# A RECONSIDERATION OF THE RACER, *COLUBER CONSTRICTOR*, IN EASTERN UNITED STATES

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A quarter of a century has passed since the publication of Ortenburger's (1928) monograph on the whipsnakes and racers. During the intervening years such factors as effect generic, specific and racial validity, distributional problems and the evaluation of diagnostic characters in these snakes have been quite generally discussed in many short papers. Yet, the taxonomic status and relationships of the various subspecies are still incompletely known. This seems especially true of those forms which inhabit the coastal areas of southern United States. Descriptions have been based on characters present in a few specimens at hand, with little knowledge of the extent of variation, either individual or geographic.

This study is primarily concerned with the morphological variations existing in the eastern forms. Notes and comments are presented on more western populations when they contribute to a better understanding of the variations which are found in the East.

In order to understand individual and geographic variation of southeastern forms practically all of the available material from the area was studied. Thus a total of 1,560 specimens from both institutional and private collections was examined. Since Florida was to be a focal point in the study of variation, many more specimens were examined from this state than any other (1,008). Of the remaining 552, 491 were from east of the Great Plains, and over two-thirds of these from the southeastern states.

Efforts were made to examine as many living specimens as possible, and 377 became available for study. The results were especially worthwhile for without live animals knowledge of certain colors (which fade rapidly in preservatives) would not have been available.

Throughout the course of this paper the following abbreviations are used when reference is made to specimens or to collections: AMNH = American Museum of Natural History, New York, New York; ANSP = Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania; CHM = Charleston Museum, Charleston, South Carolina; CM = Carnegie Museum, Pittsburgh, Pennsylvania; CNHM = Chicago Natural History Museum, Chicago, Illinois; UF = Department of Biology, University of Florida, Gainesville, Florida; JWC = John W. Crenshaw Collection, Gainesville, Florida; MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; RA-WTN = Ross Allen-Wilfred T. Neill Collection, Silver Springs, Florida; ST = Sam Telford Collection, Winter Haven, Flor-

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ida; T = University of Texas, Austin, Texas; TU = Tulane University, New Orleans, Louisiana; UMMZ = University of Michigan Museum of Zoology, Ann Arbor, Michigan; WA = Walter Auffenberg Collection, Gainesville, Florida.

## Taxonomy

There are two major groups included within the genus *Coluber,* the whipsnakes and racers. As now recognized there are eight subspecies of the racer, *Coluber constrictor.*[2] Together they are distributed throughout the United States, from coast to coast, and from the Gulf of Mexico and Guatemala northward into southern Canada. Although widely distributed, there are probably no true desert forms. However, some populations occur in mountainous areas, between, or even surrounded by truly arid conditions. They do not seem to occur on the tops of high mountains.[3] The range of *Coluber constrictor mormon* extends from the Pacific Coast to, and including most of, the Rocky Mountains; *Coluber c. flaviventris* is found in the Great Plains, from the eastern slopes of the Rocky Mountains to the forested provinces of eastern North America; *Coluber c. stejnegerianus* occurs from Guatemala northward to Nueces County, Texas, along the Gulf Coast; while *Coluber c. paludicolus* is found in the Everglades of southern Florida and on Cape Canaveral, Brevard County, Florida. These four subspecies are light in color. They may vary from green through brown to bluish-gray. The belly is always light. Another form, *Coluber c. anthicus,* of western Louisiana and eastern Texas, is spotted with yellow, buff, or bluish, on a blue, black, or tan ground color. The remaining three races are slaty-black above and below. The light-colored chin contrasts with the dark belly or throat. These are distributed throughout eastern North America. *Coluber c. priapus* is found in the Coastal Plain from North Carolina southward throughout most of Florida, westward to the Mississippi River, and thence northward to southern Illinois and Indiana along the Mississippi and Ohio River Valleys. *Coluber c. constrictor* is found from the eastern edge of the Mississippi Valley to the Atlantic Coast in the northeast, and to the Fall Line in the southeast. In the northeastern parts of its range it is found as far northward as Halifax, Canada. *Coluber c. helvigularis* subsp. nov. is found in the area of the Chipola and Appalachicola River Valleys of western Florida (fig. 1).

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[2] Etheridge (1952) has shown that the supposedly diagnostic characters of *Coluber ortenburgeri* fall within the variation of *Coluber c. stejnegerianus,* and that the former should be regarded "at most" a subspecies of *constrictor.* In view of the lack of any diagnostic character which would serve to separate the two forms I see no reason for retaining *ortenburgeri* as a nominal subspecies. The name should be referred to the synonymy of *Coluber c. stejnegerianus. Coluber c. haasti* of Bell (1952) is not regarded as a valid form for reasons to be given later in this paper.

[3] Brimley (1942) stated that *C. c. constrictor* is not found above 4,000 feet in North Carolina. Linsdale (1940) stated that *C. c. mormon* is found between 4,000 and 6,000 feet elevation in Nevada.

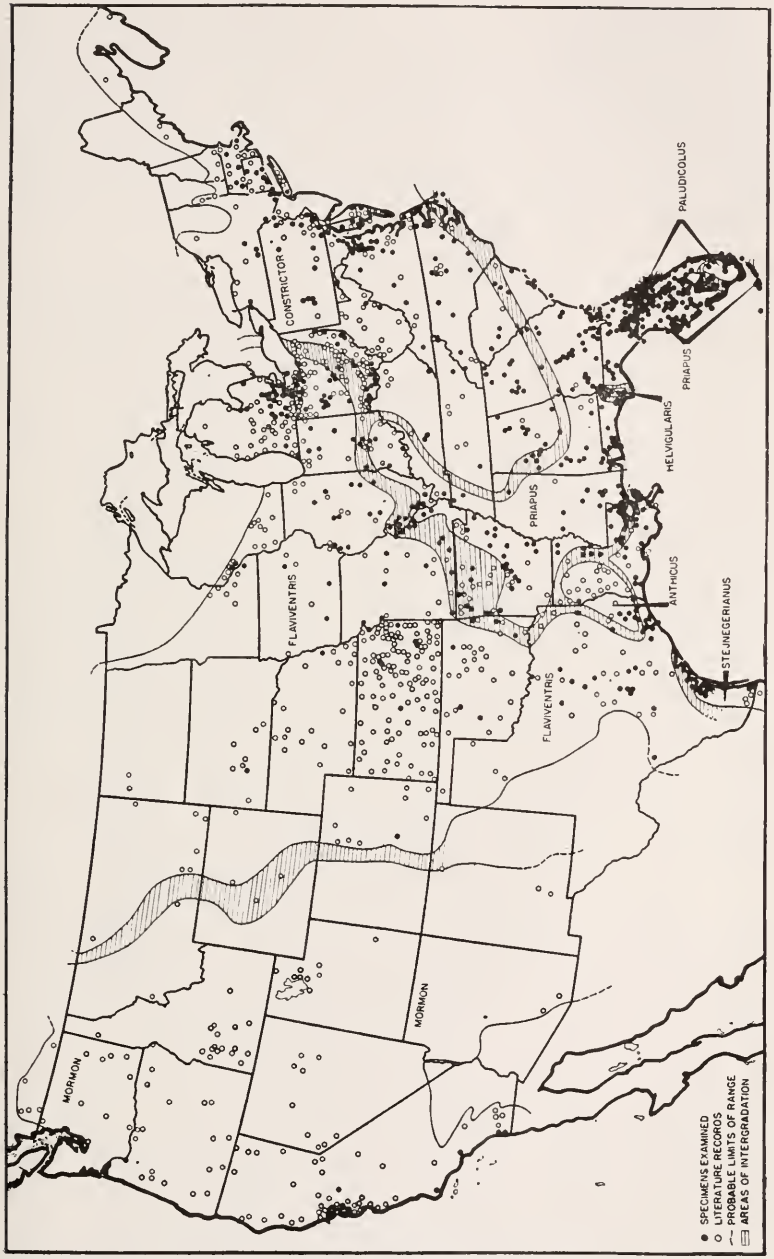


Figure 1. Distribution of the subspecies of *Coluber constrictor*.

All of these races are known to intergrade with one another at the mutual borders of their ranges with the exception of *C. c. mormon* and *C. c. flaviventris.* Intermediate populations between these two forms probably occur, although as yet none have been reported. Intergradation (if it does exist) is to be expected in Montana, where a record for *C. c. mormon* brings this racer's range within 130 miles of that of *C. c. flaviventris* (Stuart, 1930:44). Intermediate populations will probably also be found to occur throughout, or near, the Front Ranges of the Rocky Mountains.

Besides these eight recognized races there are several populations of varying sizes which, judging from their morphological characters, may be incipient subspecies. Areas in which these populations occur are listed here, although they will be discussed later in the paper. (1) The Outer, or Lower Florida Keys: speckled individuals reminiscent of intergrade specimens between *C. c. priapus* and *C. c. anthicus* are available from certain of these islands. However, they coexist with typical, uniformly black specimens and probably represent nothing more than mutant individuals. (2) The Mississippi Delta and the associated mainland: *C. c. flaviventris* from this area seems to be rather distinct from populations throughout the remainder of the range of this subspecies. These differences mainly concern coloration and scutellation. (3) Eastern Steppe Province: populations of *C. c. flaviventris* from the states of Ohio, Michigan, Indiana and Illinois differ from populations of the same subspecies from the Great Plains. The name *Coluber c. foxi* Baird and Girard, has recently been revived for this population (Schmidt, 1953:187). However, from the specimens which I have examined I am forced to conclude at the present time that a gradual cline exists between the Great Plains and Eastern Steppe populations. Further work should be conducted in these areas, especially Missouri and Iowa, to determine the nature and extent of the area of intergradation and degree of homogeneity of characters in the regions pertinent to an understanding of the situation. Until this is done it may be more advantageous to retain *C. c. foxi* in the synonomy of *flaviventris.* This interpretation has been followed throughout the present paper. (4) St. Johns River Valley, Florida: specimens of *C. c. priapus* from Seminole County to Lake Okeechobee along the lowlands of the St. Johns River are intermediate between *C. c. priapus* and *C. c. paludicolus.* This population is homogeneous and can be separated from either *priapus* or *paludicolus* on the basis of the amount of white on the ventral surface. However, they cannot be distinguished from intergrades between *priapus* and *paludicolus* from other areas where ranges of the two subspecies meet. Preliminary investigation suggests that the St. Johns River lowlands receive considerable gene-flow from Everglades populations in other species of snakes as well, *e.g. Liodytes alleni, Thamnophis sauritus, Lampropeltis getulus, L. doliata,* and *Diadophis punctatus.* The two areas are separated by a very low stream divide, and the ecological characters of both provinces are quite similar.

The condition seems somewhat comparable to that between the *flaviventris—foxi—constrictor* complex, and in this paper the lower St. Johns River specimens are considered as representing an intergrade population. However, further study may show that they deserve nominal status. At the present time no real advantage would be gained by recognizing these specimens as a separate race, for the implication would be that they had attained an evolutionary level equal to that of the other accepted subspecies in North America. In view of our present knowledge this hypothesis seems untenable.

## Key to Adult Specimens

1. Dorsal surface and most of ventral surface slaty black. ..... 2

   Dorsal surface lighter, being greenish, olive, brownish, bluish, or spotted. Ventral surface light, being whitish, yellow or light slaty blue. ..... 4

2. Enlarged basal hemipenial spines up to 2½ times the length of the adjacent proximal spines; in large adults there is usually very little white on the chin and throat. The supralabials are usually almost completely black in large adults. The iris is always brown or dark amber, never bright red or orange. ..... *Coluber constrictor constrictor*

   Enlarged basal hemipenial spines at least 3 times the length of the adjacent proximal spines, and are usually 4 times the length of these spines; in large adults from peninsular Florida there is usually a considerable amount of white on the chin and throat; the supralabials are usually half white and half black in specimens from peninsular Florida, darker on the Florida Keys and throughout the remainder of the range. The iris is usually brown, but may be amber, red, or even orange in specimens from central peninsular Florida. ..... 3

3. Chin light tan or brown, or mottled with light tan or brown; never all white or blotched with black. Supralabials and infralabials always with a light tan or brownish suffusion. Iris in adults always brown, never bright red or orange. ..... *Coluber constrictor helvigularis*

   Chin white, or mottled with black, never light brown or tan. Supralabials and infralabials white, black, or with both colors present, never distinctly light tan or brown except near the area of intergradation with *paludicolus*, or in isolated populations in western peninsular Florida. Iris brown, red, amber, or orange. ..... *Coluber constrictor priapus*

4. Dorsal surface spotted with white, yellow, buff or dark blue. ..... *Coluber constrictor anthicus*
   Dorsal surface not spotted, unicolor. ..... 5
5. Usually 7 supralabials, average adults over three feet. ..... 6
   Usually 8 supralabials, average adults under three feet. ..... 7
6. Subcaudals less than 99; ventral color usually some shade of yellow, but may be grayish, bluish-white or yellowish-white; iris usually brown, but may be reddish in specimens from southeastern Louisiana; practically never any darker clouding on the belly; 1st supralabial rarely in contact with the loreal. ..... *Coluber constrictor flaviventris*
   Subcaudals more than 99; ventral color whitish, never distinctly yellow; iris always reddish, amber or orange, rarely brown; usually with light brownish-gray or powder blue cloudy markings on the belly; 1st supralabial commonly in contact with the loreal. ..... *Coluber constrictor paludicolus*
7. Infralabials usually eight; dorsal color greenish. ..... *Coluber constrictor stejnegerianus*
   Infralabials usually nine; dorsal color usually olive. ..... *Coluber constrictor mormon.*

For the most part this study has concerned itself with the variations existing in the four eastern races of *Coluber constrictor: constrictor, priapus, paludicolus,* and *helvigularis* (new subspecies). Variation in the portion of the range of the race *flaviventris* which is found east of the Mississippi river is discussed in somewhat less detail. An abbreviated synonymy and description of the four subspecies mentioned above follow:

### *Coluber constrictor constrictor* Linnaeus
### Northern Black Racer

*Coluber constrictor* (part) Linnaeus, 1758: 385 ("Habitat in America septentrionale").
*Bascanion constrictor* Baird and Girard, 1853: 93.
*Bascanion foxii* (part) Baird and Girard, 1853: 96.
*Coryphodon constrictor* (part) Dumeril, Bibron and Dumeril, 1854: 183.
*Masticophis flagelliformis testaceous* (part) Jan, 1863: 65.
*Coryphodon constrictor vertustus* (part) Jan, 1867: fig. 3.
*Bascanion flaviventris* (part) Dumeril and Bocourt, 1870: 697.
*Bascanion constrictor flaviventris* (part) Yarrow and Henshaw, 1879, App. L. of App. N. N.
*Zamenis constrictor* (part) Boulenger, 1893: 387.
*Zamenis constrictor flaviventris* (part) Ditmars, 1907: 285.
*Zamenis constrictor constrictor* (part) Ellis and Henderson, 1913: 103.

*Coluber constrictor constrictor* (part) Stejneger and Barbour, 1917: 79.

*Coluber constrictor flaviventris* (part) Ortenburger, 1928: 175.

*Diagnosis.*—A subspecies of *Coluber constrictor* in which the ventral and dorsal coloration of the adults is slaty black; the enlarged hemipenial spine is less than three times the length of the adjacent proximal spine and the eyes are always brown or dark amber.

*Holotype.*—None assigned, but the type locality is probably in the vicinity of Philadelphia (Dunn and Wood, 1939).

*Description.*—Dorsal surface in adults uniform slaty black, fading to dark olive gray where it integrades with *flaviventris.* Scales with a satiny luster. Top and sides of head slaty black like the remainder of the body and tail. In full grown specimens the supralabials practically all black, but in some adults, or in smaller specimens, black above and white below. Ventral coloration dark slaty black to dark gray. Chin usually white and in large specimens more or less spotted with black, sometimes practically all black. Iris usually dark brown or dark amber.

Juvenile specimens possess a distinct pattern until after the first year. Ground color slaty gray or brownish-gray. There are 48 to 71 saddle-shaped blotches of dark gray, dark brown or reddish-brown, edged with darker gray or black, arranged in a single series down the back, and extending down the sides to the second or third scale rows.

On the side of the body, alternating with the dorsal saddles, are faint darker spots one to two scales long and wide. They may occur singly or in pairs, one spot being above the other. Small black punctations may occur over the same area.

On the anterior half to two-thirds of the belly there are many small semicircular or crescent-like gray, black, or brownish spots, usually two on each scute, which are usually found on the lateral edges of the ventral plates.

Supralabials cream or white, with a dark brown or black edge on the posterior margin of each plate. Infralabials white or cream, and unspotted.

Specimens in the transitional stage of color suffusion are usually very dark gray dorsally, with faint indications of dorsal spots anteriorly. Top and sides of the head usually black. The snout may be lighter, depending on stage of transition. Supralabials usually black above and white below.

The ventral coloration of the juveniles is frequently retained though the color of the dorsal surface may be typical of mature specimens. At one stage of the transition, when the ventral coloration begins to turn darker, the underside of the tail and the anterior third of the belly remain light, while the middle portion of the belly slowly turns darker. The darker coloration moves in from the lateral portions of the ventral plates, and in some specimens there remains a light area, appearing somewhat as a stripe extending down the center of the

belly. Specimens which are further along in the transition usually have uniform, slaty black bellies. Blotches or spots of black or very dark gray are frequently found on the throat. The dark ventral spots of the juveniles may be retained for a long time, as has been shown by Pope (1944: 172), who mentioned seeing traces of juvenile belly markings on a specimen of *flaviventris* that was 42 inches in length.

