 1960); *New Hanover County* (Funderberg, 1958).

ECOLOGY

The pine woods snake is too secretive and difficult to find to be studied easily in the field, but the study of specimens, habitats, and distribution provides information of ecological import, and observations on a dozen or so individuals in captivity give additional clues to the species' nature.

HABITATS

PINE FLATWOODS. Several types of flat pine forests comprise the high flatwoods of the upper coastal plain and the low flatwoods of the lower coastal plain. The pine flatwoods are vegetational associations distinct from the pine or pine-oak forests of the hills and ridges, nor are they to be confused with the New Jersey pine barrens, which are of different origin and greater antiquity (*vide* Harshberger, 1916). A generalized profile of coastal plain pine forests is given by Wahlenberg (1946, fig. 14).



Figure 3. Low pine flatwoods near Hatchet Creek, Alachua County, Florida.
Robert McFarlane

The low flatwoods (figs. 3 and 4) seem to be the main habitat of *Rhadinaea flavilata*. These woods are probably confined entirely to nearly level Pleistocene terrace deposits of the lower coastal plain.

"Low pine barrens" and "pine savannas" are among the older names for this association, but the term used here is more descriptive and is the one most frequently used in recent literature.



Figure 4. A cutover section of low pine flatwoods near Hatchet Creek, Alachua County, Florida. The pine woods snake and other small reptiles and amphibians frequent pine logs with loose bark. *Robert McFarlane*

The low flatwoods are characterized by flat, poorly drained topography on which slash pine (*Pinus elliottii*) or longleaf pine (*Pinus palustris*) is usually the dominant tree. Characteristic plants include wire-grasses (*Aristida* spp.), gallberry (*Ilex glabra*), saw-palmetto (*Serenoa repens*), pitcher plants (*Sarracenia* spp.), St. John's-worts (*Hypericum* spp.), huckleberries (*Vacciniaceae*), *Sabbatia* spp., polygalas (*Pilostaxis* spp.), butterworts (*Pinguicula* spp.), *Lobelia* spp., ground orchids (*Ibidium* and *Limodorum* spp.), Easter-lilies (*Atamosco* spp.), and *Sphagnum* spp. Cypress ponds and their associated flora are often a conspicuous element of the low flatwoods. Frequently present is a hardpan which allows water to stand for long periods in wet weather (fig. 4) and prevents the rise of capillary water during dry spells; consequently many flatwoods are seasonally subjected to the extremes of flooding and drought. Occasional fires are conducive to the preservation of the flatwoods; without fire, plant succession would probably proceed to a broad-leaved forest (*vide* Laessle, 1942).

The distribution of *Rhadinaea flavilata* closely approximates that of the low pine flatwoods. The western extent of the snake's range in eastern Louisiana corresponds to the western limits of the slash pine flatwoods, and it is not found south of the flatwoods in Florida (fig. 5). To the north and east its known distribution nearly corresponds to that of the "*Campulosus-Sarracenia* association," which Wells (1924) states lies south of a line drawn through Cape Hatteras, North Carolina; this association appears to be nothing more than a cut-over flatwoods in which longleaf pine was the dominant tree (*vide* Wells, 1924). I do not know the exact northern limits of the low flatwoods, but they probably do not extend much beyond southeastern Virginia. The narrow coastal range of *R. flavilata* seems to agree with the inland distribution of the low flatwoods.

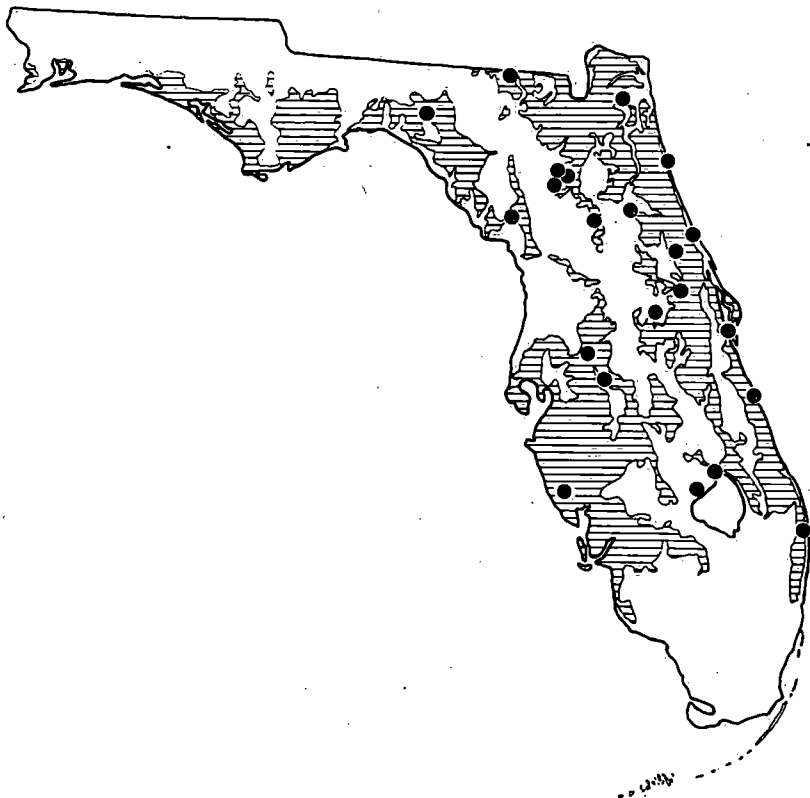


Figure 5. Distribution of *Rhadinaea flavilata* and the pine flatwoods in Florida. Drawn from a *Generalized Vegetation Map of Florida* (Florida Agri. Exp. Station, University of Florida, 1938).

The close association between *R. flavilata* localities and the flatwoods in Florida can be seen in fig. 5. That the same general habitat is occupied in other parts of the range is indicated by the following references. Use of the words "low," "flooded," and "cypress" indicates that flatwoods are being discussed, and not the pine-oak associations that grow on sandy, rolling terrain. ALABAMA: Allen (1932) found two specimens in Harrison County, under the bark of pine stumps. In Mobile County, Löding (1922) reported the species to be "not uncommon in low cut-over pine lands under logs in early spring." MISSISSIPPI: Malnate (1939) quoted Stewart Springer as having found *flavilata* near Biloxi, in "a pine woods flat with occasional gum- and cypress-surrounded ponds, and the entire area is flooded once in two years." In the panhandle counties, Brode and Allison (1958) found it to be a common inhabitant of pine stumps, in communities designated as "cypress-bay" and "pine and live oak . . . on or near a stream." NORTH CAROLINA: Schmidt (1916) found a specimen under a pine log (in flatwoods?) near Councils, in Bladen County. White (1960) collected two specimens from pine stumps in a "pine plantation" in Brunswick County (the associated fauna indicates this to be a flatwoods; table 1). SOUTH CAROLINA: Malnate (1939), in Berkely County, found a few specimens under leaves and soil, in "rather open pine woods: . . . flooded with each rain"

HAMMOCKS. A few pine woods snakes have been found in Florida's hardwood forests at places not far removed from flatwoods. Walter Auffenberg found a specimen (UF 10030) under a piece of paper in a hammock at Daytona Beach, Volusia County, and Goin and Goin (1953) record the species from a hammock in Alachua County. Several have been found in yards in Gainesville, Alachua County. Carr (1940) found two under a board in a Gainesville sawmill, and I have heard of another Gainesville specimen that was taken from a woodpile. A specimen (UF 3271) from Jacksonville, Duval County (not a hammock area), was found in a lumber yard. These records suggest the possibility that individuals occasionally are transported from the flatwoods in shipments of pine (the main timber tree of the Southeast). Nevertheless, I have no doubt that *flavilata* does enter hammocks of its own accord.

COASTAL ISLANDS. *Rhadinaea flavilata* has been found on several islands off the coasts of North Carolina and Florida. It was found "near marshy ground" at the type locality on Bogue Banks, N. C. (Coues and Yarrow, 1878); specimens also have been taken on nearby Shackleford Banks (Robertson and Tyson, 1950; Engels, 1952) and Harkers Island (Engels, 1952). These islands support dry woodlands

and marsh, but, so far as I know, nothing resembling a flatwoods. Bogue Banks and Shackleford Banks are off-shore bars of submarine origin. *Rhadinaea* probably reached these islands in partly decayed logs carried by flood waters, as Engels (1952) suggested.

C. M. Bogert (*in litt.*) reports that the specimens from Anastasia Island in St. Johns County, Florida, were found on an old railway bed under ties partly covered by sand. Possibly, Anastasia Island was connected at one time to the mainland, from which it is not far removed; Neill (1954b) assumes a former land connection to explain the existence of the fresh-water *Siren lacertina* on nearby Merritt Island.

OTHER HABITATS. Funderberg (1958) reports that *Rhadinaea* was found in an area of upland bogs and longleaf pine-oak vegetation (a sandhills association) in New Hanover County, North Carolina. Campbell and Stickel (1939) quote a letter from H. K. Gloyd saying that a Louisiana specimen (probably CAS 12132) was found "among loose bark, leaves, and other debris on one of the alluvial ridges between the swamps." Smith and List (1955) found three specimens in driftwood on a floodplain 6 miles north of Biloxi, Harrison County, Mississippi (near flatwoods?).

MICROHABITATS. Literature references and notes with museum specimens show that *Rhadinaea flavilata* occurs in various microhabitats. Individuals have been found under logs, leaves, pieces of paper, in woodpiles, and buried in loose soil. Wilfred T. Neill (pers. comm.) has found the species in crayfish burrows during dry weather. Most specimens have been found under the loose bark or in the decaying interiors of pine logs and stumps (fig. 4).