Dorsal scale rows normally 17-17-15. Reduction takes place by loss of the third or fourth lateral scale row. Occasionally an additional vertebral reduction by loss of the seventh or eighth scale row. Ventrals from 161-193 (mean 178.2±1.2), males 177.3±1.9, and females 178.8±1.3; subcaudals from 72-101 (mean 96.2±1.5), males 99.8±1.9, females 93.2±1.7; supralabials usually 7, from 8-11; preoculars normally 2, occasionally 1 or 3; postoculars 2, frequently 3; temporals 2-2-2, but quite variable. Anterior chin shields shorter than the posterior pair; loreal present, usually longer than high, and occasionally divided; body elongate, with a long and slender tail.

Large specimens are about five feet long. Ortenburger (1928: 196) mentioned a large specimen 1660 mm in total length as the largest that he had measured. Babbitt (1932: 27) reported a specimen 1854 mm long and has told me that he measured a specimen from Simsbury, Conn., which was 1905 mm in length. Roddy (1923: 32) recorded one from Pennsylvania "over six feet". Another large specimen which was 1886 mm in total length was reported by Atkinson (1901: 146).

The hemipenial characters are as follows: organ slightly bilobed, with a single sulcus; spines number 89-130, in 6-9 rows, covering about one-third of the length of the organ; the tip is smooth with a raised margin formed by the edges of the distal calyces, these edges being made up of several minute, flat, blunt, spine-like processes; three large spines are set around the basal portion of the organ. These large spines are usually from 2-2½ times longer than their predecessors in the same row. The base of the organ is smooth, but occasionally may be covered with very small spinules.

Maxillary teeth 14-16; dentary teeth 17-22; palatine teeth 13-15; and pterygoid teeth 20-26.

*Range.*—By and large *C. c. constrictor* is an eastern humid forest form. It ranges from Halifax, Canada, south through eastern Maine to northern North Carolina. Further inland it is found north of the Fall Line, throughout the Piedmont and Appalachian Mountain and Plateau provinces. It occurs as far westward as the Mississippi Valley in the states of Mississippi, Tennessee and Kentucky. The range has been shown to be correlated with the unglaciated regions of Ohio, occurring only in the eastern and south-central parts of that state (Conant, 1938: 50).

*Remarks.*—Occasional light-bellied adults are found in various parts of the range. They resemble intergrades between *flaviventris* and *constrictor* from Ohio in that they are black dorsally and have light gray or yellowish-gray ventral surfaces. Eckel and Paulmier (1902:

371) reported such an individual from New York which was "yellow" ventrally.

*Coluber constrictor priapus* Dunn and Wood
Southern Black Racer

*Coluber constrictor* Holbrook, 1843: 55.
*Bascanion constrictor* (part) Baird and Girard, 1853: 93.
*Coryphodon constrictor* Gunther, 1858: 108.
*Zamenis constrictor* (part) Boulenger, 1893: 387.
*Coluber constrictor constrictor* (part) Stejneger and Barbour, 1917: 79.
*Coluber constrictor priapus* Dunn and Wood, 1939: 4.
*Coluber constrictor haasti* Bell, 1952: 21.

*Diagnosis.*—A subspecies of *Coluber constrictor* in which the dorsal and ventral coloration is mostly slaty black; the enlarged basal hemipenial spine is three or more times the length of its predecessor in the same row. The iris is usually brown or dark amber, but may be red in both juveniles and adults from Florida.

*Holotype.*—ANSP 16111, collected by George B. Wood. The type locality is West Palm Beach, Palm Beach County, Florida.

*Description.*—For the most part very similar to *Coluber c. constrictor.* Dorsal surface of adults uniform black with a satiny luster. Top and sides of head black. Snout brownish in many half grown specimens or even adults. Supralabials usually quite dark, practically always showing slight traces of white on lower portions of at least the anterior plates. Large adults from Florida frequently have these scales colored black above and white below. Ventral coloration dark slaty gray to slaty black. In some specimens from the northern parts of its range, as well as those from the Florida Keys, there is no white on the throat, while in others from peninsular Florida the white may extend a considerable distance on the throat and anterior parts of the belly. In some specimens from central Florida this white color may extend for nearly two-thirds the entire length of the venter. Chin usually white, but may be spotted with black or very dark gray, and is frequently so suffused by black that only a few traces of white are discernible. Iris usually brown, but sometimes dark amber. In Florida the iris may be reddish, or even orange.

The coloration of juvenile specimens is very similar to that of *constrictor,* except that in central Florida the dorsal saddles may be brownish-red, and the posterior ventral plates may show a distinct reddish or even a pinkish tinge. There are 47-73 saddles along the back. Small lateral spots alternate with the larger dorsal blotches. Ventral spots one-fourth to one-eighth as wide as ventrals. These markings usually brownish or even black in color, but may be reddish or orange in specimens from Florida. The transitional coloration is seemingly identical with that of *constrictor.*

Dorsal scale rows 17-17-15. Reduction occurs laterally on the third or fourth scale rows. Occasional specimens are examined that also

have a vertebral reduction by a loss of the seventh or eighth scale rows. Ventrals 154-199 (mean 178.0±0.58), males 177.2±0.87, females 179.1±0.84; subcaudals 70-119 (mean 99.8±0.62), males 101.1±0.61, females 96.3±0.98. Supralabials usually 7, but vary from 6-9; infralabials 6-12, usually 8; preoculars 2, rarely 3; postoculars 2, occasionally 3; temporals 2-2-2, but quite variable. Anterior chin shields shorter than posterior pair; loreal present, longer than high, rarely divided and in specimens from Florida frequently in contact with the first supralabial, rarely so in specimens from other parts of its range.

At least the Florida specimens of this race seem smaller than most examples of *constrictor* that I have examined. Whether or not this is true of populations in the more western or northern parts of the range I cannot say with any degree of certainty. Of the southeastern specimens that I have examined, the largest was a male 1320 mm in total length. Ditmars (1936: 94) has mentioned that individuals from the southeastern states are not as large as those from more northern states. This seems to be true, for the average length of 171 Florida specimens with a uniform coloration is 920 mm while from New York 34 similarly-colored specimens average 1041 mm.

Hemipenial spines as in *constrictor,* except that the enlarged basal spines are much longer, practically always three times the length of the adjacent proximal spines of the same row. They vary from one to 5½ times the length of these adjacent spines. Smaller spines from 72-132, disposed in 6-10 rows, covering about one-third of the organ.

Maxillary teeth 14-17; dentary teeth 16-20; palatine teeth 13-16; and pterygoid teeth 20-30.

*Range.*—The range of *C. c. priapus* includes the southeastern Coastal Plain from northeastern North Carolina, including all of Florida except the Everglades, and associated regions, Cape Canaveral, Brevard County, and the Chipola and Appalachicola River Valleys in northwestern Florida. The populations on the Lower Florida Keys are typical of this race. It also occurs along the Gulf Coastal Plain to the Mississippi River, thence up its valley, including the northwestern part of Louisiana and a large portion of Arkansas, except the Boston Mountains and adjacent areas, and northward to the vicinity of St. Louis, Missouri. In the Ohio River Valley it is found in southern Illinois and Indiana. It occurs in the states of Kentucky and Tennessee where they border the valley of the Mississippi River.

*Remarks.*—Black-colored specimens from outside of the range as just described have been reported. A specimen "slaty black above" has been reported from Eddyville, Iowa by Guthrie (1926: 177). Anderson (1942: 211) mentioned two specimens taken near Independence, Missouri that were black dorsally and blue-gray ventrally. These would seem to be intergrades, although the author noted that other specimens from the area were colored like typical *flaviventris.* Burt and Hoyle (1934: 34) reported a "blue-black" specimen taken

in Rogers County, Oklahoma, well within the range of *flaviventris.* Branson (1904: 412) stated that although present in Kansas, black-colored racers are rare in that area. Strecker (1908: 73) stated that a black *Coluber constrictor* was taken in the Bosque Hills, north of Waco, McLennon County, Texas, and in 1915 (p. 35) reported that they were taken "as far south as Bosque and McLennon Counties". Strecker and Williams (1927: 21) reported that a half-grown specimen from San Marcos, Texas was typical of the race *constrictor,* being black in color. They added that similar specimens are found in the hill districts of Travis County and other sections nearby. This does not seem to have been mentioned in the literature since 1927, and students familiar with this area do not seem acquainted with this color variety.

The distribution of this race in the western portions of its range is not well known. All of the specimens I have examined from states west of the Mississippi River have a hemipenial spine characteristic of the race *priapus.* The nearest typical specimen of *C. c. constrictor* comes from east of the Mississippi River. On this basis I have assumed that all reliable records of black-colored snakes from west of the river refer to individuals genetically more similar to specimens of *priapus* than to *constrictor.*

It will be noted that the range of this form combined with the range of *C. c. constrictor* is not the same as that indicated by Ortenburger (1928: 183 ff.), who included Arkansas within the range of *flaviventris.* A number of the specimens examined from Arkansas are black on both dorsal and ventral surfaces. For example, AMNH 64730 from Big Buffalo River, near Pruitt, Ark., is black above and below, with a white chin. The supralabials are black above and white below. AMNH 64731 from Little Rock, Pulaski County, is black above and the anterior portion of the ventral surface is white and heavily mottled with black. The supralabials are black above and white below. I have included these and similar specimens in the race *priapus.* Only one specimen is referable to *flaviventris* among those which I have seen from Arkansas (CM 25025, from McGehee, Desha County). This individual is grayish above and very light-colored below. The supralabials are dark gray above and yellow below.

The literature includes references to black-colored snakes from Arkansas, usually identified as *constrictor* by the authors. Thus Taylor restricted the range of *flaviventris* in Arkansas to the northwestern portion of the state and listed both Washington and Benton Counties. On the other hand, Burt (1935: 312) reported *flaviventris* from Boone, Carrol, Cleveland, Madison, Crawford, Pope, Saline and Washington Counties, indicating a much more extensive range. Such references might be indicative of interdigitation between the races. Dellinger and Black (1932: 21) referred to this situation in stating the following:

> "Most students believe that there is a great deal of

> intergradation between the two subspecies of *constrictor* found in Arkansas, and that the ranges of both forms overlap to a considerable extent. For the most part *flaviventris* is found in the hills and *constrictor* [*priapus*] in the lowlands . . . but the separation is far from distinct . . . [and] we believe the disposition of these forms as made by Ortenburger is preferable."

It is unfortunate that none of these authors described or mentioned intergrades from these areas. Intermediate specimens do exist, such as those from the lower tier of counties in the southwestern corner or Missouri. In USNM 99600 from Berryville, Carrol County, Arkansas, the dorsal surface and supralabials are black. Ventrally it is very light colored, indicating some genetic affinities with *flaviventris,* and is best described as an intergrade. CM 25018 from 3.7 mi. west of Wynne, Cross County, CM 25083, 2 miles west of Fayetteville, Washington County and CM 25004 from Berryville, Carrol County (all in Arkansas) are similar, being black dorsally and bluish-gray ventrally. Until further study is conducted in this area (preferably of an ecological nature) the best disposition of specimens from Arkansas is to call all racers that are black both dorsally and ventrally, and which possess white chins, *priapus.* All specimens that are black or bluish-black dorsally and light gray or bluish-white ventrally should be called intergrades, and all individuals bluish, brownish, or gray dorsally and white, gray, or yellowish below, *flaviventris.*

Although Brown (1950) cited no records of black-colored racers from Texas, *priapus* probably occurs there. Its range would seem to embrace only the northeastern corner of the state. Strecker (1908: 73) mentioned specimens of *constrictor* (probably *priapus*) from northeastern Texas. I have heard of three other specimens from this area that are very dark, but which, unfortunately, I could not examine. Whether or not black racers are found in eastern Oklahoma is unknown. Ortenburger (1926, 1927, 1928 and 1930a and b) and Smith and Leonard (1934) did not mention *C. c. constrictor* in the state. Blair and Hubbell (1938) indicated that the Mississippi Biotic Province extends into the southeastern corner of Oklahoma. This is the warmest and most humid part of the state, and the plant associations are typical of those of the Coastal Plain. A common snake of the Coastal Plain, *Farancia abacura,* has recently been recorded from this region (Burger, 1948: 133). A *Coluber constrictor* (T 14003), from 3 miles northeast of Procter, Oklahoma, is black dorsally and bluish-white ventrally. Unfortunately, the specimen is rather small and exact identification is difficult. However, its coloration is reminiscent of young intergrade specimens between black and light colored races in other portions of North America. Another specimen (T 6513) from 1 mile south of Nashola, Oklahoma, resembles an intergrade specimen in color, although it seems closer to *priapus* than to *flaviventris,* being black dorsally and bluish-black ventrally. The supralabials are practically all black. Burt and Burt (1929: 10) recorded a specimen of *flaviventris* from Wister, Le

Flore County, Oklahoma in the extreme southeastern part of the state that somewhat confuses the issue. If populations of black-colored racers occur in both northeastern Texas and southeastern Oklahoma these will undoubtedly be found to represent the subspecies *priapus.*

As mentioned above, Ortenburger placed southern Illinois within the range of *flaviventris.* This is difficult to understand in view of his color descriptions of this race and of *constrictor.* One of the specimens, the color of which was described as typical of *flaviventris* is from Hillsboro, Illinois. It was "blackish mouse gray" on the dorsal surface and lateral tenth of the ventral plates. Below it was "light olive gray" on the median half of the belly. In describing the typical coloration of *constrictor* a specimen was chosen from Marion County, Florida. The dorsal surface was "blackish mouse gray", covering the lateral fifth of the ventral plates. The middle portion of each scute was "Hathi gray", and the anterior edges "light olive gray". Obviously these two specimens were very similar. At most the Illinois specimen was an intergrade. That southern Illinois contains other areas with black-colored racers is indicated by numerous references in the literature. Lueth (1941: 29) and Cagle (1941) mentioned *C. c. constrictor* from extreme southern Illinois. In 1942 Cagle (p. 187) stated that most specimens from Union and Jackson Counties were intergrades between *flaviventris* and *constrictor.* Blanchard (1924: 536) reported two specimens of *C. c. constrictor* from Johnson County, Illinois. Ditmars (1936: 59) mentioned *constrictor* from Swallow Rock, Jackson County, Illinois. USNM 94362 from the same locality is intermediate in that the belly is fairly light. On the other hand, the supralabials and dorsal surface are both black. This specimen, though similar to *flaviventris* in its belly color, is closer to *priapus* (*constrictor* of earlier workers). Of four adults from Olney, Illinois (USNM 13833, 14150a, b and c) three are intermediate. One is a good example of the race *priapus.* This specimen is black dorsally and ventrally. The chin is white and this color extends posteriorly to the eighth ventral plate. The supralabials in all are black above and white below.

Mittleman (1947: 481) has already called attention to the black-colored racers of southern Indiana. Of five specimens from wheatland, three are referable to *priapus.* Two are intergrades. A specimen from New Albany is typical of the race *priapus.*

*Coluber c. priapus* also extends into extreme southeastern Missouri. It probably occurs in a narrow band along the Mississippi River. I have examined intermediates from St. Louis, Montgomery, Oregon, Ozark, Jackson, Jefferson and Cape Girardeau Counties, Missouri.

*Coluber constrictor haasti,* recently described by Bell (1952: 21), is referred to the synonymy of *Coluber c. priapus,* because the characters given as diagnostic are not confined to the Florida Keys and they are frequently, and in some cases characteristically observed in other localities.

*Coluber constrictor paludicolus* Auffenberg and Babbitt
Everglades Racer

*Coluber constrictor constrictor* Conant, 1930: 60.
*Coluber constrictor priapus* Allen and Slatten, 1945: 26.
*Coluber constrictor paludicolus* Auffenberg and Babbitt, 1953: 44.

*Diagnosis.*—A light-colored racer, bluish-gray, greenish-gray, or occasionally brownish-gray dorsally. Ventrally whitish or light powder blue, with or without darker cloudy markings. Gulars frequently tinted with brown and the iris is usually red, sometimes orange or bright yellow. It differs from *flaviventris* in a higher number of subcaudals, a higher mean number of ventrals, the high frequency of contact between the 1st supralabial and the loreal and in the juveniles which have a smaller number of dorsal blotches.

*Holotype.*—USNM 131900, collected March 23, 1950, by Lewis Hall Babbitt, three miles west of Kendall, Dade County, Florida.

*Description.*—Dorsal coloration usually bluish-gray, but varies from greenish-gray to greenish-brown. A few are decidedly tan. Ventrally yellowish-white to white, frequently bluish-white. Ventral markings of adults, when present, may be in the form of cloudy blotches ranging from powder blue to grayish-brown or light tan, and in some specimens placed along the edges of the ventral plates so that there is formed a distinct light median line. Posterior gulars and lateral scales of the anterior part of neck usually tinged with light brown. Small black punctations may be scattered on the ventral surface. Top and sides of head usually olive. Snout frequently tan. Supralabials bluish-gray above, usually with a band or area of tan or grayish-brown below this. The bottom third of each plate is white, or in some cases yellowish. Chin white, but may be yellowish. Iris usually red, frequently orange, amber or even bright yellow, rarely brownish-red in adults.

Juveniles with 42 to 65 reddish-brown dorsal saddles, frequently decidedly reddish, or even pink. The smaller alternating lateral spots are reddish. Ground color grayish brown. A distinct pinkish or reddish hue is present posteriorly. Ventral surface pinkish-white anteriorly and decidedly pinkish posteriorly. Ventral spots usually small, scattered and reddish to reddish-brown in color. Many specimens have no ventral markings at all.

Dorsal scale rows usually 17-17-15, the reduction at the lateral third or fourth scale rows. Occasional specimens have an additional vertebral reduction of the seventh or eighth scale rows. Head plates normal in number. The 1st supralabial frequently in contact with the loreal, which is rarely divided. Ventrals 177-190, mean $184.0 \pm 0.36$, males $183.7 \pm 0.56$, females $187.0 \pm 1.07$. Subcaudals 99-117, mean $107.2 \pm 0.45$, males $107.8 \pm 0.81$, females $106.9 \pm 1.01$. Total length divided by the tail length varies from 3.2 to 3.8.

The largest specimen of this race examined is 1689 mm, while the mean length of 22 uni-colored specimens is 1119.2 mm. Hemipenial characters and dentition the same as in *priapus*.

*Range.*—This subspecies is found in two isolated populations which do not seem to be recognizably differentiated. One of these is on Cape Canaveral, Brevard County, Florida. Intergrades between this population and those of *priapus* on the adjacent mainland occur on Merritts Island (fig. 2). The other, and more widely distributed population, is found in the Everglades and adjacent areas of southern Florida, from Cape Sable throughout the southern tip of the penin-

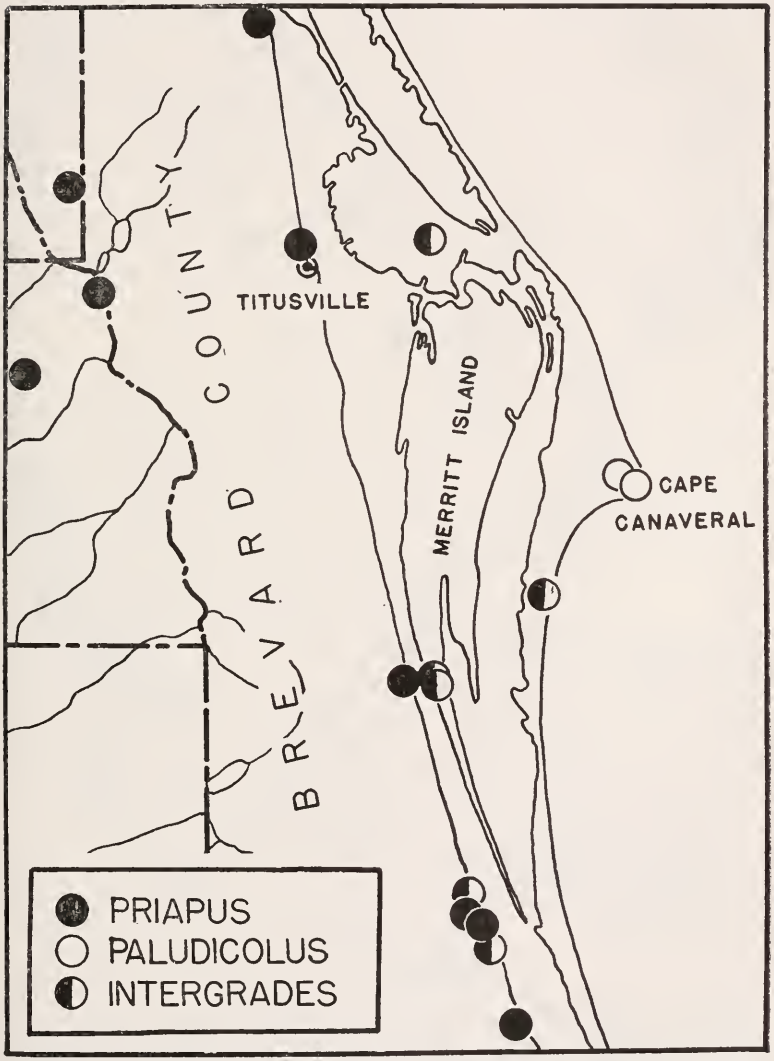


Figure 2. Distribution of *Coluber c. paludicolus* on Cape Canaveral, Brevard County, Florida.

sula, westward to the Big Cypress Swamp in Collier County, northward to the southeastern portion of the Okaloacoochee Slough in Hendry County, eastward to central Palm Beach County, and southward throughout most of Broward County with the exception of the eastern portion along the Atlantic Coast. It intergrades with *Coluber c. priapus* on both Upper and Lower Matecumbe Keys, Monroe County, and possibly on Key Largo. Intergrades are also found

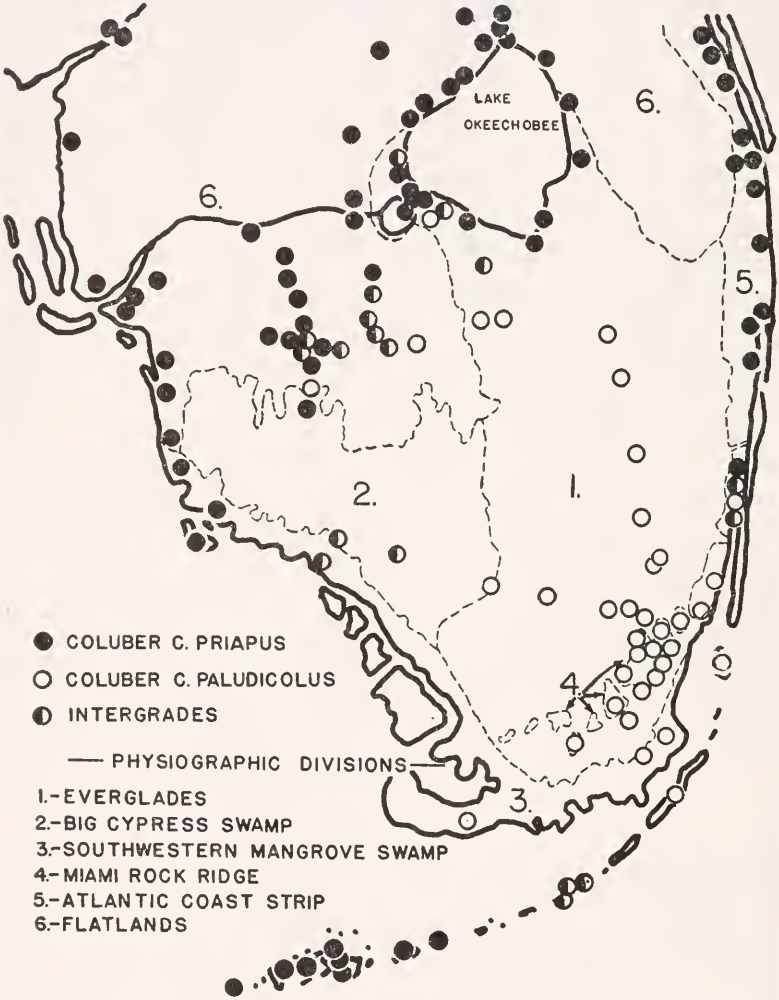


Figure 3. Distribution of *Coluber c. paludicolus* and *Coluber c. priapus* in southern Florida. For the most part, *paludicolus* is confined to the Everglades, the southern portion of the Southwestern Mangrove Swamp and the Miami Rock Ridge. It is also known from Biscayne Key in Miami Bay and Key Largo.

around the periphery of the range as stated above, except, of course, where it borders the sea (fig. 3). Intermediate specimens between *priapus* and *paludicolus* appear practically identical with those between *priapus* and *flaviventris,* or between *constrictor* and *flaviventris.* They are black dorsally and light slaty-black, gray, or light bluish-white ventrally. The supralabials are black above and light gray to white below.

*Remarks.*—Besides the two populations mentioned above, I have examined three other specimens from peninsular Florida which are colored like examples of this race. One is from "Key West, Monroe County" (USNM 14417), while the other is from "Long Pine Key, Monroe County" (MCZ 31797). These two specimens, though outside the range of *paludicolus,* probably have the correct locality data. Influence from this race could be expected over the relatively short distance to the mainland. However, USNM 83294, labeled "Gainesville", Alachua County, Florida, undoubtedly has incorrect locality data. Of close to 200 racers which I have examined from Alachua County, none approached the coloration of *paludicolus.*

*Coluber constrictor* ***helvigularis,*** subsp. nov.

Brown-chinned Racer

*Diagnosis.*—A subspecies of *Coluber constrictor* recognized by the large amount of very light brown or light tan on the supralabials, infralabials, and especially the chin and throat of adults. Although adult specimens of *paludicolus* normally have tan supralabials and posterior gulars, these two races are immediately distinguishable on the basis of their dorsal and ventral coloration. In *helvigularis* these surfaces are slaty-black, while in *paludicolus* they are much lighter.

*Holotype.*—CM 21462, collected April 9, 1942, by Coleman J. Goin, 8 miles west of Wewahitchka, Gulf County, Florida.

*Description of holotype.*—An adult female in which the top and sides of the head as well as the dorsal surface is dark slaty-black. Supralabials black above and light brown on the lower half of each plate. Infralabials and throat entirely light brown. Chin very light brown, with a few white blotches, each covering only a few scales. There are traces of a slightly darker shade of brown on the belly as well as on the underside of the tail wherever the slaty-black color, which covers most of the belly and tail, is not evident.

Supralabials 7-7, infralabials 8-8; no contact between the loreal and the first supralabial; postoculars 2-2; preoculars 2-2; temporals 2-2-2 on one side and 2-1-2-2 on the other; gulars 4. Scale rows 17-17-15. Ventrals 173, anal divided, subcaudals 102.

*Paratypes.*—Two specimens are designated as paratypes: UF 1496-7, Scott's Ferry, Calhoun County, Florida.

*Variation.*—Top and sides of the head and the dorsal surface of the body of adults black. Ventrally, however, there may be varying traces of very light brown intermingled with the more prevalent black color. Chin light brown, but with a few white blotches. Throat

either very light brown or white, the latter strongly contrasted with the brown chin. Supralabials always light tan or light brown on the lower half of each scale and black above. Snout either black or with varying traces of very light brown. Infralabials also tan or light brown.

Supralabials 7-7; infralabials 8-8; loreal in contact with first supralabial in three specimens; preoculars 2-2; postoculars 2-2; gulars ranging from 3-5, mean 4.0; temporals normally 2-2-2, but in some specimens 2-1-2-2 or 2-1-2. Dorsal scale rows 17-17-15, with the lateral reduction occurring by loss of the third or fourth scale row, from the 99th-126th ventral. Ventrals 169-174, mean $171.6 \pm 2.32$. Subcaudals 88-102, mean $97.3 \pm 1.76$. In two of the specimens the last ventral before the anal plate is divided. The hemipenial spines seem identical with those of *priapus,* including the enlarged proximal spines.

*Range.*—The flood plains and adjacent pine flatwoods along the Chipola and Appalachicola Rivers of northwest Florida. Specimens are available from Gulf and Calhoun Counties (fig. 4).

*Remarks.*—A specimen in the Ross Allen-Wilfred T. Neill collection (no. 435) which bears the data Iron City, Seminole County, Georgia, is typical of this race. The chin is heavily mottled with light brown. Both the infra- and supralabials are suffused with this color. No other specimens are available from the immediate locality. However, seven specimens are available from the area near the junction of the Flint and Chattahoochee Rivers (UF 3728-34). Five of them are from Florida and two from Georgia. Only two of these specimens have the faintest indication of brown on the chin. Those of the remaining specimens are pure white. In the collection of John W. Crenshaw there are 18 adult specimens from Baker County, Georgia. This locality is about 35 miles northeast of Iron City, Seminole County. None show any tendency toward a brownish-tinted chin. The only other specimen which is available from this section of Georgia is one from Fort Benning, Chattahooche County (USNM 80948), which is on the Fall Line. It is an intergrade between *priapus* and *constrictor* and has no brown on either the chin or labials. In southeastern Alabama I have seen a specimen from Enterprise, Coffee County (WA 2501). This locality is about 40 miles west of the Apalachicola River. The specimen shows no tendencies towards the coloration of *helvigularis.*

Intermediate specimens have been examined from Florida and extreme southwestern Georgia. CM 21464 from 12.2 miles west of Wewahitchka, Gulf County, has a light brownish tinted chin, with considerable amount of white present. This specimen, though intermediate, is closer to *helvigularis.* DBUF 2644 from Blue Springs, Jackson County, is practically identical to *priapus* except that the posterior gulars are light brownish. The supralabials also have considerable brown on them. The same is true of two other specimens from near Panama City, Bay County (USNM 81174). These last three specimens are certainly closest to *priapus,* although the presence

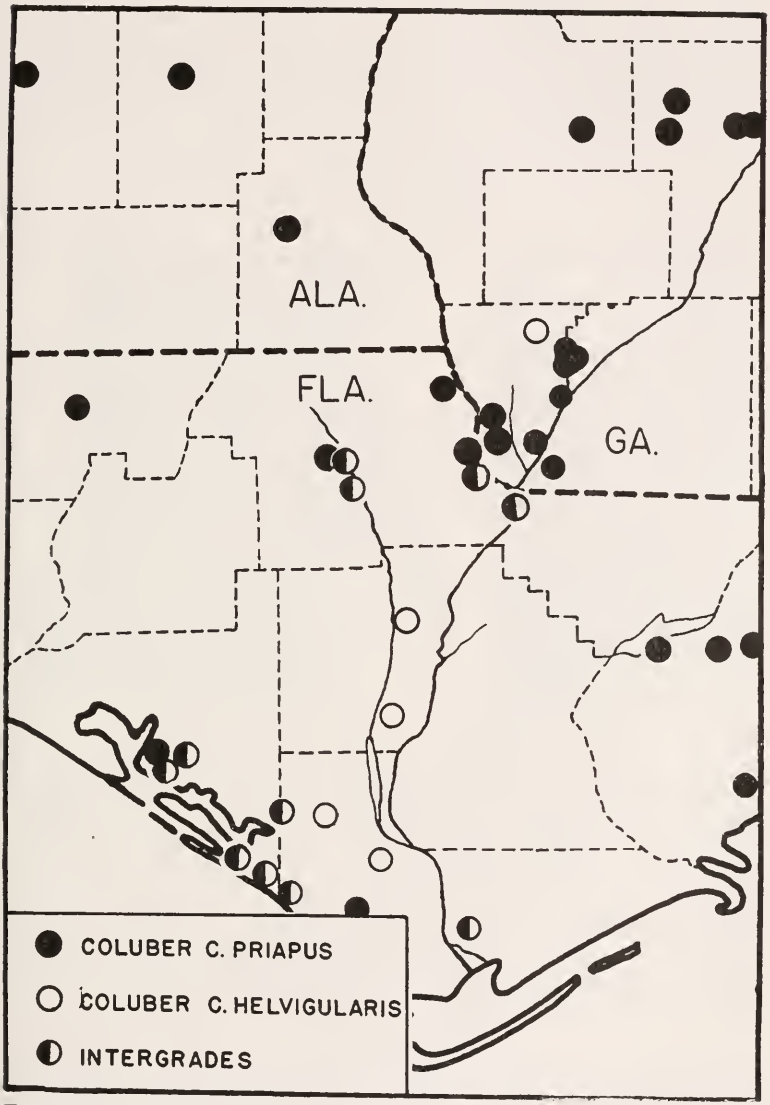


Figure 4. Distribution of *Coluber c. priapus* and *Coluber c. helvigularis*, subsp. nov.

of a considerable amount of light tan coloration shows a notable genetic influence from *helvigularis* populations farther eastward. All of these localities are about 25 miles west of the Appalachicola River. Two other specimens (WA 4001 and 4002) from 5-7 miles east of Tyndall Air Base, Bay County, Florida, are intergrades but closer to

*helvigularis.* A specimen which I have seen (no longer available) from extreme western Leon County, near Bloxham, was typical of the race *priapus.* UF 3731, from Sealy Springs, Seminole County, Georgia, has *very* faint indications of light brown on the chin. The same is true of UF 3729 from Chattahoochee, Gadson County, Florida.

## Individual and Geographic Variation

### *CORRELATED VARIATION*

Under this heading are discussed the variations in color and scutellation which are correlated with geographic locality, sex, environment, or ontogeny.

The term cline has been used to express a condition in which the values of a variable character form a slope or gradient over a geographic area. With increasing knowledge of variation systematists have come to recognize different types of clines. Although closely related, two obvious types come to attention. These are the *eco-* and *geoclines.* In the first, a character gradient is present which conforms with an ecological gradient over the same area. In the second, the character gradient simply seems correlated with distances or areas. In most cases it is obviously difficult to divorce the ecocline from the geocline.

Other than these two distinctions, character gradients may have varying slopes when the values of the character being examined are plotted against distance. Two general types of gradients seem to be recognizable by this type of analysis. One of these is the *external cline.* In this type the continuous sloping character-gradient is interrupted and may be thought of as resembling a stair case, with the separate subspecies corresponding with the treads, flat or very gently sloping, and being united by steep slopes—the zones of intergradation. The mean values for different characters of the various subspecies will often form a gradient. This condition may also be called an intergroup cline (see Huxley, 1943: 211). The other type is called an *internal cline,* which does not show any steepening of the character gradient, or cline, in certain areas, but rather a continuously sloping character-gradient with no obvious interruptions (Huxley, *loc. cit.*).