ANIMAL ASSOCIATES

FREE-LIVING ASSOCIATES. Small frogs, lizards, and snakes seem to be the only vertebrates that regularly share the flatwoods pine log and stump microhabitat of *Rhadinaea flavilata* (table 1). Frogs and lizards (and snakes?) serve as the food of *flavilata*, whereas other snakes are likely the main predators and food competitors. Perhaps the single most important associate in many flatwoods is the ringneck snake, *Diadophis punctatus*, (Myers, 1965). *Diadophis* is nearly the same size as *Rhadinaea* and occupies the same flatwoods microhabitats, but is more generalized, as indicated by its considerably wider geographic and ecological distribution and by its more varied food habits. *Diadophis* is regarded as an important food competitor, probably a competitor for space, and possibly a predator on young pine

woods snakes. It is worth noting that in Marion County, Florida, the only flatwoods area in which the pine woods snake has been found really plentiful (Allen, 1939), *Diadophis* is uncommon (W. T. Neill, personal communication).

TABLE 1. SOME MICROHABITAT ASSOCIATES OF *Rhadinaea flavilata* IN PINE FLATWOOD REGIONS.*

Species	N. C.	S. C.	Fla.	Miss.
AMPHIBIANS				
<i>Bufo terrestris</i>			X	
<i>Hyla femoralis</i>			X	
<i>Hyla squirella</i>		X		
<i>Gastrophryne carolinensis</i>			X	
REPTILES				
<i>Eumeces inexpectatus</i>			X	
<i>Lygosoma laterale</i>		X	X	
<i>Ophisaurus ventralis</i>			X	X
<i>Thamnophis sauritus</i>			X	
<i>Thamnophis sirtalis</i>				X
<i>Virginia striatula</i>	X		X	X
<i>Virginia valeriae</i>			X	X
<i>Storeria occipitomaculata</i>		X		
<i>Storeria dekayi</i>				X
<i>Diadophis punctatus</i>	X	X	X	X
<i>Lampropeltis dolia</i>	X		X	X
<i>Lampropeltis getulus</i>	X			
<i>Cemophora coccinea</i>				X
<i>Coluber constrictor</i>			X	
<i>Elaphe guttata</i>	X		X	
<i>Tantilla coronata</i>				X
<i>Micrurus fulvius</i>			X	X

*Sources: North Carolina—White (1960); South Carolina—Malnate (1939); Florida—personal observation; Mississippi—Allen (1932), Brode and Allison (1958), Malnate (1939).

The most conspicuous invertebrates found in logs and stumps in north Florida flatwoods are earthworms, centipedes, roaches, termites, and ants. The vertebrate fauna seems to avoid those logs and stumps with the heaviest concentrations of ants; the vacated tunnels of termites and ants, however, provide additional places of concealment.

Timbering practices of man help provide microhabitat space in some places (fig. 4); *Rhadinaea* and other log dwellers are at least easier to find in cut-over areas. Semi-feral pigs roam many flatwoods

and probably prey on any small creature that they uncover while rooting.

Little is known of *flavilata's* associates in habitats other than the pine flatwoods. Engels (1952) surveyed the fauna of a North Carolina coastal island where *Rhadinaea* has been found; Goin and Goin (1953) list the herpetofauna, including *R. flavilata*, of a small hammock area in northern Florida. One specimen (UF 7278) was dug up with a worm lizard (*Rhineura floridana*) in a yard in Gainesville, Florida.

PARASITES. Telford (1961) found *Monocercomonas colubrorum* Hammerschmidt and *Hypotrichomonas acosta* Moskowitz, two widespread polymastiginid flagellates of snakes and lizards, in a pine woods snake from Alachua County, Florida. The same culture (Telford, *in litt.*) later produced *Acanthamoeba* sp. (a normally free-living soil amoeba) and *Entamoeba* sp. A second specimen Telford examined was seemingly free of intestinal protozoans.

HABITATS AND BEHAVIOR

DAILY ACTIVITY. Like many snakes, *R. flavilata* probably does not have a set daily cycle, but most likely adjusts its daily activities to season and to such variables as temperature and hunger. Captive individuals are mostly nocturnal in their prowling; one specimen (TU 17353) was found crossing a highway the night of 4 July 1959.

SEASONAL OCCURRENCE. The term seasonal occurrence is a somewhat subjective index to cyclic variations in microhabitat selection. More than twice as many pine woods snakes have been captured in April as in any other month (fig. 6); there is a sharp decline in May and numbers remain small until March, when an increase is noted. March and April are apparently the most favorable months for *R. flavilata* to occupy the pine log and stump environment, where it is easily collected. This reflects more than the seasonal activity of collectors for, in the Florida flatwoods, small snakes (*Diadophis*, *Virginia*, *Rhadinaea*) of the rotting logs become progressively more difficult to find with the approach of warmer weather and drier conditions in May and June. Winter collecting in my experience, while better than during the hot summer months, yields fewer small snakes than early spring.

Few dates of collection from the Carolinas were available for inclusion in fig. 6. Because of temperature lag, the peak of activity in this region might be expected to occur in May, rather than April. Brimley (1925) found May the peak month for *Diadophis punctatus*

near Raleigh, North Carolina, but in Florida (Myers, 1965) *Diadophis* occurs at the same seasons *Rhadinaea* does.

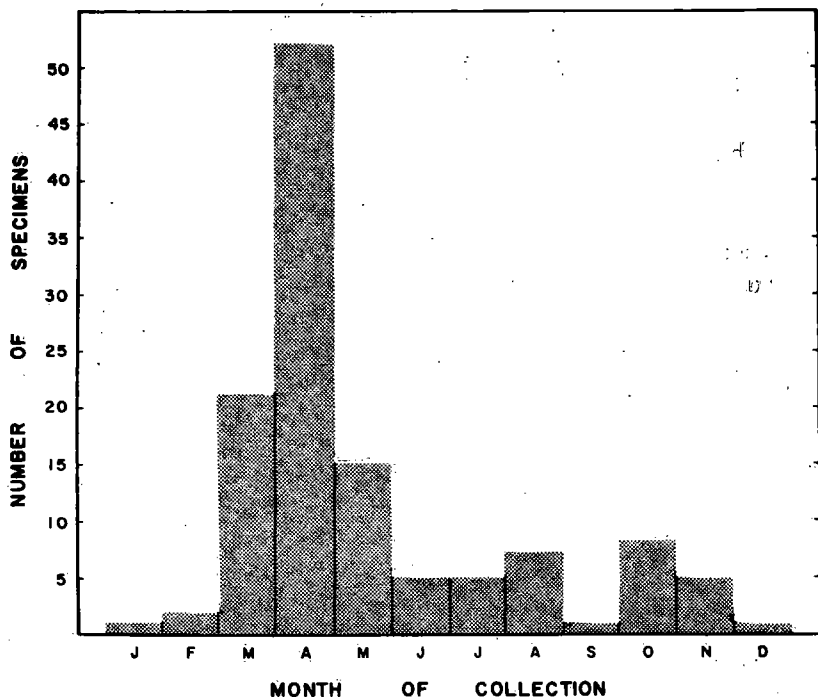


Figure 6. Months of collection for 123 specimens of *Rhadinaea flavilata*.

FOODS AND FEEDING BEHAVIOR. The diet of this species probably consists mainly, if not entirely, of small amphibians and reptiles. Malnate (1939) found the remains of small frogs (*Hyla*?) and the tail of a ground skink (*Lygosoma laterale*) in *flavilata* stomachs. In four stomachs containing food I found the following items: unidentified frog (*Gastrophryne*?, *Rana*?), tree frog (*Hyla* sp.), cricket frog (*Acris gryllus*), and the tail of a ground skink (*Lygosoma laterale*). Conant (1958) says that snakes are included in the diet, but his unelaborated statement needs confirmation. Brode and Allison (1958) state that "Some were taken from rain ponds, feeding on *Acris gryllus*."

Malnate (1939) doubts Haltom's (1931) statement that *flavilata* feeds "on small insects." I likewise question the assertion of Brode and Allison (1958) that "In the drier stumps *Rhadinaea*, *Storeria* and *Lampropeltis* fed on roaches and other insects." Such undocumented

statements have long clouded our knowledge of dietary patterns; it is difficult to judge whether they are based on fact or fancy—for instance none of the specimens Mr. Brode kindly loaned me had the stomach opened. Even when arthropods are found in the stomach, most recent writers (e.g. Neill and Allen, 1956) demand more conclusive proof that these are primary foods. I found the intestine of one *flavilata* crammed with ants, but suspect that these were secondarily ingested, perhaps with the frog *Gastrophryne carolinensis*, which lives in the same habitats with *Rhadinaea* and whose fondness for ants Anderson (1954) has documented.

In captivity *R. flavilata* has accepted a variety of salamanders, frogs, and lizards, but has refused invertebrates, baby mice, a small snake, and a few species of salamanders and lizards (table 2). It seems odd that several individuals refused small *Eumeces* (*inexpectatus* and *egregius*) but fed readily on *Lygosoma*.

TABLE 2. FOOD PREFERENCES OF *Rhadinaea flavilata* IN CAPTIVITY.