A rather special type of cline, generally termed an *ontocline,* is also shown in *Coluber constrictor.* It is an ontogenetic change that varies as a character-gradient in degree or intensity with distance.

### *External Clines*

*Length of the hemipenial spines.*—The characters associated with the hemipenes of male snakes have long been used in taxonomic studies of serpents. In general they have been used as characters of generic, or specific consequence. However, Dunn and Wood (1939: 1 ff) have shown that proportional measurements of the proximal spines may also serve as one of racial significance.

In *Coluber constrictor* the basal portion of the hemipenes is spinous. These spines are disposed in definite rows, with a gradual proximal increase in the size of the spines. At the basal end of certain of

these rows there is also a very much enlarged spine. Dunn and Wood (*ibid.*) have suggested a standardization of terms for the proportional measurements of the enlarged basal spines and the smaller preceding ones in the same rows. A basal spine that shows only a slight enlargement over the preceding one is called "not significantly enlarged". If it is two times the length of the adjacent proximal spine it is "significantly enlarged". It is called a "basal hook" if it is four times the length of the next smaller spine in the same row (fig. 5).

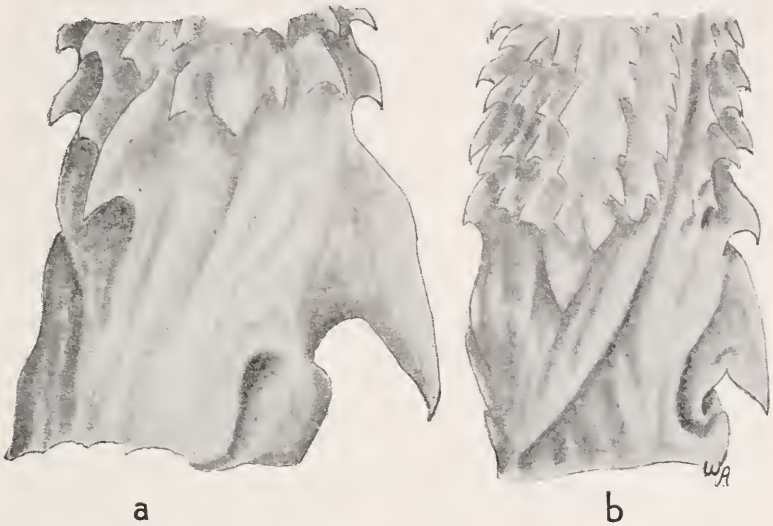


Figure 5. Variation of the enlarged basal spines on the hemipenis of *Coluber constrictor*. a. Basal portion of the hemipenis of a typical specimen of *C. c. priapus* (WA 3009, Alachua County, Florida). b. Basal portion of the hemipenis of a typical specimen of *C. c. constrictor* (WA 3670, Atlanta, DeKalb County, Georgia).

Following an examination of several male black racers from eastern North America, Dunn and Wood (*ibid.*) found that all of the Florida specimens were provided with a "basal hook", while others from New York, New Jersey, Pennsylvania and Virginia had basal spines which were, at most, "significantly enlarged". In view of this geographic variation, they proposed the name *Coluber c. priapus* as a new subspecies, which was then known only from Florida. In the present study an examination of many specimens from the eastern half of North America has shown that this race is not restricted to Florida, but has a distribution which is very similar to that of many other Coastal Plain reptiles and amphibians.

The basal spines of this species may vary in two ways: (1) the length of the spines (as shown by Dunn and Wood), and (2) the number of basal spines which may be termed hooks. The values of the former may be constant over large areas of North America, with

zones of intergradation between. However, the mean lengths in these same areas vary geographically as a gradient. In view of these two characteristics I have included this type of variation under "external clines". The latter situation (2) has already been referred to by Dunn and Wood (*ibid.*), who stated that some Florida specimens have one hook, some have two, and others even have three. This will be discussed under "internal clines".

Although the eastern limits of the range of *flaviventris* has been shown to lie westward of that indicated by Ortenburger (1928: 183 ff), specimens on the eastern side of the Mississippi River have always been referred to the race *constrictor.* In view of this it is unusual that Dunn and Wood (*ibid.*), in writing of a male from Samburg, Tennessee (ANSP 4489) that had one basal "hook", did not question the restricted Floridian range of *priapus.* Mittleman (1947: 479) has indicated that specimens of *Coluber c. constrictor* from near the area of intergradation with *C. c. flaviventris* possess the large basal hooks upon which *priapus* has been described. He raised the question that if basal hooks occur among some specimens of middle-western *constrictor,* the entire question of the correlation of these structures with geographic dispersion should be re-examined.

All of the races of *constrictor,* with the exception of *constrictor constrictor,* appear to have basal spines which may be termed "hooks". In the black-colored racers there is at least one hook present in specimens from southern Illinois and Indiana, western Kentucky and Tennessee, extreme eastern Missouri, Arkansas, northeastern Louisiana as well as the Florida Parishes, all of Mississippi except the northeastern corner, and all of Alabama, Georgia and South Carolina below the Fall Line, throughout Florida, and in coastal North Carolina north to the Cape Hatteras region. This, with the exception of the ranges of *paludicolus* and *helvigularis,* is the distribution of *priapus.*

Practically all of the specimens that I have examined from the Coastal Plain have a basal hook. However, the ratios varied from one to five and a half. In view of such individual variation mean ratios were calculated for various regions of the eastern United States to obtain an estimate of broader geographic variation. These ratios are given in Table I. It is apparent that these data fall into two groups which correspond to the ranges of the two races, *priapus* and *constrictor.*

Along the Fall Line specimens are frequently taken in which the spines are two and three quarters, three or three and a quarter times the length of the smaller spines. I have called these specimens intergrades. In eastern Ohio, where color intermediates occur between *constrictor* and *flaviventris,* the hemipenial spines do not seem to be intermediate, but resemble those of *constrictor.*

The overall ratios of specimens for the southern portion of the range (using individual ratios for calculation) was $3.7 \pm 0.67$. The corresponding value for northern specimens was $2.2 \pm 0.57$. Hence the two groups of specimens bear a difference in the mean values

that is statistically significant ($t = 5.73$).

TABLE 1.
GEOGRAPHIC VARIATION IN MEAN RATIOS OF THE LENGTH OF THE PROXIMAL HEMIPENIAL SPINES

| Area | Mean Ratio | No. of Specimens |
|---|---|---|
| Florida | 3.9 | 305 |
| Southern Georgia (below Fall Line) | 3.8 | 31 |
| Coastal South Carolina | 3.3 | 12 |
| Coastal North Carolina (excluding N.E. part) | 3.3 | 7 |
| Southern Alabama | 4.0 | 26 |
| Southern Mississippi | 3.6 | 8 |
| Eastern Louisiana | 3.6 | 21 |
| Arkansas (excluding N.W. part) | 3.8 | 23 |
| Western Ky., Tenn. & southern Ill. & Ind. | 4.0 | 11 |
| New York | 2.1 | 26 |
| Pennsylvania | 2.2 | 12 |
| Virginia | 2.3 | 15 |
| Eastern Ohio | 1.7 | 18 |
| Northern Georgia | 2.1 | 20 |
| Western North Carolina | 2.2 | 11 |

Specimens from coastal North and South Carolina frequently have basal spines which are about three times the length of the adjacent proximal spine. There is no sharp break between the specimens with small proximal spines which are only significantly enlarged, and those with true basal hooks. The region of intergradation in the coastal areas of these two states is wide and exhibits a more gentle gradient than is found in the intergradation area along the Fall Line of Georgia and Alabama.

*Color.*—It is obvious that the distinguishing character of *priapus* is restricted in its value, not only in view of the fact that it is sex-limited, but also in that it is accurately reliable in only rather large, dead or preserved specimens. Coloration is one of the predominant diagnostic characters used to distinguish the various races of *Coluber constrictor.* It has been referred to time and again in relation to southeastern populations of this species. Ortenburger (1928: 213) was one of the first workers to mention the presence of a distinguishable coloration in specimens from the southeast: "In the southeast the throat and chin are almost always immaculate blue-white, while to the north of Georgia the chin and throat are white, but more or less spotted with dark gray."

Ditmars (1936: 94; 1939: 191) mentioned this peculiarity and gave some indication of a race confined to the southern portion of the United States: "With specimens from South Carolina, Georgia and Florida the white may cover the entire upper labials, thus indicating a fairly well defined southern race."

The exact range of variation in this coloration has never been examined.

A complication in the description of color in this species is that

an ontogenetic color and pattern change occurs when the snake is about one year old. The blotched pattern of the juvenile becomes the uniform coloration of the adult through continuous and successive stages of suffusion by a darker color. Color notes taken on specimens from one area are not comparable to notes taken on specimens from other areas, unless the specimens are of the same size or age. Unfortunately the size at darkening is not the same in every individual, as has been shown by Kelly (1936: 43). In some cases the size at color transition is somewhat correlated with geographic locality. Another difficulty is that in preservatives not only does the entire specimen become more or less darkened, but certain colors, such as those of the iris and tongue, fade rapidly.

*Adult dorsal color.*—This is one of the most important criteria used in distinguishing the races of *Coluber constrictor.* Based on their dorsal coloration these subspecies fall into three main groups. They include (1) the light, usually greenish, brownish or bluish group, which is composed of the races *C. c. mormon, stejnegerianus, flaviventris* and *paludicolus.* For the most part they inhabit rather open situations, under relatively little forest canopy. They are primarily found in grasslands, and one subspecies, in marshes. Another group (2) is formed of only one race, *anthicus.* It is spotted and occurs in the pine forests of eastern Texas and western Louisiana (fig. 16). The last group (3) is black and is composed of three subspecies, *constrictor, priapus* and *helvigularis.* These are primarily associated with the forested portions of eastern United States (fig. 16). It might be added that *flaviventris* inhabits a great variety of habitats and is also the most variable as regards coloration. Specimens are lightest in the Great Plains and darkest in the northeastern portions of its range where it has invaded the forests of the glaciated regions of North America. This post-glacial eastern extension of typical steppe fauna has been frequently discussed (Schmidt, 1938; Ruthven, 1908; and Grobman, 1941).

The light-colored subspecies show perfect intergradation with darker forms at their mutual borders, and for this reason adult color is included under "external clines".

The dorsal color of the races *priapus, helvigularis* and *constrictor* is nearly always slaty black. Ortenburger (1928: 212-213), stated that ". . . specimens from southern Florida, and to a certain degree those of New England are more intensely black than those from any other part of the entire range". Undoubtedly he was writing of specimens from the Florida Keys, for southern peninsular Florida is inhabited by a very light race, *paludicolus.* This is exemplified, not only by the lighter coloration of the dorsal surface, chin, supralabials and belly of adult specimens from this area, but by the lighter-colored juveniles as well. This is opposed to the darkly-colored juveniles and adults of northern parts of the state. The light color of this Everglades population has been mentioned by Conant (1930: 60), Carr (1940: 81) and Allen and Slatten (1945: 25). Specimens

from the Keys are black dorsally, but not appreciably darker than specimens from Alabama, Mississippi, southern Georgia, or even northern Florida.

The dorsal coloration of *paludicolus* is a bluish-gray, but in some specimens is greenish-brown to greenish-gray. I have been told that specimens from Cape Sable are tan. The only individual that I have examined from this area is greenish-gray. Intergrades between this race and *priapus* occur in Collier, Hendry, Palm Beach, Broward and Monroe Counties (fig. 3).

There is a southward extension of the range of *priapus* down both the east and west coasts of the peninsula. On the east its range seems correlated with an area known as the Atlantic Coast Strip which is mostly composed of deep sands and is higher than the Everglades. Forests of pine cover most of the area, while in the dunes along the sea the vegetation is decidedly scrubby. The race *priapus* also occurs in the Pine Flatlands of the lower west coast. This area is gently rolling, with many small ponds and sloughs. Open pine forests with grasses and thickets of saw palmetto predominate the landscape. The Florida Keys are for the most part covered with scrubby bushes and trees. On the other hand, the Everglades is a shallow, praire-like basin, that, before the digging of drainage canals, was about 80 percent marshland. Trees occur only along the edges of natural sloughs or in "islands" on slightly higher ground. The conditions of these two major habitats simulate those between the forests and prairies of our middle west. The resemblance of the two prairie situations, even though one is wet and the other is dry, and the similarity of the color of the forms inhabiting both suggests that approximately equivalent natural selective factors have acted on both of these populations.

A series of seven specimens in the AMNH (6981-7) and a head (USNM 44518) from, respectively, Canaveral Light and Canaveral, Brevard County, Florida, are colored exactly like specimens of *paludicolus* from the Everglades. The color in all is greenish-gray to greenish-brown. Three of them (AMNH 6983, 6985 and 6987) have the light brownish-colored posterior gulars frequently observed in *paludicolus.* Three adult intergrades between the Cape population and *priapus* have been examined. USNM 11989, from Georgiana, Brevard County, has a coloration which resembles that of the specimens from Cape Canaveral. WA 3719, from seven miles east of Titusville, Brevard County, is intermediate. In life it was black on the anterior portion of the dorsal surface, and brownish-black posteriorly. Ventrally it was light bluish-black, and, as frequently happens in intergrade specimens from the Big Cypress Swamp of Collier County, there was a light powder blue line mid-ventrally. The gulars and middle third of the supralabials were brownish. Six specimens from Eau Gallie, Brevard County are typical of the race *priapus,* except for one, AMNH 6919. This specimen is very dark above, but quite light ventrally. The gulars are tinted with light brown.

This is also considered an intermediate specimen (fig. 2).

There are two separate populations of *paludicolus* which do not seem to differ in any color characters. The scale counts of these two populations are also practically identical. An offshore bar extends southward from Cape Canaveral for a considerable distance. One intergrade specimen has been examined from this bar.

The dorsal color clines which are found in the area of intergradation between *priapus* and *paludicolus* are exactly the same as those between *flaviventris* and *constrictor* in Ohio, or between *flaviventris* and *priapus*.

Specimens from intermediate areas are black dorsally and light ventrally. The ventral color seems to change over a greater geographical distance than does the dorsal color. For example, in southern Florida the change in ventral color from slaty black to the light color of *paludicolus* takes place over approximately 55 miles, while the change in dorsal color takes place over 30 miles at most. As would be expected, the width of the intermediate zone is dependent on the distance over which grasslands, or essentially prairie conditions, change into a forested condition. As a result, the slope of the cline is directly proportional to the proportion of prairie and forest constituents over a given area. This is exemplified by the rather short distance in which the dorsal color and topography change along the edges of the Big Cypress Swamp and the Everglades, as compared to the more gradual change in the dorsal color and topography in central Ohio.

I have seen eight specimens from Upper and Lower Matecumbe Keys, Monroe County, Florida, some 20 miles south of the mainland, which are very unusual in that many of the dorsal scales have lighter centers, so that they appear speckled. USNM 85303, from Key West, Monroe County, Florida, also has dorsal scales which have slightly lighter centers, but in addition, certain scales are distinctly tinted, though faintly, with greenish, brown, or blue. The ground color of all of these specimens is slaty black. They are reminiscent of intergrades between *anthicus* and *priapus* which I have examined from Louisiana and Arkansas, except that the speckling is not as evident. Certain specimens of *paludicolus,* which I have seen have scales whose centers are slightly darker than their edges.

*Adult ventral color.*—A resume of the general coloration of the ventral surface as found in the various races would serve no real purpose, since the belly color is seemingly correlated with the dorsal coloration. That is, subspecies dark on the dorsal surface are also darkly colored ventrally. It is only in the zones of intergradation between light and dark-colored forms that one finds snakes that are very dark above and light below. The contrast between the two surfaces is considerable. Such specimens have been described in earlier parts of the paper.

Recently Schmidt (1953: 187) revived the name *Coluber c. foxi* (Baird and Girard) for those populations of *Coluber constrictor* in-

habiting the Eastern Steppe Province of Ohio, Indiana, Illinois and Michigan. Following an examination of many specimens from Ohio and Michigan it is obvious that the adult ventral color of this population and that of the Great Plains is quite different. Ortenburger made reference to this difference (1928: 191), "The typical yellow coloration is found in Kansas; the blue-gray, in the northern part of the range". However, he failed to recognize two subspecies on this basis alone. Specimens from the states of Iowa, Illinois, and Missouri seem to indicate that the change in ventral coloration is gradual and covers a great distance; that is, it seems to exhibit an internal, rather than an external cline. Such a wide band of intergradation is incongruent with the widths of zones of intergradation between other subspecies of *Coluber constrictor* in eastern United States.

The darker ventral surface of *foxi* is interpreted in the present paper as an indication of past or present genetic influence from dark bellied forms, such as *constrictor* or *priapus.* Specimens of *flaviventris* from southern Louisiana, near the range of *priapus,* are very similar to *foxi* in the coloration of their ventral surface. This certainly indicates an approach to *priapus* in this area. It has been previously shown that the ventral coloration changes over a greater area than does the dorsal coloration in areas of intergradation between light and dark-colored forms.

Until a critical study is made of the nature and degree of intergradation between the yellow and grayish-bellied forms, and the degree of homogeneity in the two proposed nominal populations, the best disposition seems to be to regard them as slightly differing populations of the same subspecies.

Occasional specimens are taken throughout the range of *constrictor* and *priapus* that are black above and very light gray or bluish-white below. These individuals appear like intergrades between *priapus* and *paludicolus* or *flaviventris* and *constrictor.* Eckel and Paulmier (1902: 371) seem to have had such a specimen in mind when they referred to specimens from New York which were "greenish-yellow" ventrally, though black dorsally. This coloration seems most common along the Atlantic Coast, yet still unusual in these areas. Only 4.3% of the specimens from South Carolina are so colored, 1.9% in eastern Georgia, 3.2% in northern Florida and 8.2% in central Florida.

*Adult chin color.*—The chin color of adult racers has been mentioned by a number of earlier workers as a possible diagnostic character of a southeastern race. One of the difficulties in describing the coloration of racers lies in the fact that there is an ontogenetic change in coloration. All juvenile racers have a white chin, usually without markings of any kind. In the races *flaviventris, mormon, stejnegerianus, anthicus,* and *paludicolus* there is no appreciable color change to adulthood, except possibly with an introduction of a yellowish tint. However, in the black-colored racers of the eastern parts of North America specimens have chins mottled with black, or brown, as in the case of *helvigularis.* This mottled appearance is brought

about by growth and fusion of black blotches on the chin where before there were none. In this manner some specimens attain practically solid black chins.

Not all specimens from one locality exhibit the same degree of darkening on the chin. In twenty individuals from Key West, Monroe County, Florida, practically every gradation between an immaculate white chin and one which is almost entirely black is represented. The specimen with the least white on the chin that I have examined from the Florida Keys is CMNH 33816, in which only the mental scale is white. The darkest racer that I have examined is WA 2506 from 5 miles north of Florence, South Carolina. There is no pure white on any part of this snake. The anterior portion of the chin exhibits a few smoky-gray vermiculations.

Although Ortenburger (1928: 213) and Ditmars (1936: 94; 1939: 191) indicated that specimens from the southeast have less white on the chin than specimens from more northern states, an evaluation of individuals over 1000 mm in total length has indicated that the number of specimens in the southeast with black-colored chins is quite large. However, specimens from central Florida have a con-

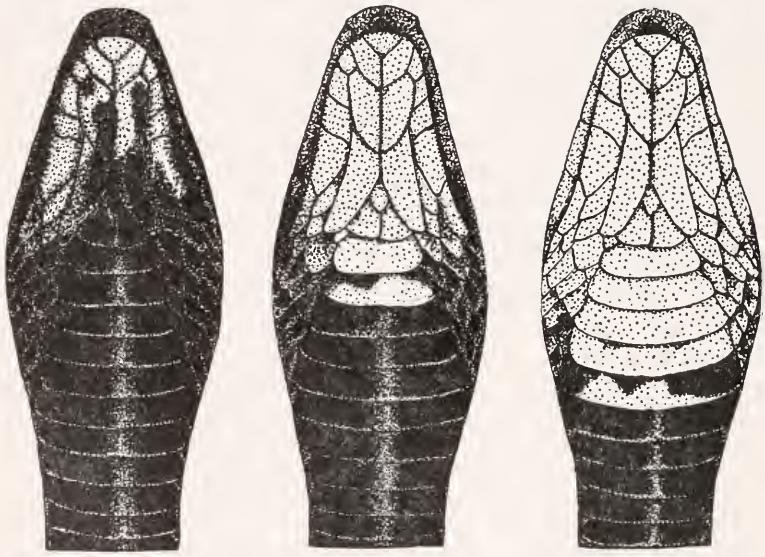


Figure 6. The amount of white on the chin of three typical specimens of *Coluber constrictor* from eastern United States. **A.** Typical adult from New York State. **B.** Typical adult from South Carolina. **C.** Typical adult from northern Florida. Any of these variations may be found in any area of eastern North America, and the amount of white on adult specimens is best measured by the mean number of white ventrals (*cf* fig. 7).

siderable amount of white on the chin and throat. This variation is best measured by tabulating the number of ventrals on which white occurs. When this is done for states along the Atlantic Coast the distribution is typical of that of an external cline. There are two areas in which the values, though distinct, are fairly constant, with a steepened gradient in the zone of intergradation between. Figure 6 shows three typical specimens from the Atlantic coastal states, while figure 7 shows the results of an analysis of the amount of white on the chin and throat of specimens over 36 inches long from various localities in eastern United States. Although a southeastern race cannot be described on this basis alone, there is an indication of a differentiated population occurring in the lowlands of the lower portion of the St. Johns River in Florida. However, these specimens are probably intergrades between *priapus* and *paludicolus,* even though considerable homogeneity seems indicated (*cf* page 92).

*Adult gular and supralabial color.*—The lateral gulars of large specimens of *C. c. constrictor* and *C. c. priapus,* except those from central and south-central Florida, are usually spotted with black. Occasional specimens have completely black gulars. In central Florida specimens usually have much white on the chin and throat, and in these the gulars are also white. In the region of the flood plains of the Chipola and Appalachicola Rivers of western Florida the entire chin and throat may be suffused with very light brown or tan. These specimens have been designated as a new subspecies, *C. c. helvigularis.* Brownish-tinted posterior gulars are also quite common in specimens of *C. c. paludicolus.* Intergrades between the latter and *priapus* frequently exhibit this coloration. Specimens from the west coast of Florida rarely have brownish-tinted gulars. This color never seems to be found in other specimens of *priapus.* Both *paludicolus* and *helvigularis* have light brown or tan on the supralabials. In both, though especially in the latter, the ventral surface is frequently clouded with light brown or tan.

Specimens with unusually-colored gulars or chins are occasionally found, such as a specimen from DeLand, Volusia County, Florida (WA 3610) in which these parts were light orange in life. In specimens of *flaviventris, mormon, stejnegerianus,* or *anthicus* the gular scales are yellow, white, or yellowish-white.

The supralabials of full grown specimens of *constrictor* are usually black with only traces of white on the lower parts of the first few plates. This is also true of large examples of *priapus* from its entire range, except individuals from central peninsular Florida. Specimens from this area usually have supralabials which are black above and white below. Half grown specimens of *constrictor* and *priapus* have these scales similarly colored. Individuals are frequently taken in south-central Florida from Lake Okeechobee south to the Big Cypress Swamp of Collier County that have supralabials which are black above, and immediately below this there is a narrow band of very light tan or light brown. The bottom third is white. In this regard

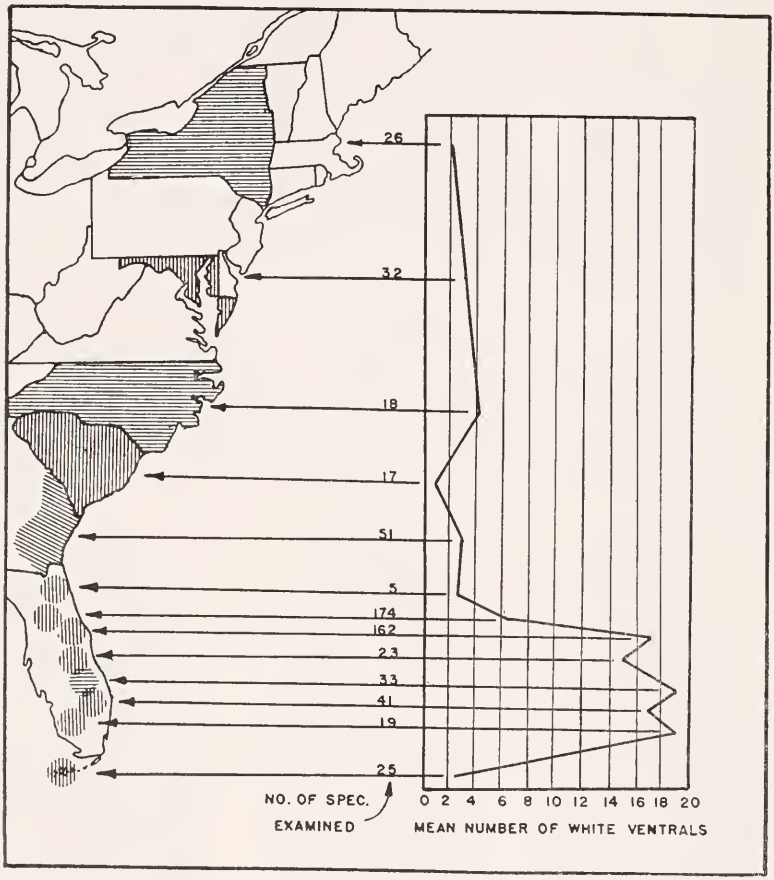


Figure 7. The mean number of white ventrals on the throats of specimens of *Coluber constrictor* from the Atlantic Coast area. The distribution of mean values in this figure is a fairly good example of an external cline in which the slope of the character-gradient is rather level over two large areas, but with a rapid increase in slope over a narrow portion of the range—the zones of character intergradation. These zones occur in northern Florida and on the Upper Keys. Although this figure would indicate the presence of another nominal population in central Florida, the character, and its distribution in this region, points to a narrow zone of frequent gene flow between two nominal populations inhabiting two rather similar ecological situations, and separated by an obviously inefficient barrier (see page 92).

these specimens show a genetic influence from populations of *paludicolus* from farther south. In this race the upper portion of each plate is dark gray or bluish-gray rather than black. Individuals with light tan or brown on the supralabials are frequently taken in the vicinity of Sarasota, Manatee County, in west-central Florida

(fig. 16). The posterior gulars of specimens from this area are tan. Individuals that possess a very small amount of light brown or tan on the supralabials are also taken in the Gulf Hammock region of western peninsular Florida. Full grown adults from northwestern Florida, except those from within, or near the range of *helvigularis,* nearly always have black supralabials. Large specimens from this area which have these plates half black and half white are much less common than in specimens from peninsular Florida.

Along the zones of intergradation with light-colored racers of middle North America the supralabials become dark blue or black above and white below, gradually fading into the lighter colors characteristic of the western subspecies. The supralabials of specimens of *anthicus* from the eastern parts of its range are black above and white below. In the western parts of its range the supralabials are dark gray or bluish above and whitish below. In the middle portions of the range of *anthicus* the supralabials are usually either all light tan, or tan above and whitish below. The color of the supralabials in *flaviventris* may range from dark bluish-gray to light brown above. Below they may vary from white to bright yellow. The latter coloration is especially prevalent in the Great Plains portion of its range, while the former is most frequently found in the northeastern parts of its range.

*Temporal coloration.*—There are certain other colors frequently found on the heads of racers which may vary geographically. One of the most obvious of these is the coloration of the temporal scales. In most subspecies of *Coluber constrictor* these scales are slightly darker than the supralabials, parietals, or lateral scales of the neck, all of which surround the temporals. However, many specimens from Michigan, Indiana, Ohio, Illinois, and especially southeastern Louisiana have very darkly-colored temporals which, in many cases, gives an impression of a vague, short, postocular stripe. This color is usually a dark grayish-blue. Whether or not populations possessing dark-colored temporals form steep gradients where they intergrade with populations having lighter-colored temporals is unknown. However, the fact that this characteristic seems to be found in rather definite areas may indicate that the zone of intergradation is narrow.

### *Internal Clines*

*Number of hemipenial spines.*—It has been previously shown that on mapping the proportionate lengths of the basal hemipenial spines in specimens of *Coluber constrictor* an external cline is indicated; *i. e.,* a definite and relatively narrow area of intergradation exists between populations having basal hemipenial hooks and those that do not. However, the *number* of hooks also seems to vary geographically, but as a steady cline or gradient, with no obvious areas of intergradation (steepening of the cline). Huxley (1943: 220) also called this a continuous cline.

The maximum number of hooks found in any specimen is three. This number occurs occasionally in all subspecies that normally possess

at least one hook. Most of the specimens of *C. c. mormon* that were examined by Dunn and Wood (1939: 1-4) had three hooks present. In an examination of twelve specimens from California eight possessed three hooks, three had two and only one had one hook. In 15 specimens of *C. c. stejnegerianus* from Nueces County, Texas, nine had three hooks, four had two and two had only a single hook. In three specimens of *C. c. anthicus* none had three hooks, one had two, and two had a single hook. Although *C. c. flaviventris* frequently has three hooks, this number seems much more common in the southern portions of its range than in the northern parts. In fact, a large number of specimens from Michigan do not have any basal hooks at all, but have basal spines which are from three to three and three-fourths times the length of the adjacent proximal spines in the same rows. Of 211 adult black racers from Florida (*C. c. priapus*) 72.0% have one hook, 14.6% have two hooks, 11.1% have three hooks and 2.3% have no hooks. The evidence, though admittedly scanty from extreme western United States, seems to indicate that a large geocline is present in the number of basal hemipenial hooks as found on *Coluber constrictor.* Three hooks are most frequently found in populations from the western states, one hook being normal in eastern populations. Of 32 adult male specimens from the states of Missouri and Arkansas, 34.3% have three hooks, 40.9% have two hooks, 21.7% have one hook and 3.1% have no hooks, indicating an intermediate condition between the two extremes, both numerically and geographically.

*Color of the young.*—The transformation of the color and pattern of the juvenile racers to that of the adult follows certain well defined trends. On the dorsal surface the suffusion of the body blotches takes place from the posterior to the anterior regions. Even on some newly hatched specimens it is quite difficult to count the total number of these markings due to a certain amount of darkening on the posterior portions of the body while the snake was still in the egg. In most newly hatched specimens the total number of these dorsal markings can be counted easily.

The mean number of dorsal blotches in young racers varies geographically, as has been shown by Ortenburger (1928: 180, 213, and 216). Populations of this species which inhabit the western portions of North America have a higher mean number of body blotches than do populations from more eastern localities. Furthermore, this geographic variation is a gradual cline, except possibly in central Ohio (Conant, 1938: 54). This character gradient is best described as a geocline, and more specifically—an internal cline.

The subspecies, *C. c. stejnegerianus,* is thought to be closest to the ancestral stock, and this form possesses the highest number of dorsal blotches. However, the total number is seldom countable due to the fact that they are rather indistinct posteriorly. They range from 42-53 on the anterior third of the body and are not saddle-shaped as in the eastern forms, but crossbands (Auffenberg, 1949: 55). *C. c.*

*flaviventris* has 43-80 blotches. Specimens of this race from southeastern Louisiana have fewer dorsal saddles than do those from more northern parts of the range. In 23 newly hatched specimens from Jefferson Parish, Louisiana (WA 3673-96), the number varies from 43-63 (mean, 55). This is considerably lower than in a series of 18 specimens of *flaviventris* from Oakland County, Michigan (WA 3026-44), in which they range from 68-76 (mean, 71.3). In Florida, from which a large number of young are available, a definite trend is indicated, whereby specimens from southern Florida seem to have fewer blotches than do those from northern Florida. Of 56 newly hatched specimens from northern Florida the total number of blotches varies from 43-73, mean 52. In 32 specimens from central Florida the number of blotches ranges from 45-76, mean 49.7. In 10 specimens from extreme southern Florida in which the total number of dorsal blotches could be counted, they vary from 40-57, mean 45.8.

Conant (1942: 195) has also shown that geographic variation exists in the coloration of newly hatched racers. He mentioned that specimens of *priapus* from five miles south of Brighton, Glades County, Florida, had body blotches which were "rich chestnut brown", while in a series from Philadelphia, Pennsylvania these markings were "dark brown". The specimens from Florida were also more reddish in other parts of the body and these colors were suggested as additional means of distinguishing juvenile specimens of *priapus* and *constrictor.*

An examination of the material has shown that not all specimens of *priapus,* or even all specimens of *priapus* from Florida, have such brilliant colors. Ditmars (1939: 192) mentioned dark brown blotches on a specimen from Marion County, Florida. Although he recognized a difference concerning the color of the chin and supralabials of adult specimens from the southeast as compared with those of the northeast, still, in describing the typical young of black racers he used a specimen from Florida. In a series of 18 specimens from Columbia County, Florida, the dorsal blotches are a very dark reddish-brown and, when placed next to a series of hatchlings from Scioto County, Ohio, no appreciable difference can be discerned. However, in eleven specimens from Alachua County, which is directly south of Columbia County, the blotches are decidedly more reddish. Another juvenile described by Ditmars (*ibid,* p. 192) from Connecticut has dorsal blotches which are "grayish-brown", being lighter than the markings of the Columbia County, Florida specimens. A hatchling from Pensacola, Escambia County, Florida, has pinkish-gray blotches, while one from Tampa, Hillsborough County, Florida, has dorsal blotches which are very dark brown.

On the whole, most juvenile specimens from northern Florida northward, including the remainder of the range of *priapus* and all of that of *constrictor,* have markings which are usually some shade of dark brown, frequently dark reddish-brown. Conant's specimens from Glades County, which is quite far southward in the state, shows

a portion of the cline exhibited by this coloration in peninsular Florida. In the Everglades of southern Florida practically all of the juveniles have light chestnut, or even reddish or pinkish blotches. Such light colors are never found in specimens from northern Florida, but are frequently found in individuals from south-central Florida. These colors are not diagnostic of the race as a whole, but the character exists as a geocline throughout peninsular Florida.

Specimens of *flaviventris* from southeastern Louisiana, which seem to have fewer dorsal blotches than do specimens of the same race from farther north, also have dorsal blotches which are decidedly more reddish than do specimens from farther north.

Conant (*op. cit.*) also mentioned the general reddish cast to the entire body as of possible significance in the identification of juvenile specimens of *priapus*. This characteristic, as with the lighter dorsal markings, is most prevalent in the Everglades race, *paludicolus*. Throughout the major portion of the range of *priapus* (excluding south-central Florida) most juveniles have a gray, or grayish-brown ground color as do specimens of *constrictor*. Of special significance is the fact that specimens of *flaviventris* from southeastern Louisiana show the reddish suffusion of the general body colors which is characteristic of juvenile *paludicolus*. Specimens of *flaviventris* from more northern parts of the range do not show this coloration, but are similar to *constrictor*.