Food accepted	Food rejected
AMPHIBIA: CAUDATA	ANNELIDA
<i>Desmognathus fuscus conanti</i> ¹	Earthworms ^{1,5}
<i>Plethodon glutinosus</i> ¹	INSECTA
<i>Manculus quadridigitatus</i> ¹	"small insects" ⁵
AMPHIBIA: SALIENTIA	wood roaches ¹
<i>Bufo quercicus</i> ^{1,2,6}	AMPHIBIA: CAUDATA
<i>Bufo t. terrestris</i> ¹	"salamanders" ⁵
<i>Acris gryllus</i> ^{1,2,4,6}	REPTILIA: SAURIA
<i>Hyla crucifer</i> ^{1,5}	<i>Ophisauris ventralis</i> ¹
<i>Hyla ocularis</i> ¹	(hatchling)
<i>Hyla squirella</i> ¹	<i>Eumeces inexpectatus</i> ¹
<i>Eleutherodactylus ricordi</i> ¹	<i>Eumeces egregius</i> ¹
<i>Gastrophryne carolinensis</i> ^{1,3}	REPTILIA: SERPENTES
<i>Rana catesbeiana</i> ⁵	<i>Diadophis punctatus</i> ¹
REPTILIA: SAURIA	MAMMALIA
<i>Hemidactylus turcicus</i> ¹	baby mice ⁵
<i>Anolis carolinensis</i> ^{1,5,6}	
<i>Lygosoma laterale</i> ¹	

Sources: ¹personal observation; ²Allen (1939); ³Campbell and Stickel (1939); ⁴Funderberg (1958); ⁵Malnate (1939); ⁶Neill (1954a).

The feeding behavior of *R. flavilata* led Neill (1954a: 59-60) to believe that it kills prey with a mild venom it introduces into wounds made by its enlarged rear maxillary teeth:

"The method of feeding was unusual. The snake would seize a frog or lizard, chew until the back teeth were imbedded, and then remain motionless. Seldom was any prey held for less than 45 minutes. Usually a frog would be held for about 70 or 80 minutes. A large, active frog or lizard was often retained for 2 or even 3 hours, until it had become quiescent. Apparently the yellow-lipped snake imbeds its posterior teeth and then waits until a mild venom has numbed the prey. These feeding habits were independently observed by Walter Auffenberg, of the University of Florida. Malnate (1939, Zoologica, (24): 364) observed this snake eating an *Anolis* in captivity. The snake seized the anole, held it until it ceased struggling, and then worked its jaws along the lizard's body to the head and immediately commenced swallowing operations. However, the entire process from the time the lizard was seized until it was completely swallowed took only 25 minutes."

Funderberg (1958) states that his specimen seemed to use no venom on cricket frogs (*Acris gryllus*) but swallowed them at once. My own observations showed that small food items often are swallowed alive, but that larger items are first killed, or at least rendered inactive, as Neill described. I have never observed any feeding that lasted over one hour; several times I have watched captives kill and swallow ground skinks (*Lygosoma laterale*) within 15 minutes.

Rhadinaea flavilata feeds well in captivity, especially if isolated with the prey in a small container. I regularly placed both snake and prey in a 1½ x 4-inch vial and left it in a darkened part of the laboratory; usually the prey animal had disappeared within an hour. Prey is usually swallowed head-first, but small frogs and lizards sometimes are taken from the rear or side.

DEFENSE. The pine woods snake exudes the amber-colored contents of its anal glands when handled, but does not attempt to bite. Whether the anal glands of snakes afford protection against some predators is not known, but seems likely.

The slender tail of *R. flavilata* breaks readily and probably helps some snakes escape predation, as 29.4 percent of all specimens examined had stub tails. Some of this breakage, however, may be due to the ophidian disease that Neill (1960) calls "tail-rot."

REPRODUCTION. Examination of the reproductive tracts of eight adult females collected in different years in Florida, Louisiana, and Mississippi gave the following results:

February (1 specimen): Largest ovarian eggs 4 mm in diameter.

Late April (3 specimens): One had three ovarian eggs, 12 x 4, 13 x 4, and 15 x 4 mm; another had three ovarian eggs, 6 x 4, 15 x 5,

and 16 x 5 mm; the third had two eggs in the oviducts, 26 x 6 and 28 x 6 mm.

May (3 specimens): Position of the eggs in two poorly preserved specimens collected May 13 could not be determined; one from each measured 18 x 6 and 28 x 7 mm. The third specimen collected May 25 had three oviductal eggs, 25 x 7, 27 x 7, and 27 x 7 mm.

July (1 specimen): collected July 4 had two ova (probably ovarian) measuring 14 x 4 and 16 x 5 mm.

The above observations of egg size and placement suggest a long egg deposition season, which is further indicated by a few records of captive layings. Funderberg (1958) reports a specimen from North Carolina that on 4 June 1958 laid four eggs which measured only 13 x 5 mm. Telford (1952 and pers. comm.) records a female 207 mm in total length that deposited four eggs averaging 20 x 4 mm. in Polk County, Florida, 19 July 1946; and a specimen collected in Polk County in June 1947 that measured 381 mm and laid four eggs averaging 18 x 5 mm on 6 July. Allen (1939) mentions a Marion County, Florida individual that laid three eggs averaging 23 x 8 mm 19 August 1937; these hatched in September. The season of egg laying seems similar to that of *Diadophis punctatus* in Florida (Myers, 1965), which is thought to lay from May or June into August, although egg laying in any one year and locality probably does not extend over so great a period.

Funderberg (1958) states that the eggs of a North Carolina specimen were white; the leathery surface was granular to the naked eye, but under magnification irregular, wavy, longitudinal ridges were visible. Curiously, these eggs were smaller than some of the ovarian ova mentioned above. Telford (pers. comm.) noted that the eggs in a clutch from Polk County, Florida were bright yellow. The natural nest has not been reported.

SEX RATIOS

The total sample breaks down nicely into a 1:1 sex ratio, but deviations from this occur in a series from Florida and in the western part of the range. In the combined sample from Alachua and Marion counties, Florida, the ratio is 37 per cent males to 63 per cent females; the exact reverse occurs in the Louisiana-Mississippi sample (table 3). If the deviations from a theoretical 1:1 ratio in these two samples reflect more than chance collecting, I am unable to account for them; there are no conspicuous differences in number of juveniles present or in times of collection.

TABLE 3. SEX RATIOS OF *Rhadinaea flavilata*. THE LARGEST SAMPLES ARE TESTED BY CHI-SQUARE FOR STATISTICAL DEVIATION FROM A THEORETICAL 1:1 RATIO.

Series	%Males: %Females	Number of males	Number of females	χ^2	P
ALABAMA	43:57	3	4		
FLORIDA (total)	44:56	47	59	1.358	<0.25> 0.20
Alachua Co.	36:64	9	16		
Marion Co.	37:63	16	27		
Alachua-Marion Co. (combined)	37:63	25	43	4.764	<0.05> 0.025
All other counties	58:42	22	16		
GEORGIA	—	0	1		
LOUISIANA	62:38	8	5		
MISSISSIPPI	63:37	27	16		
LOUISIANA- MISSISSIPPI (combined)	63:37	35	21	3.500	<0.10> 0.05
NORTH CAROLINA	57:43	4	3		
SOUTH CAROLINA	50:50	4	4		
ALL STATES COMBINED	50:50	93	92		

VARIATION

All observed structural variations are treated in this section. Most variation in this and other species of snakes presumably has a genetic basis, but studies by Fox (1948) and Fox *et al* (1961) show that environment may have major morphological influence in some cases. Until such problems can be studied and discussed in more detail, it seems best to classify variations of snake species without regard to possible genetic or environmental causes. The following scheme seems useful.

- A) Intrapopulational variation
 - 1) Ontogenetic variation
 - 2) Sexual dimorphism
 - 3) Uncorrelated variation
- B) Interpopulational variation
 - 4) Geographic variation

Overlap is frequent between classes 1 and 2. Class 3, uncorrelated variation, is equivalent to the "individual variation" of most

authors, which seems to me a poor term because all variation relates ultimately to the individual. Uncorrelated variation is that which is not basically related to age or sex, although differential mortality rates may sometimes superimpose an age or sex correlation.

Interpopulational, or geographic variation can be variously subdivided, but, as *R. flavilata* provides few good examples, this is not attempted here. The study of geographic variation is essentially the study of shifting frequencies of a character or attribute between populations. Whatever pattern such shifting involves, be it mosaic or smooth or stepped clines, it must be remembered that geographic variation is not something completely apart, but rather is compounded from any or all of the three classes of intrapopulational variation. The only exception is the relatively rare intraspecific situation (absent in *R. flavilata*) where a geographically variable character shows no intrapopulational variation, its frequency being either 0 or 100. In the pine woods snake geographic variation is compounded mainly from uncorrelated variation, partly from sexual variation, and, so far as known, not at all from ontogenetic variation.

Table 4 lists the variable characters determined for *Rhadinaea flavilata* and the classes of variation to which they are assigned.

TABLE 4. CLASSIFICATION OF OBSERVED VARIATION IN *Rhadinaea flavilata*.

Character studied	Type of variation			
	Ontogenetic	Sexual	Uncorrelated	Geographic
Color brightness and pattern	X			
Anal ridges	X	X		
Sexual segments of kidney	X	X		
Tail length	X	X		
Total and body lengths		X		
Anal sacs		X		
Tail breakage		X		
Number of subcaudals		X		
Number of ventrals		X		X
Color pattern			X	X
Labials			X	X
Temporals			X	X
Dorsal scales on neck			X	X
Labial and ventral color			X	
Loreals			X	
Oculars			X	
Divided or half-ventrals			X	
Fused subcaudals			X	
Number of teeth			X	

Characters that vary in more than one way are so indicated in the text. In the following accounts, individuals with total lengths (preserved) over 250 mm are considered adult, and those under 200 mm juvenile, as explained in the discussion of anal ridges.

ONTOGENETIC VARIATION

COLOR AND PATTERN. Most snakes probably undergo some ontogenetic changes in color brightness (= value or brilliance) and saturation. Young *R. flavilata* seem somewhat brighter than adults. Malmate (1939) mentions that some individuals have an indistinct light yellow patch on each side of the neck. The prominence of these occipital spots seems determined partly by age, as they were conspicuous on three juveniles from Okeechobee County, Florida and on one juvenile from Berkely County, South Carolina, but absent or faint on other juveniles and adults.

ANAL RIDGES. These structures are discussed more fully on pages 72-73. Anal ridges are absent on most juveniles, but present on some adult females and most adult males (fig. 9).

KIDNEYS. The kidney in juvenile males is similar to that in females lacking noticeably enlarged "sexual segments" of the urinary tubules. For more details see below.

TAIL LENGTH. This is also a sexually dimorphic feature (fig. 8); tails average proportionally shorter in juveniles of both sexes than in adults. Nine juvenile males have a mean tail/total length ratio of 30.0 per cent (range 28.7-30.7), whereas 47 adult males have a mean of 32.6 per cent (range 30.2-35.9). Corresponding percentages for nine juvenile females and 42 adult females are 28.6 (27.0-30.6), and 29.8 (27.5-32.0), respectively.

SEXUAL DIMORPHISM

Aside from differences in the reproductive organs, the sexes of *Rhadinaea flavilata* were found to vary in the following ways.

KIDNEYS. The adult male kidney is relatively larger than that of the female, and is white with a convoluted surface caused by enlarged segments ("sexual segments") of the urinary tubules. The juvenile and female kidneys are smoother in texture and darker in color. Kidney texture in *Rhadinaea flavilata* is similar in general appearance to that in *Diadophis punctatus* (see Myers, 1965). The function of this dimorphism in the kidneys of some snakes and lizards is unknown.

ANAL SACS. The anal sacs (also called musk or scent glands) of snakes are paired structures lying in the base of the tail and opening

into the cloaca. In the males the sacs lie dorsad from the hemipenes; and for this reason occupy a lesser circumference than in females. The function of these structures is not known with certainty, but as the contents are discharged when *R. flavilata* and most other snakes are handled, they may have some protective value. The sacs are well developed in juveniles.

The length of the anal sacs was determined in only 26 specimens, but the data suggest that the sacs tend to extend more caudad in males than in females (table 5). This is perhaps a compensation for the smaller diameter of the sacs in males.

TABLE 5. LENGTH OF THE LEFT ANAL SAC IN *Rhadinaea flavilata*.

Sex	Number of subcaudals spanned						No.	Mean
	9	10	11	12	13	14		
Males	0	1	7	4	3	1	16	11.8
Females	2	3	2	2	1	0	10	10.7
Both sexes	2	4	9	6	4	1	26	11.3

SIZE AND PROPORTIONS. Females attain greater total length than do males (fig. 7). The seven largest specimens (365-387 mm total length) are females. Assuming individuals over 250 mm total length to be adults, 46 adult males with complete tails average 301.83 ± 4.15 mm in total length, and 45 adult females 325.40 ± 5.20 mm. These differences are due to the greater body (snout-vent) length attained by females (fig. 9), as males usually have longer tails than do females of equivalent length (fig. 8). The largest male (St. Johns County, Florida) is 363 mm in total length and has a tail length of 125 mm;

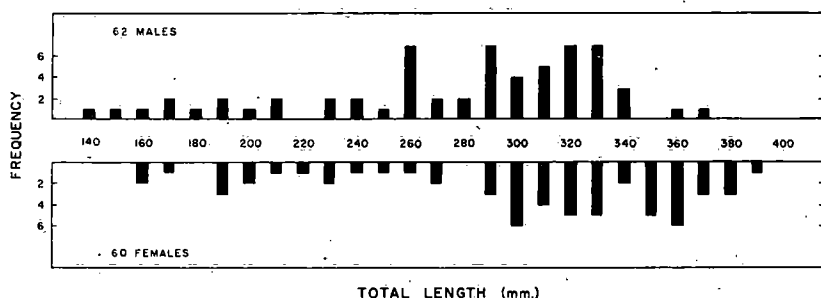


Figure 7. Observed frequency of total lengths in *Rhadinaea flavilata*. Individuals with incomplete tails are excluded.

in contrast, the largest female (Alachua County, Florida) is 387 mm in total length but has a tail measurement of only 114 mm. Mean proportional tail to total length for 60 males is 32.0 per cent (range 28.7-35.9), and for 57 females is 29.5 per cent (range 27.0-32.0).

The presence of the hemipenes and associated muscles is undoubtedly the basis for longer tails in male snakes generally, while the value of additional space for egg or embryo development is logically the selective agent responsible for larger body size in the females. Because of the hemipenes, the base of the tail in male *R. flavilata* is noticeably wider than in females.

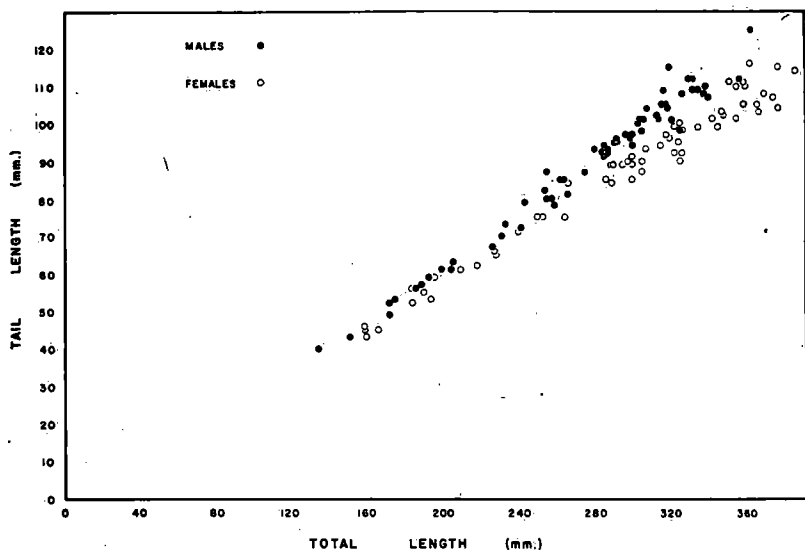


Figure 8. Tail length to total length relationships in *Rhadinaea flavilata*. Individuals with incomplete tails are excluded.

ANAL RIDGES. This term was coined by Blanchard (1931) for the keel-like ridges on dorsal scales in the anal region of certain otherwise smooth-scaled snakes, including *Rhadinaea flavilata*. In snakes of the genera *Carphophis* and *Diadophis* Blanchard found such structures characteristic of males over certain lengths, and seldom present in females and young males. Blanchard and other workers have logically assumed that the ridges indicate the approximate size at which sexual maturity is reached. This belief has been objectively documented for *Diadophis punctatus* in Florida (Myers, 1965), but the function of the structures remains uncertain.

In *Rhadinaea flavilata*, anal ridges are present on all male specimens over 164 mm snout-vent length (fig. 9) or 243 mm total length. Therefore all specimens over 250 mm total length are arbitrarily considered to be adults, and all specimens under 200 mm to be juveniles. Malnate (1939) mentioned two males of 275 mm and 305 mm total length that lacked anal ridges. Possibly Malnate overlooked poorly developed ridges on these specimens because of poor magnification or lighting. Nevertheless occasional large *Diadophis* males lack anal ridges (Blanchard, 1931, 1942; Myers, 1965), and so might some large *Rhadinaea* males. Malnate (1939) also said that anal ridges were not present on any females examined, but they appear on 34 of 87 females I examined (fig. 9).

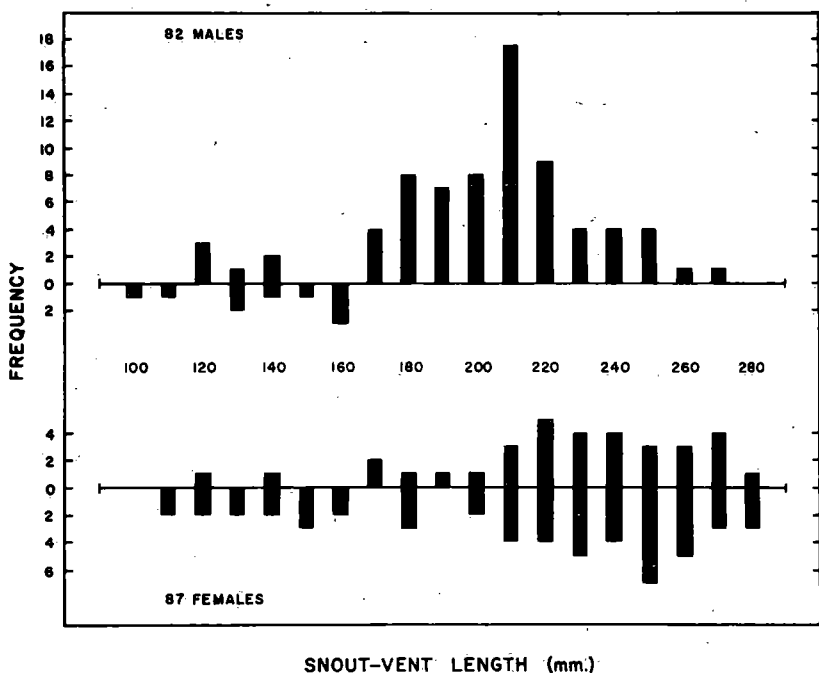


Figure 9. Distribution of anal ridges by size and sex in *Rhadinaea flavilata*. Specimens plotted above the horizontal lines have anal ridges, those below lack them.

The degree of development of anal ridges varies considerably in *flavilata*, but females tend to have them less strongly developed than males. The most conspicuous anal ridges are found in the larger males, but some of the largest specimens have them poorly developed.