The ventral color of juveniles from south-central Florida is also different from that of specimens in the Philadelphia area (Conant, *ibid*). This difference involves both the ground color and the small ventral spots. Conant's specimens from Glades County, Florida had "spots on the belly orange brown; ground color of belly (posteriorly) bright pinkish orange". Specimens from the Philadelphia area had ventral spots which were "very dark brown or black", and the ground color of the belly was "bluish-gray". Ditmars (1939: 192), regarding a juvenile from Marion County, Florida, wrote of "brick-red" ventral spots. In 18 juveniles from Columbia County, Florida, the posterior ground color of the belly is not pinkish and the ventral spots are dark reddish-brown. In USNM 17655 from Tampa, Hillsborough County, Florida, the ventral spots are reddish-brown. In USNM 4736 from Micanopy, Alachua County, Florida, these spots are brown, while in eleven others from Alachua County (WA 3647-56, and 3680) the ventral markings are light reddish-brown. In WA 3657 from 4 miles north of Kissimmee, Osceola County, Florida, the ventral spots are dark pinkish-orange. These few examples indicate that the color of the ventral spots is probably clinal in the state of Florida. Juvenile specimens from northern areas of the peninsula usually have reddish-brown ventral spots with no reddish suffusion posteriorly, while those from southern Florida have reddish ventral spots with a similar color suffusion posteriorly. Thus, for the same reason that the color of the dorsal blotches cannot be used as a diagnostic character of the race *priapus*, neither can the color-

ation of the ventral spots be so used; namely, the character is an internal cline in Florida (fig. 16). The ventral spots of both *flaviventris* from southeastern Louisiana and *paludicolus* are decidedly reddish or orange. The general ground color of the belly is slightly pinkish in specimens from both localities. The ventral color of juvenile *flaviventris* from the northern parts of its range resembles that of juvenile *constrictor.*

Throughout the entire range of *constrictor,* and most of that of *priapus* (except south-central Florida), the ventral markings are rather large. They are about one-fourth to one-sixth as wide as the width of the ventral plates themselves. In *priapus* from south-central Florida, as well as in *paludicolus,* these markings are much smaller. They are practically never larger than one-eighth the width of the ventral plates and are frequently absent entirely. This reduction in the size of the ventral spots in specimens from southern Florida is again paralleled in *flaviventris* from southeastern Louisiana. The small number of live specimens which I have examined from this area have fewer and smaller ventral markings than do specimens from Michigan and adjacent states.

*Scutellation.*—Certain scales of the head and body of racers have been shown to vary geographically (Ortenburger, 1928: 174 ff). This is especially true of the number of ventral and subcaudal scales, both of which form continuous clines.

*Ventral scales.*—It was first pointed out by Ortenburger (*ibid.*) that the mean number of ventral scales in *Coluber constrictor* varies geographically as a continuous gradient. The highest means are found in Florida and the extreme northeastern portions of the United States, while the lowest mean count is found in southern Texas. This last area is inhabited by the subspecies *stejnegerianus.* During the early part of the century only a few specimens of this race were available and it was thought to represent nothing more than a variant of *C. c. flaviventris.* During the past few years many specimens have become available and studies of this form by Mulaik and Mulaik (1942: 13-15) indicated that the form deserves subspecific designation. Later studies (Auffenberg, 1948: 53 ff), based on a much larger number of specimens than were available to Ortenburger, showed that the mean number of ventral scales of this race is lower than that of any other subspecies in North America.

It is significant that of the specimens from Florida, those from the southern parts of the peninsular have a higher mean number of ventral scales than do those from the more northern portions of the peninsula. This portion of the state is believed to have been populated from more northern localities. This, in part, constitutes the basis of Ortenburger's hypothesis which states that low ventral scale counts in *Coluber constrictor* are ancestral to higher ones. On the whole the present study has corroborated this hypothesis, though certain complications have become evident with additional material.

In Trapido's study of the genus *Storeria* (1944), as well as in

Ortenburger's monograph of the whipsnakes and racers, the cline in the number of ventral scales is more rapid and exaggerated in Florida than in any other portion of the ranges of the genera involved in these studies. This is also true of the subcaudal scale counts.

According to Ortenburger the mean number of ventral plates in specimens from the northern parts of Florida is 177.4. For the southern portions, this average is stated as 181.6. Figure 8 shows


Figure 8. Mean number of ventral scales for various localities in Florida, based on data from localities from which at least five specimens were available. The data presented on the map represent scale counts of 872 specimens.

the results of mapping the mean number of ventral scales in 872 specimens from the state of Florida. Means are shown for various localities, but only if at least five specimens are available from that area. A number of other specimens (136) were examined, but not included due to the unreliability of the counts of only a few specimens scattered over rather large areas. Also drawn on the map are the physiographic provinces of the state as outlined by Cooke (1939:

14). Because the specimens from the extreme southern parts of the peninsula are so noticeably different from those on the Keys, the mean number of ventral scales was tabulated separately for these two areas. By separating these counts the mean number of ventral plates for the populations of the Lower Keys is 176.7±.49, while in a large sample of specimens from Alachua County, in northern Florida, the mean is 178.3±0.38. On the other hand, specimens from Dade County, at the southern extremity of the peninsula, have a mean of 184.0±.36. It is obvious that the number of ventral plates of the specimens from the Keys is much closer to those from Alachua County in northern Florida than to the geographically closer locality of Dade County.

The difference between the means for northern and southern Florida, as found by Ortenburger, is 4.2 scales. By separating the Keys populations from those of the southern mainland I find a difference between the populations of northern and southern peninsular Florida of 6.7 scales ($P = > .001$). Specimens from Cape Canaveral, Brevard County, which are identical in color with the Everglades race, *paludicolus,* also have a higher number of ventrals than do populations of typical *priapus* from the mainland (fig. 8). From the Cape the mean is 184.6±0.39, while for the adjacent mainland population of *priapus* it is 182.0±0.52. However, the difference between the means of the two populations is not significant. It should be pointed out, however, that the samples from both of these areas are rather small.

Series of specimens from a number of localities over the state of Florida suggest that the cline in the number of mean ventral scales is not simply north-south in the peninsula. In figure 8 there is shown a Central Highlands District. This area may be termed the backbone of the state, and is composed of significantly older formations than are the surrounding Coastal Areas (Cooke, 1939, 1945; MacNeill, 1951, *et al*). Large portions of it are the site of the Floridian Archipelago, formed during former high sea levels and which may be important in the distribution of the fauna of the extreme southeastern states. Within each one of these districts there seems to be a slight suggestion of a north-south trend in the number of ventral scales. Specimens from the northern portions of each district have lower counts (though not statistically significant) than do those from the southern parts of the district. The mean for the entire northeastern part of the Coastal Lowlands is 180.1±0.42, while for Dade County, in extreme southern peninsular Florida, it is 184.0±0.36. In the Central Highlands the mean in the entire northern portion is 178.2± 0.32, while in the extreme southern tip of this district it is 179.6± 0.65. Specimens from the western panhandle of the state have the lowest mean number of ventral scales of any area in Florida. This region includes the northwestern Coastal Lowlands, the Western Highlands, Mariana Lowlands and the Tallahassee Hills. The mean for this entire region is 174.1±0.72.

Reference has been made to specimens from Sarasota County, on the west coast of Florida which approach intergrade coloration (*paludicolus* X *priapus*). It seems significant that this region also has a higher mean number of ventral scales than the surrounding counties, and that this count approaches that of the race *paludicolus*. In the region of Lake and Sumpter Counties in central Florida, the number of ventrals (181.3) is higher than in populations to the north or south of them. This general region also seems to be the one in which it is believed a seaway extended from the east to the west coasts of Florida during a large portion of the early Pleistocene. Whether or not there is any direct correlation is unknown at present. Specimens from the geologically recent portions of Florida, comprising the Pamlico Terrace of the extreme eastern coastal strip and much of southern peninsular Florida, have the highest mean number of ventrals of any area in the state. The mean number of ventral scales for all of the western "panhandle" is $174.1 \pm 0.72$; for the Central Highlands, $178.1 \pm 0.35$; and for the peninsular Coastal Lowlands, $181.8 \pm 0.38$. There is a difference of 4.0 scales ($P = >.001$) between the means for the western districts and the Central Highlands; and 3.7 scales difference ($P = >.001$) between the means for the Central Highlands and the peninsular Coastal Lowlands. In the specimens from Sumpter and Lake Counties in the middle portion of the Central Highlands, the mean is 181.3, while to the north the mean for Marion and Alachua Counties is 177.5. The difference between the two areas is 3.5 scales, but is not statistically significant. The mean for Orange, Polk and northwestern Osceola Counties (south of Lake and Sumpter Counties) is 176.8, the difference between them being 4.2 scales. Again, the difference is not significant, but only suggestive. The difference between the means of specimens from the Everglades and the Keys is quite great, being 7.3 ($P = >.001$). This difference, though actually gradual, takes place over approximately 150 miles. Although the difference between the mean number of ventral scales within the State of Florida is quite small, it seems significant that the differences among the mean number of ventrals of a sample of *stejnegerianus* from extreme southern Texas, and another sample of *flaviventris* from Nebraska is 10 scales ($P = >.001$). This involves a distance of approximately 1,500 miles.

An isophene is drawn for the various mean numbers of ventral scales in Florida in figure 9. This is based entirely on figure 8. Figure 10 shows the results of drawing an isophene of the mean number of ventral scales throughout the United States. Due to the proportionately lesser number of specimens used in this evaluation as compared with that of Florida, this representation is more generalized than that for Florida. However, it is evident that there are two areas with very high mean ventral scales: (1) the New York, Pennsylvania, Maryland and eastern Ohio region; and (2) the eastern and southern coastal regions of peninsular Florida. The area with the lowest mean count is in southern Texas. The pattern is one of more


Figure 9. An isophene based on the mean number of ventral scales of specimens from Florida, based on data obtained from figure 8.

or less concentric circles away from this area having a low mean number of ventral scales. It will also be noted that the counts are lower along the northern parts of the entire range of the species. This is especially evident in the New England States, where the counts drop from a mean of 180.1 in New York state to practically 170 in Maine. This has been thought to be due to the effects of minimum vital conditions found in this northern region (Ortenburger, 1928: 231), and not an integral part of the inherent tendencies along the paths of dispersal.

*Subcaudal scales.*—The geographic variation of the subcaudal scales is very similar to those of the ventral scales. Analysis of the available data by Ortenburger (*op. cit.*) indicated that a geocline exists in the mean number of subcaudals. The present study has substantiated these data, at least for the eastern United States.

Figure 11 is an isophene drawn from the available material of eastern United States. Unfortunately, a large number of specimens have broken tails, so that even large series from one locality have

many specimens that cannot be utilized for an analysis of this character. As a result, the isophene based on subcaudals is necessarily more generalized than that for the ventral plates.

Similarities between the two isophenes (figs. 10, 11) are apparent. This is especially true in Florida. The western portion of the state has the lowest mean number of subcaudals of any area in the state ($97.5 \pm 1.02$). The southern portion of the peninsula has a higher mean number of caudals ($107.9 \pm 0.82$) than does the northern part of the peninsula ($103.2 \pm 0.93$). On the Keys the mean number is $102.5 \pm 1.31$, being more similar to the mean of the population from northern peninsular Florida. It is also significant that the isophene representing a mean number of 105 caudals is very similar to that representing a mean of 180 ventrals in figure 9. In New York State, where specimens also have a high number of ventral plates, the number of subcaudals is also relatively high, but not significantly higher than those from many other portions of the eastern United States.

*Reduction of scale rows.*—Ortenburger (1928: 205) discussed the mean point of reduction of the dorsal scale rows, especially in terms of geographic variation. He showed that the point of scale row reduction is "farther posteriorly in specimens from the Northeast and from the Southeast than from the southwestern part of the range". This is to be expected if the point of decrease is correlated with the total number of ventral scales in this species. The mean number of ventral scales at which this reduction occurs in specimens from Alachua, Marion and Columbia Counties, Florida, is $108.4 \pm 1.32$; for specimens from Volusia and Seminole Counties, Florida; it is $109.0 \pm 1.02$; for the Keys, $107.5 \pm 1.72$; and from Collier and

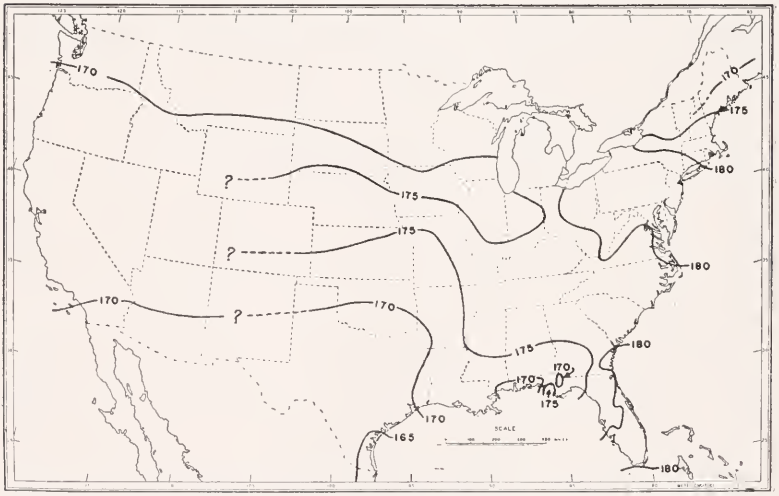


Figure 10. An isophene based on the mean number of ventral scales of specimens of *Coluber constrictor* from the United States.

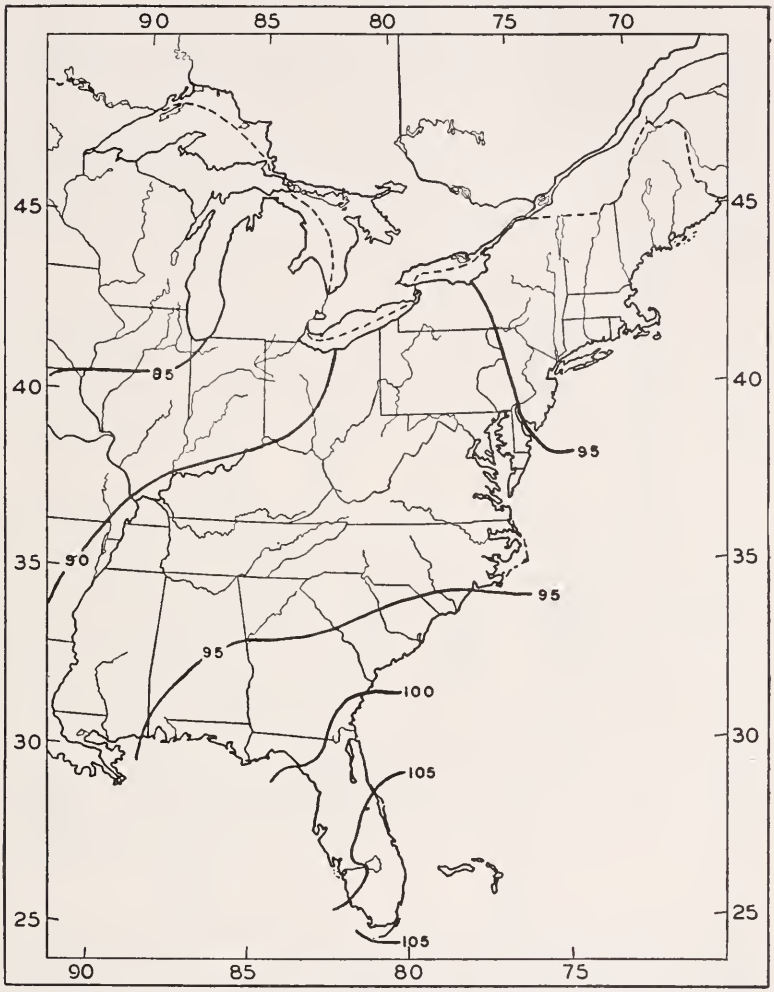


Figure 11. An isophene based on the mean number of subcaudal scales in specimens of *Coluber constrictor* from eastern United States.

Dade Counties in extreme southern Florida it is 115.7±1.01. As in the distribution of the number of ventral and subcaudal scales, the populations from the Keys are more similar to those from northern peninsular Florida than to those from the geographically closer locality of extreme southern mainland Florida. Populations from localities between the northern part of the peninsula and the Everglades of southern Florida have the scale reduction occurring between the 108th and 115th ventral plates and exhibit a geocline in that the scale reduction is found farther back on the body as populations are

encountered which have progressively higher ventral scales. When the mean number of ventral scales of any population is divided by the mean ventral scale at which the scale reduction occurs, the resultant ratio varies from 1.6 to 1.8.

*Osteology.*—During the latter part of this study some skulls of *Coluber constrictor* were examined. Certain variations became evident, but because of the small number of prepared crania most of these cannot be discussed at present with any degree of certainty. However, one character-gradient dealing with the bones of the skull is rather obvious. This is the shape of the premaxillary.