TAIL BREAKAGE. Incomplete tails are present in 27 males and 28 females, or 29.4 per cent of the total sample. There is no significant sexual dimorphism in the place of breakage, although the break is closer to the anal plate in some females than in males. The hemipenial muscles normally extend to the 21st subcaudal (to the 24th in an Alabama specimen), and only one male, with 18 pairs of caudals, has less than this number. Seven females, however, have 20 or fewer pairs of caudals. Females with broken tails have 12-70 pairs of subcaudals remaining, with a mean of 38.75 ± 3.30 ; males have 18-69 pairs with a mean of 42.37 ± 2.59 .

VENTRALS. The number of ventral plates varies both geographically and sexually. For the entire sample the number of ventrals in males ranges from 112 to 134, and for females 118 to 139. For given populations the overlap is not nearly so great, and the means are well separated (fig. 11); females usually average four or five more ventrals than males (table 6). The greater number of ventrals in females is correlated with larger body size.

TABLE 6. SEXUAL DIMORPHISM OF *Rhadinaea flavilata* IN NUMBER OF VENTRAL PLATES.

Series	Males			Differences		Females		
	N	M	SE	DM	CD	N	M	SE
North and South Carolina	8	119.88	—	8.40	6.77	7	128.28	—
Alabama, Louisiana, and Mississippi	37	123.30	.31	4.70	3.74	26	128.00	.58
Alachua and Marion counties, Florida	25	125.32	.28	4.70	3.68	43	130.02	.37
Entire range	91	124.20	.28	5.50	4.33	93	129.70	.30

N = number; M = mean; SE = standard error of mean; DM = difference between means; CD = coefficient of divergence (in per cent).

SUBCAUDALS. Males have longer tails (fig. 8) and hence more subcaudal plates than females. For the entire sample males have 68-83 pairs of subcaudals, females 59-75 pairs; there is little or no geographic variation (fig. 12). In given populations males average five or six more subcaudals than females (table 7). As expressed by the coefficients of divergence (tables 6, 7), sexual dimorphism is more marked in subcaudals than in ventrals.

TABLE 7. SEXUAL DIMORPHISM OF *Rhadinaea flavilata* IN NUMBER OF SUBCAUDAL PLATES.

Series	Males			Differences		Females		
	N	M	SE	DM	CD	N	M	SE
North and South Carolina	8	71.62	—	4.62	6.67	4	67.00	—
Alabama, Louisiana, and Mississippi	22	72.64	.55	5.95	8.54	13	66.69	.99
Alachua and Marion counties, Florida	18	73.61	.51	5.58	7.88	33	68.03	.51
Entire range	60	72.87	.31	5.24	7.46	60	67.63	.40

N = number; M = mean; SE = standard error of mean; DM = difference between means; CD = coefficient of divergence (in per cent).

UNCORRELATED VARIATION

Several uncorrelated variations of *Rhadinaea flavilata* seem to have distributional significance and are discussed under geographic variation. These are certain aspects of color pattern and of labial, temporal, and dorsal scale scutellation. It seems likely that additional data would give geographical significance to many of the remaining uncorrelated variations. Only in the case of an aberration of the last ventral plate are there sufficient data to indicate an uncorrelated variation that may not undergo interpopulational shifts in frequency.

COLOR AND PATTERN. Color pattern variation is discussed under geographic variation. Also of possible geographic significance is the coloration of labials and venter, but too few color descriptions of living individuals are available to document this. Cope (1871) says that the labials and venter of the type specimen (North Carolina) were white; this was in life, for Cope received the type alive (Coues and Yarrow, 1878), kept it alive for several months (Cope, 1900), and published his description of the specimen less than two months after receiving it. Ditmars (1907) states without elaboration that the upper lip is "bright-yellow." In a combined description of two living specimens from Florida and Mississippi Brown (1901) states that the ventrals and labials were light yellow. Malnate (1939) gives the following description, probably from South Carolina specimens: "(color nomenclature from Ridgway) . . . Ventral surface pale martius or marguerite yellow, fading to whitish on the chin and throat . . . Labials light maize yellow or sulphur yellow." Ventral coloration

of living specimens from northern Florida ranges from white to chartreuse (yellow-green), and the labials are white, sometimes with a trace of the brown head coloring as well as the usual black spotting. A specimen in the Duke University collections has bright yellow labials—from a slip of yellow paper that faded in the jar of preservative.

LOREALS. A male from Mississippi lacks a loreal on the left and has the right one very much reduced.

OCULARS. A female from Hancock County, Mississippi has the right preocular fused with the supraocular. Netting (1936) notes that a supposed Texas female has the same condition on the left side of the head. Pseudo-oculars rarely appear anterior to the lower edge of the eye, but these arise from labial divisions as discussed under geographic variation.

LABIALS AND TEMPORALS. All variation in these plates is for convenience considered under geographic variation, although it is possible that a few rare conditions of the supralabials and temporals might be uninfluenced by geography.

DORSAL SCALES. See under geographic variation.

VENTRALS. The last ventral is abnormal in 11 per cent of all specimens examined. In most cases (17 of 21) only a half-ventral is present; in the others two half-ventrals lie side by side, giving the appearance of a full plate divided sagittally. The percentage of aberrant specimens is nearly the same in the Florida and western samples, but higher in a series from the Carolinas (table 8). The Carolinas sample was tested for statistical difference from the combined Florida and western sample. The results ($\chi^2 = 0.509$; $P < 0.50 > 0.30$) suggest that this anomaly is not characteristic of any one part of the country; also no evidence suggests that local popula-

TABLE 8. ABERRANCY* OF THE LAST VENTRAL PLATE IN *Rhadinaea flavilata*.

Series	No. aberrant	Total sample	% aberrant
FLORIDA	12	110	10.9
WESTERN (Alabama, Louisiana, and Mississippi)	6	64	9.3
NORTHERN (North and South Carolina)	3	15	20.0
Total	21	189	11.1

*"Divided" or "half-ventral," probably indicative of vertebra duplication.

tions vary significantly from one another in this respect. There is no sexual dimorphism, as 11 variants are males and 10 females.

Rarely do aberrations occur other than in the last ventral. Half-ventrals are present on the anterior part of the body in two males (Mississippi and Florida). A female from Florida has several anterior ventrals "divided."

King (1959) demonstrated that half-ventrals correspond to vertebral duplication (duplicate accessory processes and rib) on one side of the body. Consequently a ventral scute that seems to be divided at the midline probably represents two half-ventrals corresponding to vertebral duplication on both sides. The half-ventral is illustrated diagrammatically by King (1959, fig. 1-E) and Peters (1956, fig. 3-1; 1960, fig. 2-1); the "divided" type of ventral is illustrated by Peters (1956, fig. 3-2; 1960, fig. 2-2). The conditions observed in *Rhadinaea flavilata* are similar to these illustrations; the other types of anomalous ventrals figured by King and by Peters were not observed. King (1959) mentions that half-ventrals were found in *Rhadinaea*; this statement was based on *R. flavilata* (King, verbal communication), although I can state that it also occurs in other members of the genus.

SUBCAUDALS. Two males and two females have one or more single subcaudal plates. A specimen from Okeechobee County, Florida has the first caudal undivided, and one from Alachua County, Florida has the last undivided. One of two snakes collected 5 miles west of Slidell, St. Tammany Parish, Louisiana has the first two plates undivided, the other has the second, third, and fourth plates entire.

DENTITION. No attempt was made to ascertain possible geographic variation in the number of teeth, which does occur in some

TABLE 9. VARIATION IN THE NUMBER OF TEETH IN FLORIDA SPECIMENS OF *Rhadinaea flavilata*.

Bone	No. bones	Number of teeth												
		11	12	13	14	15	16	17	18	19	20	21	22	23
MAXILLARY (anterior to diastema)	16				14*	2								
PALATINE	13	8*	3	2										
PTERYGOID	12									1	2	1	5	2
DENTARY	12									5*	6		1	

*Location of counts for Polk County specimen (1 maxilla, 1 palatine, and 1 dentary were available). All other specimens from Alachua County.

snakes (e.g. *Coluber constrictor*, Auffenberg, 1955). A small series of skeletons from Alachua County, Florida and one from Polk County, Florida indicate the extent of variation in one geographic area (table 9).

Malnate (1939) apparently attempted to count the teeth of *R. flavilata in situ*, and perhaps for this reason obtained lower counts than given in table 9.

GEOGRAPHIC VARIATION

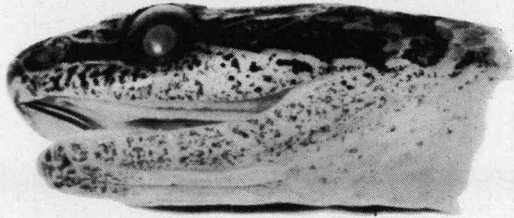
COLOR PATTERN. The most conspicuous geographic variation in *R. flavilata* is the dark pigmentation on the labials (fig. 10), which increases from south to north. In Florida the labials are usually unmarked except for a few plates anterior to the eyes, although some Florida individuals show scattered spots of pigment on all the supralabials and most of the infralabials. In specimens from Alabama, Louisiana, and Mississippi most of the labials are usually spotted and generally more pigmented than in Florida individuals. Some South Carolina specimens have still more pigment, and in North Carolina all the labials and even the genials may be profusely pigmented. Some snakes from the Carolinas resemble southern specimens in labial pigmentation, but no southern individual (Florida, Georgia, Alabama, Mississippi, or Louisiana) remotely approaches the extreme peppered condition shown in fig. 10.

The dorsal stripe also varies geographically. When present this stripe consists of a band of diffused pigment on the vertebral scale row, the pigment normally being restricted to the distal ends of the vertebral scales. The stripe is absent in about 45 percent of the Florida sample and usually only faintly indicated in the rest. Only about 10 percent of the Alabama, Louisiana, and Mississippi specimens lack a middorsal stripe, and it is usually more distinct than on Florida specimens. One of eight specimens from South Carolina does not have a vertebral stripe, but on most it is distinct. The stripe is best developed in the North Carolina sample (seven specimens); vertebral scale row pigmentation is more or less continuous on four specimens, a rare condition anywhere else in the range. I fail to detect geographic variation in the lateral stripe, which is rarely absent but is often weak. Neill (1963: 205) mistakenly attributes presence or absence of striping in *flavilata* to polychromatism, but variation in this character is continuous.

VENTRALS AND SUBCAUDALS. The number of ventrals decreases slightly from south to north (fig. 11). Geographic variation in the

number of subcaudal plates is either nonexistent or too slight to demonstrate in the available sample (fig. 12.)

NORTH
CAROLINA



SOUTH
CAROLINA



FLORIDA



Figure 10. Geographic trends in labial pigmentation of *Rhadinaea flavilata*. *Top*—DU specimen from 24 miles SW Morehead City, Carteret County, North Carolina; *Center*—CM 25190, Berkely County, South Carolina; *Bottom*—specimen from Alachua County, Florida. Robert McFarlane

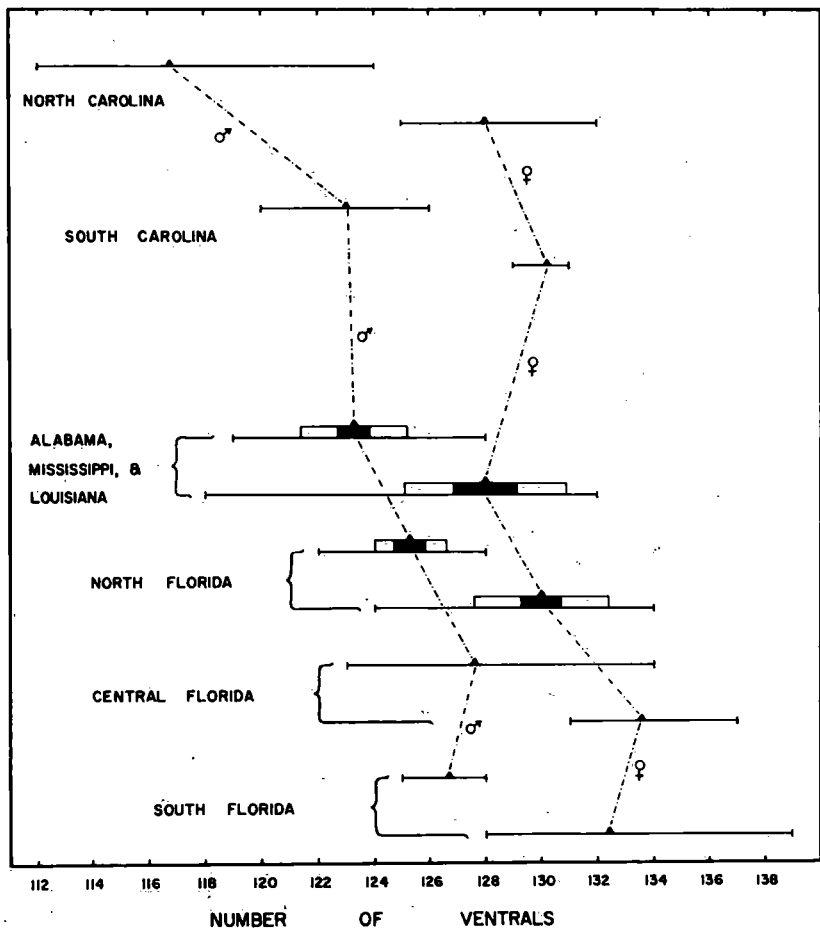


Figure 11. Geographic and sexual variation in the number of ventral plates in *Rhadinæa flavilata*. Horizontal lines represent the ranges of variation, and small triangles the means. A solid rectangle represents two standard errors on each side of the mean; this plus the open rectangle, one standard deviation on each side of the mean.

Sample sizes: *North Carolina*—4 males, 3 females; *South Carolina*—4 males, 4 females; *Alabama, Mississippi, and Louisiana*—37 males, 26 females; *North Florida* (Alachua and Marion counties)—25 males, 43 females; *Central Florida* (Brevard, Orange, Polk, and Seminole counties)—5 males, 5 females; *South Florida* (Glades, Okeechobee, and Palm Beach counties)—4 males, 5 females.

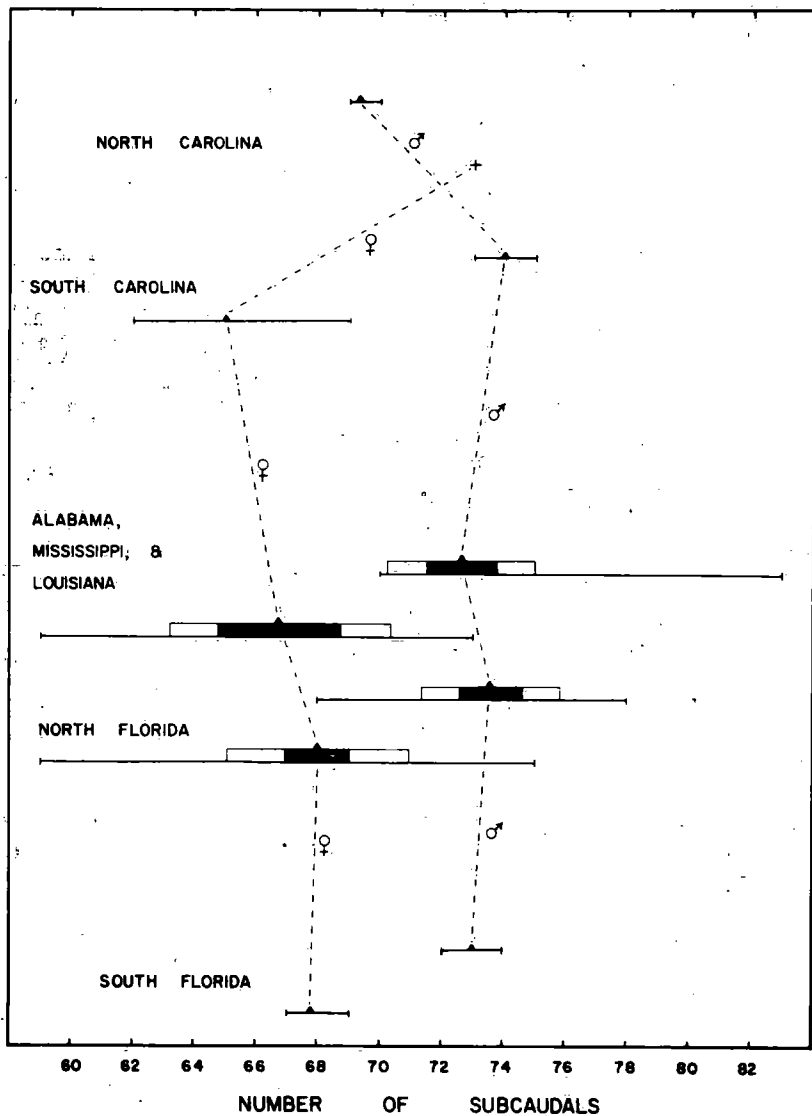


Figure 12. Geographic and sexual variation in the number of subcaudal plates in *Rhadinaea flavilata*. See fig. 11 for interpretation.

Sample sizes: *North Carolina*—4 males, 1 female; *South Carolina*—4 males, 3 females; *Alabama, Mississippi, and Louisiana*, 22 males, 13 females; *North Florida* (Alachua and Marion counties)—18 males, 33 females; *South Florida* (Glades, Okeechobee, and Palm Beach counties)—4 males, 3 females.

INFRALABIALS. The lower labials usually number 9/9, but there are occasionally 7, 8, or 10. Observed variation is listed in table 10; several formulae (e. g. 7/7) that may exist in nature were not observed. Sexual dimorphism appears not to be involved in deviations from the normal (13 males to 18 females). Deviations in upper and lower labial counts occur independently more often than not; only four specimens (from Florida) showed deviations in both the supra- and infralabial formulae.

Reduction or increment of the infralabials occurs most commonly in Florida (table 10); elsewhere such cases are known only from Alabama (1) and Mississippi (2). The Florida sample differs significantly even when compared only to the western population ($\chi^2 = 13.396$; $P < 0.001$). A greater percentage of variant specimens occurs in the Alachua-Marion counties sample than all other Florida locali-

TABLE 10. VARIATION IN THE NUMBER OF INFRALABIALS OF *Rhadinaea flavilata*.*

	Number of labials (left/right)											
Series	7/8	7/9	8/8	8/9	9/8	9/9	9/10	10/9	8/10	10/10	Total	
FLORIDA	1	1	7	5	5	70	4	4	1	1	99	
Alachua Co.			3		3	16	1	1			24	
Marion Co.		1	3		2	25	2	3	1	1	38	
Brevard Co.				2		3					5	
Duval Co.				1							1	
Okeechobee Co.			1	1		5					7	
Orange Co.				1							1	
St. Johns Co.						3	1				4	
Other counties (8)						14					14	
Unknown	1**					4					5	
GEORGIA						1					1	
WESTERN (Alabama, Louisiana, and Mississippi)			1			61		1		1**	64	
NORTHERN (North and South Carolina)						15					15	
UNKNOWN ("Texas")						1					1	
Total	1	1	8	5	5	148	4	5	1	2	180	

*A mutilated male with the formula 10/? (St. Johns Co., Fla.) was not included, nor were a few similar specimens with formulae 9/? or ?/9.

**Specimens mentioned by Malnate (1939, p. 363) that were not available for the present study.

ties combined (table 10); but the difference is not statistically significant ($\chi^2 = 1.139$; $P < 0.25 > 0.20$).