*Premaxillary shape.*—Bogert (1947: 11) has mentioned the use of this bone as a possible indicator of phylogenetic relationships among various genera and species of snakes. In *Coluber constrictor* the premaxillary is roughly "skate-shaped", having two "wings" extended out in a horizontal plane, perpendicular to the axis. At the posterior inner edge of these flat, lateral "wings", are two posterior projections of the processes.

An examination of 32 specimens for this character has disclosed that a geocline seems to exist from *mormon* and *stejnegerianus* through *flaviventris* to *priapus.* This cline is concerned with the shape and plane of the axis of the two posterior processes mentioned above. In *flaviventris, mormon* and *stejnegerianus* these processes are rather short, being shortest in the last two subspecies. In all of these races they lie in a nearly horizontal plane, but decidedly less so in *flaviventris.* In *constrictor* they are in a horizontal plane, but longer than in *flaviventris.* They are longest of all in southeastern specimens of *priapus* and *paludicolus,* and are, furthermore, twisted in these two races so that the outer edges of the two posterior processes have been rolled upwards, causing them to lie in a vertical, rather than a more or less horizontal plane. The shape and nature of the axis of these processes varies both geographically and individually.

The shape of the lateral "wings" of the premaxillary may also vary individually and geographically. In the western races the tips of these processes usually form less acute angles than do the tips on specimens from the east, and especially the southeast. In some of these specimens this tip may be formed into a sharp, slightly recurved hook.

In the description of a fossil Pleistocene snake, *Coluber acuminatus,* Cope (1899: 197) described the shape of the premaxillary as "subconic", and "narrower and more protuberant than in *Z. constrictor* . . . with which I have compared it". The degree of protuberance of the anterior tip of this bone is variable, individually, geographically and ontogenetically. Adult specimens from the southeastern states have a much more protuberant profile than specimens from the western states. Juvenile specimens from the southeastern states have a less protuberant profile than do the adults from these areas and are

similar to adult specimens of more western races.[4]

*Dentition.*—That the number of teeth in this species varies geographically has already been shown by Ortenburger (*op. cit.*). Moreover, the number of teeth increases from the western races to those of the eastern parts of North America. Figure 12 shows the range of variation in the number of dentary, palatine, pterygoid and maxillary teeth in the races of *Coluber constrictor.*

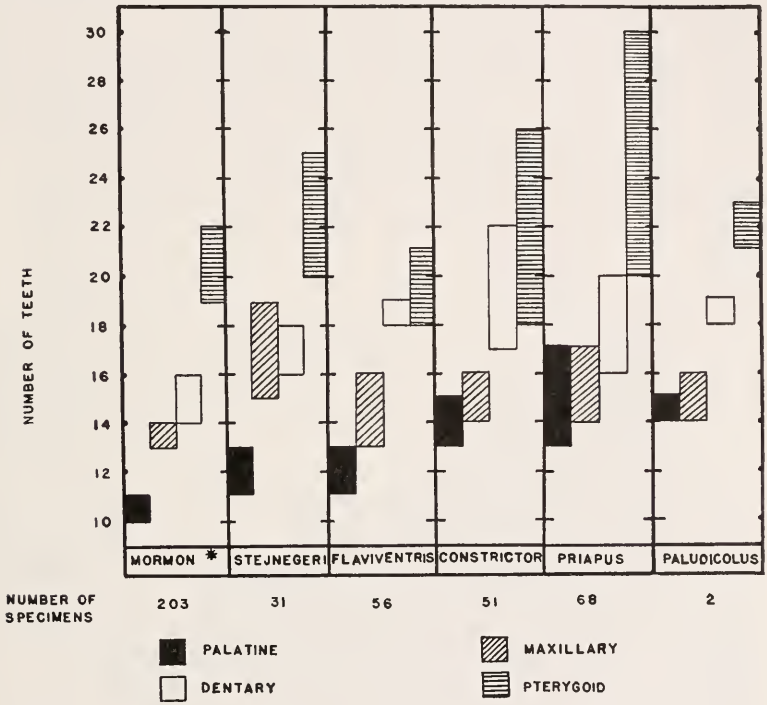


Figure 12. Range of variation in the number of teeth in some of the subspecies of *Coluber constrictor.* The relationship of the number of palatine and dentary teeth is especially interesting. In *priapus* the numbers overlap slightly, while in the other races the numbers of these teeth are discrete. There is an apparent increase in the number of palatine teeth from the western to the eastern races. There is also a general increase in the numbers of other teeth. The decrease in number of dentary teeth from *constrictor* to *priapus* and *paludicolus* is interesting in view of a general increase from *mormon* to *constrictor* (* data from Ortenburger, 1928: 174).

[4] A paper by the author (in print) compares the variation in the skeletal elements of *Coluber constrictor* with *Coluber acuminatus,* and shows that *acuminatus* should be referred to the synonymy of *Coluber constrictor.*

*Ontoclines*[5]

*Color of the iris.*—The color of the iris in specimens of *Coluber constrictor* is important. Conant (1942: 195) has suggested that the red eyes observed in both adult and juvenile racers from Florida may be characteristic of the race *priapus,* and may be of value in distinguishing both sexes of this subspecies from *constrictor.* The latter usually have brown-colored eyes. The range of variation, either individual or geographic, was practically unknown, although Perkins (1949: 10) suggested that the degree of consistency in this character needed more confirmation, especially in adults.

In all living examples of *constrictor, flaviventris* and *priapus,* in the more northern and western portions of its range, the iris is usually brown. Sometimes it may be dark amber, tan or reddish-brown, but never distinctly reddish or orange. Specimens with a red, or orange iris occur in Florida. However, analysis of this character is complicated by the simultaneous existence of a geocline and an ontogenetic change in the color of the iris in specimens from peninsular Florida.

Of the living adults that I have examined from the extreme northern portions of Florida, none possesses red eyes. However, of eleven newly hatched specimens from Columbia County, which is situated in the northern part of the peninsula, four possessed red eyes, while those of the remainder were brown. Both parents of these hatchlings (WA 3345-6) had brown-colored eyes. The female parent of nine red-eyed hatchlings from Alachua County, which borders Columbia County on the south, was also brown-eyed. Seven other newly hatched specimens from Columbia County and six others from Alachua County had brown eyes. In eight young from Kissimmee, Osceola County, in central Florida, seven had red eyes and those of the remaining snake were brown. Moreover, there were many adults from Osceola County that had red eyes, while in Alachua County there were only a few. Of 38 living specimens of *paludicolus* from southern Florida, practically all of the juveniles *and* adults had red eyes. Those that were not red were yellow, or rarely reddish-brown. In the case of specimens from northern Florida, the number of young with bright red eyes (25.3%), and the fact that only a very few red-eyed adults were taken (5.2%) seem to indicate that this character is, at least in part, ontogenetic. That is, most red-eyed juveniles simply change to brown-eyed adults. This is somewhat substantiated by the brown-eyed parents of red-eyed juveniles. In living specimens from the Kissimmee area, not only are red eyes more frequent in newly hatched specimens than in those from northern Florida (69.8%), but many retain this color into maturity (58.2%). In extreme southern Florida, practically all of the juveniles possess red eyes (78.4%). None seem to change this color, for a large number

[5] An ontocline may be either a geo- or ecocline, and at the same time an external or internal cline. It is a condition in which an ontogenetic change varies geographically as a character-gradient.

of the adults examined were also red-eyed (75.3%). The relationship of the color of the eyes in juveniles and the geographic locality of various populations is shown in figure 13.

That the eyes of juvenile snakes from northern peninsular Florida change color is strongly substantiated by living specimens of all ages in which all gradations from red to brown have been observed. In specimens with red eyes the first indication of change is in the lower half of the iris, next to the pupil (fig. 14). Here there is formed a reddish-brown crescent that gradually gets larger. In specimens of about 30-40 inches there is frequently noted a red crescent on the upper portion of the iris, while the remainder is brown. This crescent in the iris of adult specimens is probably an indication of its previously red-colored iris as a juvenile.

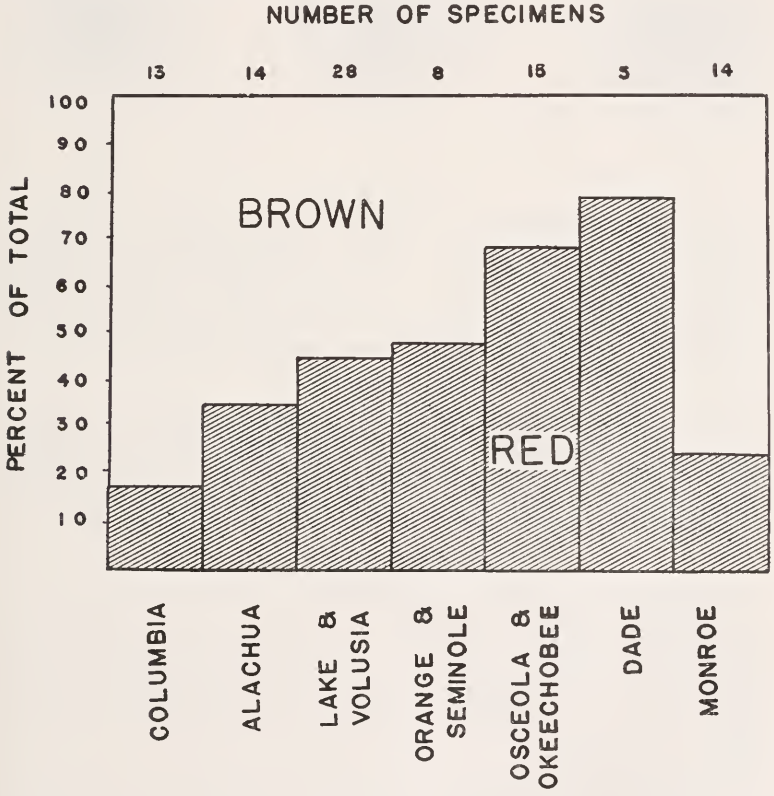


Figure 13. Geographic variation in the coloration of the iris in juvenile specimens of *Coluber constrictor* from Florida. Note the gradual increase in the number of red-eyed specimens from Columbia County to Dade County, Florida, and the similarity between the specimens from the Outer, or Lower Keys and northern peninsular Florida.

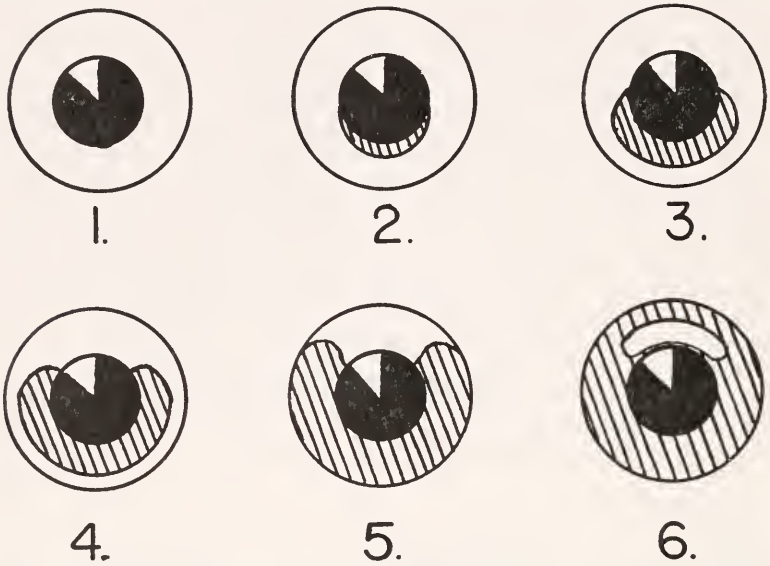


Figure 14. Ontogenetic changes in the coloration of the iris of specimens of *Coluber constrictor.* Shaded areas represent regions of the iris which are dark brown in life. Clear areas represent regions which are bright red or yellow in life. The eyes, numbered 1-6, show the change of red-eyed hatchlings through successive stages in which the brown color increases, to the practically all brown eye of the adult. Faint traces of red are usually found above the pupil in even very large adults (6).

Another interesting parallel between the race *paludicolus* and specimens of *flaviventris* from southeastern Louisiana is that the iris of juveniles from both areas is usually reddish. All the live juvenile specimens of *flaviventris* which I have seen from Michigan and Ohio have brown eyes (fig. 16).

### *Dimorphism*

*Geographically variable dimorphism.*—A character not mentioned by any earlier workers, and of frequent occurrence in the southeastern part of North America, is the contact of the first supralabial and the loreal. This is made possible by an elongation of the upper posterior corner of the first supralabial making contact with the lower, anterior corner of the loreal. It may be present on one side, but not on the other.

The presence of a contact between these two scales is found mainly in specimens from the southern states, and then only in a fair degree of regularity. However, it seems to be generally absent in specimens from the northern portions of the ranges of *C. c. flaviventris* (except in Michigan, and Ohio, where it occurs in 12.2 percent) and *C. c. constrictor.* It is absent in the few specimens of *flaviventris* that I

have examined from the central parts of its range, as well as in all specimens of the race *mormon*. It occurs in at least 10% of all specimens of *priapus* except those from extreme eastern North Carolina (fig. 16). I have found this contact in 6.6% of the specimens of *constrictor* from north of the Fall Line in Georgia, and in 7.1% of the specimens from Tennessee. It does not seem to occur in any other portions of the range of this form.

In the southern portions of the states of Mississippi, Alabama, Georgia and South Carolina, this contact occurs in at least 15% of the specimens, while in northern peninsular Florida it occurs in 10-35% of the specimens. In the central part of the peninsula it occurs in 25-45%, while in the southern counties it is found in 40-50% of the individuals.

Although a cline is indicated by the frequency with which this contact is found, this cline is not steady and gradual. Various inconsistencies occur throughout the peninsula, such as, for example, the counts obtained from specimens from northern Florida. Of one hundred and seventy-eight specimens from Alachua County 45.9% have a contact between these two scales. However, in specimens from adjacent counties it occurs in only 20-30% of all of the individuals examined. In Volusia County, from which 134 specimens are available, it occurs in only 10%, while in the surrounding counties it occurs in closer to 30% of the individuals examined (102). In Pinellas County it is found in 50% of the specimens, while in adjacent counties it occurs in 26.9-34.3%.

The means for the degree of frequency in which such contact occurs for northern, central and southern Florida are, respectively, 28.2%, 33.8% and 44.2%. Thus, there is a tendency for more specimens to have a loreal-first supralabial contact in southern Florida than in the northern parts of the state. Furthermore, such contact seems confined to the southern half of the United States, and is more frequent below the Fall Line (fig. 16). It also seems significant that the population from the Florida Keys have this contact in a degree of frequency (27.3%) which is more similar to that of northern Florida (28.2%) than to that of southern Florida (44.2%).

*Sexual dimorphism.*—Aside from rather obvious sexual dimorphism such as that concerning the reproductive organs, certain other characters are evidently related to the sex of the individuals. However, most of these differences are not obvious, and are based on mean values of significantly large samples.

*Scutellation.*—The only scale character which I have found exhibiting statistically significant sexual divergence is the number of caudals, but only on the basis of local populations. A comparison of the mean number of caudals for males and females of large samples from restricted localities indicates that differences in the means are significant ($P = > 0.001$). On the other hand, when the means for all of the males and females are analyzed, the observed differences are not significant ($P = < 0.03$).

Other scale characters, such as the point of reduction of dorsal scale rows and the total number of ventrals, have been mentioned by Ortenburger (1928: 185) as showing sexual dimorphism, expressed by mean values. However, on statistical analysis such differences as might exist in these characters could be due to effects of random sampling ($P = <0.03$).

A valuable statistic, the coefficient of divergence, has been given for a few species of snakes. A comparison of the coefficients of divergence that have been determined for the ventrals and caudals of two species by Klauber (1940: 208), two races by Grobman (1941: 21) and one by Dowling (1950: 21), as well as those of the eastern races of *Coluber constrictor,* are shown in Table 2. As in other species for which such coefficients are available, *Coluber constrictor* exhibits more divergence in the mean number of caudals than in the number of ventrals. In fact, sexual differences in the mean number of ventrals do not approach statistically significant levels, even for large samples from restricted localities ($P = 0.8$-$0.3$).

TABLE 2.
COEFFICIENTS OF SEXUAL DIVERGENCE

| Form | Number of Specimens | Ventrals | Caudals |
|---|---|---|---|
| *Lampropeltis g. californiae* | 271 | .009 | .073 |
| *Opheodrys v. vernalis* | 391 | .006 | .147 |
| *Opheodrys v. blanchardi* | 56 | .072 | .163 |
| *Phyllorhynchus d. perkinsi* | 225 | .073 | .256 |
| *Seminatrix p. pygaea* | 203 | ? | .228 |
| *Coluber c. constrictor* | 278 | .008 | .068 |
| *Coluber c. priapus* | 1008 | .010 | .049 |
| *Coluber c. flaviventris* | 102 | .012 | .071 |
| *Coluber c. paludicolus* | 58 | .017 | .008 |

Although the coefficients of divergence of the mean number of ventral scales of the eastern races of *Coluber constrictor* seem to form a group, the same is not true of the caudal scales. The coefficient of sexual divergence in the mean number of caudals in *Coluber c. paludicolus* is quite different from those of the other subspecies, and the low value of this statistic may be of some diagnostic importance.