Infralabial variation is best explained by assuming the division or fusion of plates during embryonic development. The reduction to 8 plates involves the fusion of the eighth and ninth or the second and third plates; a reduction to 7 plates involves both of the above combinations. An increase to 10 plates is the result of a division in one of the first several plates (second to fourth, apparently) or in one of the last. Fox *et al.* (1961) report a significant correlation between low supra- and infralabial counts and low environmental temperatures during embryonic development in the snake *Thamnophis elegans*.

SUPRALABIALS. The upper labials usually number 7/7, but occasional combinations of 7/8, 8/7, and 8/8 appear with equal frequency to one another. No apparent sexual dimorphism is involved, as six males and nine females were among the variants studied.

Deviations from the normal count may appear anywhere in the range, but seem most common in Florida (table 11) where 81 percent of the observed variation occurred. Statistically the Florida sample does not differ significantly from the rest of the range ($\chi^2 = 3.398$;

TABLE 11. VARIATION IN THE NUMBER OF SUPRALABIALS OF *Rhadinaea flavilata*.

Series	Number of labials (left/right)				Total
	7/7	7/8	8/7	8/8	
FLORIDA	91	4	5	4	104
Alachua Co.	19	1	3	2	25
Marion Co.	38	1	1	1	41
Polk Co.	3	1			4
Seminole Co.				1	1
Unknown	3	1	1		5
Other	28				28
GEORGIA	1				1
ALABAMA	7			1*	8
LOUISIANA	13				13
MISSISSIPPI	42	1			43
NORTH CAROLINA	7				7
SOUTH CAROLINA	7		1		8
UNKNOWN ("Texas")	1				1
Total	169	5	6	5	185

*A specimen mentioned by Malnate (1939, p. 363) that was not available during the present study.

$P < 0.10 > 0.05$), although the probability obtained is not much above the level (0.05) here accorded significance. While the possibility of chance collecting cannot be ruled out, I suspect that supralabial numbers do vary more frequently in Florida. Most supralabial variants in Florida occurred in the large Alachua-Marion counties sample (table 11), but no significance can be attached to this in comparison with the rest of the state ($\chi^2 = 0.0237$; $P < 0.90 > 0.80$).

Several anomalous supralabial conditions were observed. A female from Alachua County, Florida and another from adjoining Marion County each have a small extra plate (pseudopreocular) added at the anterodorsal corner of the third labial on the left. In a Georgia female a small plate present above the third labial on both sides of the head gives an apparent preocular formula of 2/2. A female from Putnam County, Florida has the first labial on the left excessively elongated along the horizontal axis.

Some specimens have an extra plate between the fifth labial (sixth labial in a specimen with 8 supralabials) and the first temporal. In the sample from Alabama, Louisiana, and Mississippi, 19 have such a plate on one or both sides of the head and 43 do not. The anomaly is absent in the small series from Georgia and the Carolinas but present in four of 104 specimens from Florida. By comparing the Florida sample with the western one it is seen that geographic differences are probably not due to chance alone ($\chi^2 = 21.134$; $P < 0.001$). This is the only head plate anomaly found to be characteristic of the western population. No sexual dimorphism seems to be involved, for the ratio of 15 aberrant males to 8 females can be explained on the basis of an unbalanced sex ratio in the western sample (table 3).

As with the infralabials, supralabial variation is best explained by assuming the division or fusion of plates during embryonic development. The addition of extra plates at the dorsal borders of the third and fifth labials is caused by a division of those plates, as is evident from their reduced area and altered shape. Increase from a normal number of seven to one of eight seems to be the result of a vertical split of the second or third labial, most often the latter. The single instance where the first labial was elongate probably was caused by a fusion of the first two plates and a division of the third.

TEMPORALS. The normal temporal formula is 1 + 2, but these plates are frequently altered by division, fusion, enlargement, or reduction; 33 percent of all specimens examined have one or more aberrant temporals, but usually on only one side of the head. The following kinds of variation were observed.

1) Vertical division of one or rarely both plates in row 2. This gives the formula $1 + \frac{1}{2}$, $1 + \frac{2}{1}$, or rarely $1 + \frac{2}{2}$. (52 specimens: Florida 36, Louisiana 5, Mississippi 9, North Carolina 1, South Carolina 1).

2) Reduction in size of one or both plates in row 2, usually with a noticeable enlargement of an adjoining post-temporal. (7 specimens: Florida 6, Mississippi 1).

3) Fusion of the top plate in row 2 with the adjoining post-temporal, thereby forming an elongated plate. (7 specimens: Florida 6, South Carolina 1).

4) Enlargement of the bottom plate in row 2 and a corresponding reduction of the top plate. (2 specimens: Florida 1, Mississippi 1).

5) Fusion of both plates in row 2 on the left side of the head. (1 specimen: Mississippi).

6) Fusion of the single plate in row 1 with the top plate in row 2 on the right side of the head. This was the only observed instance in which the first temporal was affected. (1 specimen: Mississippi).

The various temporal conditions are so mixed in some samples that they are best considered all together. Only 11 specimens had the same temporal aberration on both sides of the head; only four specimens had more than one kind of temporal defect; aberrations occurred as frequently on one side of the head as on the other. As they occurred in 34 males and 28 females, no sexual dimorphism is evident. Although the observed sex ratio in the Alachua-Marion counties, Florida population was 37 per cent males to 63 per cent females, temporal variants occurred in nearly a 1:1 sex ratio (16 males: 17 females); however, no statistical significance can be attached to these differences ($\chi^2 = 2.360$; $P < 0.20 > 0.10$).

Temporal plate anomalies may be slightly more common in Florida than elsewhere (table 12), but differences based on the available sample are not really significant ($\chi^2 = 3.442$; $P < 0.10 > 0.05$). The issue is further confused by sample bias: The number of anomalous specimens in the Alachua-Marion counties series differs significantly from the rest of the Florida specimens combined ($\chi^2 = 7.035$; $P < 0.01 > 0.005$). Specimens with aberrant temporals are also

known from Brevard, Duval, and Volusia counties on the east Florida coast; 6 of 12 individuals from these counties have anomalous temporals compared with 25 normal specimens from 11 other Florida counties (table 12). This distribution is not random ($\chi^2 = 10.444$; $P < 0.005 > 0.001$), and the amount of temporal plate aberrancy in Florida differs significantly from one local population to the next.

TABLE 12. GEOGRAPHIC DISTRIBUTION AND FREQUENCY OF SPECIMENS OF *Rhadinaea flavilata* HAVING ANOMALOUS TEMPORAL PLATES.

Series	Anomalous	Normal	Total	Per cent anomalous
FLORIDA	42	67	109	38.5
Alachua Co.	12	13	25	48.0
Marion Co.	21	21	42	50.0
Brevard Co.	3	2	5	60.0
Duval Co.	1	3	4	25.0
Volusia Co.	2	1	3	66.7
Counties unknown	3	2	5	60.0
Other counties (11)	0	25	25	0.0
GEORGIA	0	1	1	0.0
WESTERN	17	46	63	27.0
Alabama	0	7	7	0.0
Louisiana	5	8	13	38.5
Mississippi	12	31	43	28.0
NORTHERN	3	12	15	20.0
North Carolina	1	6	7	14.3
South Carolina	2	6	8	25.0
UNKNOWN ("Texas")	0	1	1	0.0
COMBINED	62	127	189	32.8

DORSAL SCALES. The dorsal scale row formula is normally $18 + 17 + 17 + 17$, but occasionally the first count (immediately behind the head) is reduced to 17 or very rarely increased to 19. Deviations were observed in Florida and Mississippi specimens (table 13). A significantly higher number of deviations occurred in Florida than in the western sample ($\chi^2 = 5.822$; $P < 0.02 > 0.01$). The Alachua-Marion series showed no significant difference from other Florida localities combined ($\chi^2 = 0.075$; $P < 0.80 > 0.75$).

TABLE 13. GEOGRAPHIC VARIATION IN NUMBERS OF DORSAL SCALES ON THE NECK OF *Rhadinaea flavilata*.

Series	Number of scales on neck			Total	Per cent deviation from normal (18)
	18	17	19		
FLORIDA	77	23		100	23.0
Alachua Co.	17	8		25	32.0
Marion Co.	32	8		40	20.0
Brevard Co.	2	2		4	
Duval Co.	1	2		3	
Glades Co.		1		1	
Levy Co.		1		1	
Taylor Co.		1		1	
Other counties (9)	22			22	
Counties unknown	3			3	
GEORGIA	1			1	0.0
WESTERN	55	3*	1*	59	6.8
NORTHERN	14			14	0.0
UNKNOWN ("Texas")	1			1	0.0
Total	148	26	1	175	18.2

*From Mississippi.

SUMMARY. Interpopulational variation in *Rhadinaea flavilata* is compounded from intrapopulational uncorrelated variation, except for the geographic changes in numbers of ventral plates, which first vary according to sex. Clinal variation is seen in features of color pattern and ventral numbers, pigmentation increasing from south to north and ventrals decreasing. Other geographically variable characters vary regionally and/or microgeographically: Variation in labial numbers, presence of anomalous supralabials, and deviation from an anterior count of 17 dorsal scale rows, all occur in highest frequencies in Florida. An extra plate between the fifth supralabial and anterior temporal occurs most frequently in the western portion of the range in Alabama, Mississippi and Louisiana. Frequency of occurrence of anomalous temporal plates seems to vary from population to population on a distinctly microgeographic basis.

Except for clinal changes in color pattern, geographic variation in the pine woods snake is not striking. The present study confirms Malnate's (1939) view that no subspecies are recognizable.

AFFINITIES

Rhadinaea flavilata is a relatively generalized member of its genus, as shown by the following characters: 1) Dorsal body scales in 17 rows and not reduced posteriorly. 2) Two enlarged and ungrooved rear maxillary teeth, set off by a diastema. 3) Hemipenis clearly single, capitate, and calyculate. 4) Oculars 1 + 2, temporals 1 + 2. The species is unusual in normally having only 7 supralabials, and is unique in its strong tendency toward a uniform golden-brown dorsal color (most species are conspicuously striped) and in its northern distribution, widely isolated from other species of the genus.

Concerning a more specific relationship for *R. flavilata* within the genus, I concur with an idea advanced independently by Malnate and by Bailey 27 years ago. Malnate (1939) suspected that the dorsal striping on some *Rhadinaea flavilata* indicated relationship with *R. laureata* (Günther) of the highlands of western Mexico. Bailey (1940, p. 16) expresses the same conclusion as follows (remarks in brackets mine):

"A third species, *laureata*, offers a clue to the relationships of the isolated *flavilata* of the southeastern United States. In these species the upper labials are normally 7, a reduction from the usual 8 in other forms. Recent examination of a living specimen of *flavilata* revealed further similarities to *laureata* which were unsuspected from preserved material. The head is uniform above for 2 or 3 scales on the neck, as in *laureata*, and a very faint trace of striped body pattern is present in *flavilata* for which the same scale-row relationship is found as in *laureata*. [In *flavilata* the middorsal stripe, when present, occupies the vertebral scale row, whereas in *laureata* this stripe includes the paravertebral rows. The weak lateral stripes in *flavilata* and *laureata* bear exactly the same scale-row relationship.] The stripes of *laureata* show unmistakable signs of diffusion (see Pl. I) which is simply further developed in *flavilata*, resulting in an almost unicolor pattern [except that body stripes are fairly well developed in North Carolina]. In keeping with this general pattern weakness, the white collar of *laureata* is lacking and the light temporal stripes are less distinct in *flavilata*."

An additional characteristic shared by *flavilata* and *laureata* is the color pattern of the chin and lips. *R. laureata* throughout its range has the labials and genials profusely peppered with dark pigment as in some *R. flavilata* from North Carolina (fig. 10). The fact that this pattern occasionally occurs in other sections of the genus (e.g. in *R. pachyura fulviceps*) does not lessen its significance as an indicator of relationship between *flavilata* and *laureata*.

EVOLUTION

The following hypothesis presumes that *Rhadinaea flavilata* or an ancestral predecessor reached the southeastern United States

via a coastal route from the west. This assumption is based on the present coastal distribution of *flavilata* and its apparent relationship to Mexican *Rhadinaea* (especially *laureata*). A number of other animals seem to have had similar origins (Blair, 1958; Goin, 1958).

Fossil vertebrae assigned to *R. flavilata* are known from Pleistocene localities in Florida as follows: Reddick I B, Marion County (Auffenberg, 1963); Williston, Levy County (Holman, 1959); and Saber-tooth Cave, Citrus County (Holman, 1958). The Reddick and Williston localities seemingly represent the third (Illinoian) glacial stage (Holman, 1959); the Saber-tooth Cave deposit is assigned to the last (fourth or Wisconsin) glacial stage (Holman, 1958). The present-day habitat preferences of *R. flavilata* may have been developed early, for Holman (1958, 1959) interprets the Williston and Saber-tooth Cave faunas as indicative of pine flatwood regions with associated ponds. Thus *flavilata* possibly migrated into the southeastern states during the second glacial period, when the Gulf Coast probably afforded a low, damp corridor from the west and southwest. An earlier entry is possible, even into Florida, where land may have persisted since Miocene time (Vernon, 1951 and Vernon in Goin, 1958). Auffenberg (1963) shows Recent Florida snake genera present in the Pliocene and visualizes little change in distribution of snake genera since then. He further states that, "On the basis of data obtained from the amphibians of the Florida Middle Pliocene . . . there is every reason to believe that it was between Lower Miocene and Middle Pliocene that Florida felt the effects of a western herpetofaunal immigration. This is also suggested by the presence of certain genera of snakes in the Middle Pliocene which are thought to have their ancestral home in southwestern North America (*Crotalus*, *Micrurus*, etc.)." He also suggests an eastward coastal immigration "during the time represented by Stratum 2 at Vero," which is subsequent to the entry of *Rhadinaea*.

Regardless of exact time of arrival, the east-west distribution of this species was perhaps reduced by climatic changes during glaciation, quite possibly in the third (Illinoian) glacial period. The third great glacier extended farther south than any of the others, and climatic changes are thought to have driven many warmth-requiring animals into separate refuges in Mexico and Florida. At that time *flavilata* was presumably isolated in Florida where it has survived to the present. During the late Pleistocene the Florida land mass was occupied by such now-extinct animals as lions, saber-tooth tigers, camels, horses, mammoths, mastodons, ground sloths, giant armadillos, dire wolves, and peccaries (Simpson, 1929). But where-

as the mammals (and birds) underwent considerable extinction, the snake fauna of Florida differs little between late Pleistocene and modern times (Auffenberg, 1963).

With the retreat of the Pleistocene ice sheets and subsequent climatic changes, *R. flavilata* spread out of Florida and followed an expanding habitat westward and northward. The hypothesis of a relatively recent dispersal of a homogeneous stock into relatively uniform habitat (pine flatwoods) explains nicely the absence of any marked geographic variation in the species. Resemblance in color pattern of North Carolina *flavilata* to Mexican *laureata* suggests that the pine woods snake retains primitive characteristics at the northern limits of its range. Because a northward shift in climate since glaciation is very probable, possibly the tendency toward loss of color pattern and toward increased variability in scutellation in the southern populations represent adaptation to a changing environment. Much variability in scutellation is anomalous, indicating that southern populations are in some ways less adjusted than northern ones, which exist in a climate closer to that for which *flavilata* has been longest adapted.*

Thus it seems that the southern populations of *Rhadinaea flavilata* are evolving faster than the northern ones, presumably in response to a warming postglacial climate. Though laboratory studies have shown temperature increase to be an effective mutagen in *Drosophila*, it is not wise to demand a genetic basis for all cases of intraspecific variation in snakes. Scutellation variations similar to some in *Rhadinaea* have been induced experimentally in *Thamnophis elegans* by lowering environmental temperatures during embryonic growth (Fox *et al.*, 1961). Possibly *R. flavilata* is also showing phenotypic susceptibility to environmental change, but the implications of the *Thamnophis* study are not easily applied. The two main reasons for this difficulty are: 1) In the absence of adequate breeding data, nearly impossible to obtain for many or most snakes, one can seldom distinguish between heritable and non-heritable variation; comparing environmentally-induced variation in *Thamnophis* with evolutionary trends in this and other genera, it seems certain that a single kind

* Telford (1966) presents an excellent analysis of variation in southeastern snakes of the genus *Tantilla*, in which the peninsular Florida species, *T. oolitica* and *relicta*, "clearly show a trend toward more aberrant individuals than does *T. coronata*" which occurs north of the peninsula. The fact that the peninsular *Tantilla* are comprised of rather isolated demes does not seem sufficient to explain this particular case of regional variation; one would expect a low frequency of aberrations in some demes to balance out a high frequency in others, unless a nonrandom factor were involved. I suggest that these differences in *Tantilla* may be related to the phenomenon discussed here in *Rhadinaea flavilata*.

of variation is sometimes strictly phenotypic and othertimes genetic, even possibly within single species. 2) We lack comparative data on the potential effects of temperature on the developing embryo. Can, for example, the same sort of phenotype be induced by lowered temperatures in some species of snakes and by increased temperatures in others, or can temperature shifts to either side of the physiological optimum induce similar results in the same species? These are a few questions that come to mind when assuming environmental causes of variation in the scutellation of *R. flavilata*. Ventral plate numbers in the pine woods snake are lower in the north in accordance with the findings in *Thamnophis*, but what about scales and plates that are most variable in the warmer parts of the range? If some of this variability is indeed nonheritable and if it is induced by temperatures below physiological optimum (as in *Thamnophis*), we must assume that, because of genetic adaptation to overall warming trends, the southern populations have become more responsive than northern ones to local periods of cool weather during ontogeny.

Such speculation as above is warranted by the extreme importance of the work of Fox *et al.*, but should not be extended to overshadow suggestive, albeit indirect, evidence that some interpopulational variation in *flavilata* is attributable to non-selective genetic mechanisms. Differences between local populations in frequency of anomalous temporal plates, for example, are easily explained by genetic drift or the founder principle (see Mayr, 1963 and Ford, 1964, for recent discussions of such mechanisms). Regional differences may also have arisen by non-selective genetic mechanisms under certain circumstances; fragmentation of the pine flatwoods, as in northwestern Florida, provides sufficient isolation to maintain regional differences developed from pioneer stock. An extra plate between a supralabial and the first temporal occurs in 30.6 percent of the western population, but in only 3.8 percent of Florida snakes; that this is a genetic trait responsive to drift in pioneer populations is strongly suggested by the fact that of the four (of 104) Florida individuals having the extra plate, three are from an island population (Anastasia Island, St. Johns County) represented by only five specimens.

In addition to mechanisms discussed above, natural selection probably accounts for some geographic variation. The basis for selection may be that *R. flavilata* has shifted habits in response to climatic change directly, or to some ecological situation for which higher temperatures increase the number of favorable mutations. As inferred from study of variation and relationships, the principle

evolutionary trend is reduction—in color pattern, in supralabials, and perhaps in certain other head plates. Such traits are most developed in truly fossorial snakes and lead me to suggest that *flavilata* is becoming more secretive in habits. Certainly the pine woods snake is not often found away from cover, in contrast to several species of tropical *Rhadinaea* with which I have had field experience.

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