*Size and proportion.*—Very few specimens were measured during the course of this study, partly because of the difficulty encountered in obtaining accurate measurements of preserved specimens. However, measurements of 103 living specimens seem to indicate that females attain a larger size than do males of the same subspecies. The mean length of 51 male specimens of *Coluber c. priapus* is 943 mm, while the mean for 26 females of the same race is 955 mm. The largest specimen of this race that I have examined is a male, 1473 mm in total length. Of 13 male specimens of *paludicolus,* the mean is 951 mm, while for eight females it is 1043 mm. The largest specimen is a female, 1689 mm in total length. The mean length of 13 male specimens of *constrictor* is 949 mm, while for 12 females

it is 999 mm. The largest example of this race which I have measured is a female, 1588 mm in total length.

Ortenburger (1928: 186) has shown that there is considerable sexual dimorphism in proportionate tail length; "the male has a much longer tail than the female; the averages are 0.254 and 0.233 respectively". He has also shown that there is a positive correlation between the number of caudals and the proportionate tail length within each sex.

*Environmentally Produced Characters*

For the most part practically all of the characters used in the description of variations of snakes, either individual or geographic, are assumed to be genetic in origin. However, Fox (1948) has shown that the number of scales on various parts of at least certain species of snakes may be influenced by environmental conditions.

Character-gradients, or geoclines, are frequently found to have as their basis of expression, environmental factors which exist in a similar gradient. This has been shown both experimentally and in field studies for a number of species of fishes (Tåning, 1952; Hubbs, 1922a, 1922b, 1940; Jordan, 1893; Schultz, 1926). In all of these studies temperature was of utmost importance in the expression of meristic characters. It is entirely within the realm of possibility that the number of caudal and ventral scales in *Coluber constrictor,* as well as other clinal characters, are environmentally influenced during development of the embryo within the egg, either by temperature alone, or in combination with other ecological factors. Aside from these possibilities of environmental influence on the embryo of young racers, it was found that such factors may affect the appearance of racers *after* they are hatched. This change is concerned with the color of the ventral surface.

*Coloration of the ventral surface.*—Cope (1900: 793) mentioned black punctations on the ventral surface of a racer from Galveston, Texas (USNM 10481). This coloration is a common phenomenon in many individuals from southern United States, even being evident on the black bellies of many specimens of *priapus.* These marks are rarely encountered in specimens of *flaviventris* or *constrictor* from the northern parts of their ranges. I have never noticed such marks on newly hatched or juvenile specimens. They are present on adult specimens of *flaviventris* from east central Texas, and are very evident on adult *anthicus.* The latter frequently has such marks on the first few rows of dorsal scales as well as on the ventral surface. They are also common in many adult specimens of *priapus* from southern Mississippi, Alabama, Georgia, South Carolina and Florida. Many specimens of *paludicolus* also have them (fig. 16).

Close examination of these minute black punctations shows that a very large number of them contain a small mite (*Ophioptes* sp., near *tropicalis* Ewing), which is buried beneath the noncellular outer layer of the skin. Presumably they are not discarded when the skin is cast. In preservation the mite is pale buff to white, and the black

punctations are composed of very minute black specks or streaks.

The taxonomic implications of this phenomenon are intriguing. The distribution of specimens with black punctations on the venter may indicate the Coastal Plain range of the mite. Of more significance is the fact that this distribution may reflect a physiologically variable character in which the racers from southern United States may be more susceptable as host animals to the parasitic mite, and that the mite is actually found over a much greater range.

The influence of the environment on cold-blooded vertebrates, and especially reptiles, is very little known. Of particular importance to the taxonomist interested in these groups is its effect on meristic characters. Jordan (1893) found a general correlation between water temperature and the number of vertebrae in marine fishes, while Schultz (1926) showed the existence of a similar phenomenon in the fresh water fish *Notemegonus crysoleucas.* Both of these studies were based on field data and indicated that most species of fishes tend to have a higher number of vertebrae or fin rays with decreasing temperatures. Hubbs (1922a and b, 1940) and Tåning (1952) worked with specimens in which the temperature during the developmental period was controlled. The results of these experiments tended to substantiate theories based on field data. It was also found that decreasing oxygen pressure and rapid changes in temperature during the sensitive period of embryonic development produced a difference in the mean number of vertebrae (Tåning, 1952). Field observations concerning the effect of salinity on meristic characters have been rather inconclusive.

In reptiles the only studies of this nature have been on one ovoviviparous species of snake, *Thamnophis e. atratus* (Fox, 1948). The subject is of vast importance in the study of herpetology in view of our present practice of utilizing the mean number of scales in the description of nominal populations. As in fishes, racial studies involving geographical variation are more difficult than previously supposed because of the possibility of dependence of some meristic characters on environmental factors. The subject affords many opportunities for worthwhile contributions to our knowledge of variation.

### *UNCORRELATED VARIATION*

In this section are discussed all of the external morphological variations which do not seem correlated with age, sex, environment or geographic locality.

#### *Scutellation*

*Dorsal scales.*—For the most part, practically all of the specimens of *Coluber constrictor* have a dorsal scale formula of 17-17-15 rows. However, occasionally specimens are examined that have a vertebral reduction in addition to the normal lateral type. Ortenburger (1928: 204-205) stated that this type of reduction occurred only rarely in *Coluber constrictor,* being found in only 4 out of over 400 examined. However, of 86 specimens of *priapus* that I have examined for this

character, I find that it occurs on the body in 5.6%. A vertebral reduction occurs over the anal plate in 34.3%, and on the base of the tail just behind the anal plate, in 60.1%. A typical dorsal scale formula of a specimen possessing a vertebral reduction on the body is given in the manner suggested by Dowling (1951: 131-133). The specimen is from Columbia County, Florida.

$$21\ \frac{3}{3}\ \frac{4(2)}{4(3)}\ 19\ \frac{3}{3}\ \frac{4(8)}{4(9)}\ 17\ \frac{3}{3}\ \frac{4(100)}{4(102)}\ 15\ \frac{7}{8(146)}\ 14\ \frac{7}{7(148)}\ 13(178)$$

The high incidence of a vertebral reduction in *Coluber* and the fact that the race *ruthveni* of *Masticophis taeniatus* is more or less characterized by having no vertebral reduction (58% of the specimens have a scale formula of 15-13 *fide* Ortenburger, 1928: 87) lends support to the proposition that perhaps the two genera should be united, and not given generic distinction as indicated by Inger and Clark (1943: 492). No subspecies of *Coluber constrictor* is characterized by having a vertebral reduction, although the condition seems to occur sparingly throughout the range of the species.

*Scales between the chin shields.*—The presence or absence of small scales between the posterior chin shields of specimens is also of taxonomic importance (Inger and Clark, *ibid.*). A small proportion of the specimens (24.5%) examined do not have these scales present between the chin shields. When present, they vary from 1-8.

*Supralabials.*—The number of supralabials in this species may vary from 3-12. Both extremes are rather rare and are produced by a considerable amount of fusion or splitting of the scales. They usually range from 6-8. In the eastern races they are usually 7 (mean 7.2). Occasionally 8 supralabials (7.1%) are found in specimens from eastern United States. Although this number is characteristic of two races (*stejnegerianus* and *mormon*) from the western parts of North America, it is not found in any definite area in eastern United States in a higher frequency than in any other, and the number seems uncorrelated with locality in this area. The mean number for *flaviventris* is $7.11 \pm 0.11$, for *priapus* it is $7.10 \pm 0.09$, for *paludicolus* $7.05 \pm 0.27$, and for *helvigularis* $7.01 \pm 0.34$. The possibility of sexual dimorphism is discussed under infralabials.

*Infralabials.*—The number of infralabials in the races of *Coluber constrictor* from the eastern portion of North America varies from 6-12, usually 8-9, mean $8.36 \pm 0.31$. The occurrence of a number of infralabials other than 8 or 9 does not seem correlated with any geographic region. The mean number for *flaviventris* is $8.75 \pm 0.57$, for *constrictor* $8.31 \pm 0.82$, for *priapus* $8.32 \pm 0.48$, for *paludicolus* $8.41 \pm 0.78$ and for *helvigularis* $8.51 \pm 0.92$. The suggested geographic variation is not statistically significant ($P = 0.03$).

Ortenburger (1928: 186 *ff*) mentioned the possibility of a slight sexual dimorphism in the number of supralabials and infralabials, at least in the race *flaviventris*. However, statistical analysis shows that the observed results could have been obtained from random

sampling (P = 0.3). Table 3 shows the mean number of infralabials and supralabials for a sample of *flaviventris* from Michigan, Ohio and Indiana, and a sample of *priapus* from northern Florida. The mean numbers of these scales in males and females are not significantly different and the coefficients of divergences are low, as would be expected (P = 0.8-0.3).

TABLE 3.
NUMBER OF SUPRALABIALS AND INFRALABIALS

| Subspecies | Sex | Number of Specimens | Supralabials Mean | Supralabials C. D. | Infralabials Mean | Infralabials C. D. |
|---|---|---|---|---|---|---|
| *Coluber c. flaviventris* | ♀ | 59 | 7.12 | .005 | 8.66 | .017 |
| | ♂ | 53 | 7.08 | | 8.51 | |
| *Coluber c. priapus* | ♀ | 154 | 7.12 | .005 | 8.36 | .014 |
| | ♂ | 231 | 7.08 | | 8.28 | |

*Postoculars.*—The number of postoculars varies from 2-4 (mean 3.01±0.08). The occurrence of either 2 or 4 postocular scales does not seem correlated with any geographic area, as it occurs rarely throughout the entire range of the species. The small differences among the mean number of these scales for specimens from various parts of the United States do not reach statistical significance.

*Preoculars.*—The preoculars are usually 2, rarely 1, mean 1.97± 0.06. The occurrence of 1 preocular is not correlated with any geographic area of North America.

*Loreal scale.*—The loreal scale is usually single (97.01%) but may be divided into two or three smaller scales. The shape is usually square to slightly higher than long. The posterior edge may be straight or slightly convex. Variations as might exist seem individual rather than geographic.

*Temporals.*—The number of temporals is quite variable. They are usually disposed in three pairs, one behind the other, indicated by the formula 2-2-2 (80.5%). Four pairs are also common (16.9%), shown by 2-2-2-2, or in two pairs (1.3%), indicated by 2-2, or even five pairs (1.3%), 2-2-2-2-2. Frequently an additional scale may be present in any vertical row, in which case the formula is expressed as 2-2-3, 2-3-2, or 3-2-2. Three scales may occur in more than one row, as 3-3-2, 3-3-3, or 2-3-3. Occasionally the pair of scales in each vertical row may be reduced to form a condition expressed as 1-2-2, 2-1-1, etc. Frequently an additional scale is present between two pairs of scales, so that the formula is expressed as 2-2-1-2, 3-1-2-2, etc. Practically all combinations of numbers from 1-5, either in pairs or not, are found. There is no apparent correlation with geography. The lowest number of temporals which I have counted is expressed as 2-2, the highest as 3-3-2-2 and 2-3-3-2, both totaling ten scales in all.

### *Color*

In general, the coloration of individuals, both juveniles and adults, is correlated with geographic locality and has been discussed previ-

ously. However, certain facets concerning the coloration of the eastern races, such as the manner in which the juvenile pattern changes to that of the adult, seem uncorrelated with geographic locality. This is also true of aberrant colors of both young and adult specimens.

*Ontogenetic color and pattern changes.*—It has been mentioned that the transformation of color and markings of juvenile specimens, which are blotched, to the adults, which are uniform in color, follows rather basic patterns. On the dorsal surface the markings are first obliterated posteriorly. This suffusion slowly moves anteriorly. On many newly hatched specimens, such posterior suffusion is already present, so that accurate counts of the total number of blotches is difficult. Numerous authors have reported that these markings disappear completely during the second or third year. The total length at which this suffusion is complete is about 500 mm. WA 3423 from Astor Park, Lake County, Florida, which is 458 mm in total length, has a dorsal surface spotted with faint dark brown blotches. In WA 3204 from the same locality and 519 mm in total length, there is no indication of any dorsal markings. A specimen from Winter Haven, Polk County, Florida (SRT 250), which is 623 mm, does not have any visible dorsal markings. In USNM 4423 from Georgetown, South Carolina, which is 526 mm in length, the ventral spots are quite evident while the dorsal spots are completely suffused by black. Practically all of the specimens which I have examined that are under 480 mm in total length, had visible dorsal spots, while most of those over 600 mm showed no indication of such markings. McCauley (1945: 74) stated that in Maryland the largest specimen that he has examined that had noticeable dorsal blotches was 584 mm. The smallest one that was completely transformed was 640 mm.

In the subspecies with a dark, slate-colored belly (*priapus, constrictor* and *helvigularis*) there is frequently observed a light stripe extending down the middle of the ventral surface. Loennberg (1894) described such a specimen from Arcadia, DeSoto County, Florida, in which there is a median stripe of small white, cloudy spots. This is a consequence of the method by which the ventral suffusion takes place. A specimen 521 mm in total length, from 4 miles north of Kissimmee, Osceola County, Florida, was kept alive for a long period and notes were taken on color changes that occurred over a period of nine months. Ventrally this specimen was bluish-gray with pinkish-orange ventral spots (Sept. 14, 1951). By November 16 there was a noticeable area of dark grayish-blue on the lateral edges of the ventral plates in the mid-body region. This left a lighter stripe of the original ground color down the center of the belly. Anteriorly, and on the underside of the tail, the specimen was still light-colored. By April, 1952, it was 617 mm in total length. The darker pigment which was slowly suffusing the midbody outer surfaces of the ventral plates was slaty-black and the light mid-ventral stripe became very evident.

This observed change is also borne out by many living and pre-

served specimens. In most adult individuals the belly is slaty-black with only the chin and first few ventral plates being white. The underside of the tail is also frequently white. This coloration seems typical of most large specimens from peninsular Florida. Large individuals from New York, New Jersey and other northeastern states usually have much more black on the chin, throat and underside of the tail. In many specimens from such widely separated states as New York and Florida, the anterior portion of the underside of the body and throat may be white, blotched with black. A similar condition is also frequently noted on the underside of the tail. McCauley (1945: 74) reported a specimen from Allegheny County, Maryland,

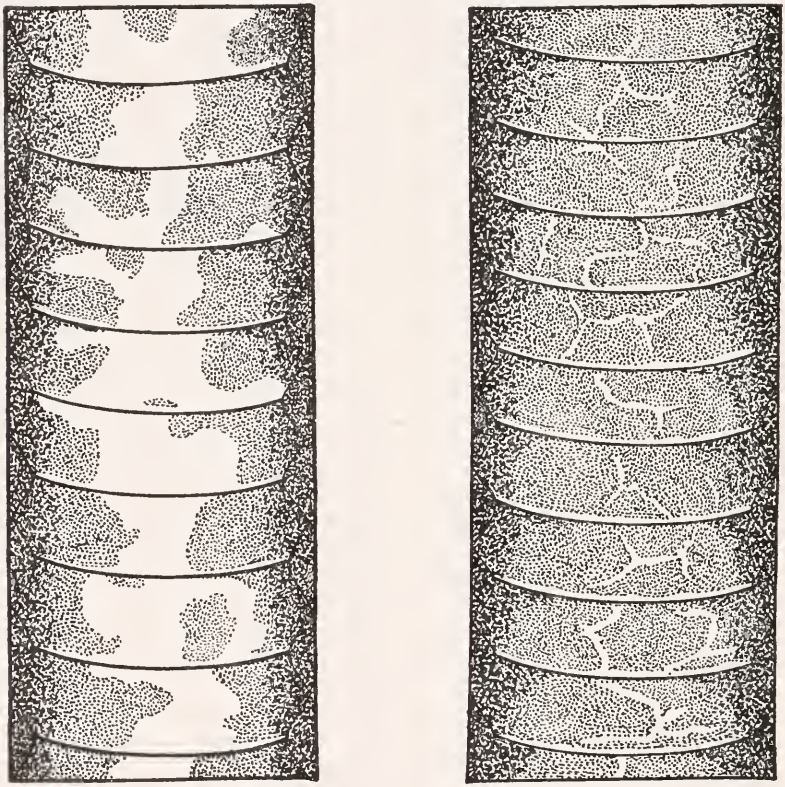


Figure 15. Ontogenetic color and pattern changes in subadult specimens of *Coluber constrictor* from eastern United States. Black blotches on the anterior portion of the belly of young subadults (A) slowly get larger. This causes light, faint reticulations to be formed in older specimens (B). The final stage is complete fusion of the blotches, causing a uniform coloration.

1130 mm in length, which was mottled with black about 100 mm down the belly. UMNZ 57059 from Enterprise, Volusia County, Florida, has very large blotches on the anterior portion of the ventral surface. The same is true of AMNH 6719, labeled "Arkansas". WA 3561 from Astor Park, Lake County, Florida, is similar. None of these specimens are full-grown, but are about 760 mm in total length. They all come from areas in which full-grown specimens have a black throat and belly. This would seem to indicate that while the mid-body ventral suffusion takes place over a large area on the lateral surfaces of the ventral plates, in the region of the throat this suffusion takes place by a gradual growth, and finally, a coalescence of slaty-black blotches. In many specimens from Florida that are between 760-1020 mm in total length, the anterior portion of the belly and throat is mostly black, but with faint reticulations of bluish-white. These specimens represent the next to the last stage in the ventral ontogenetic color change, in which the black blotches are practically completely fused (fig. 15).

In the races that have a light-colored ventral surface (i. e., *flaviventris, anthicus, mormon, stejnegerianus,* and *paludicolus*) the ventral markings of the juvenile may be retained for a long time. This is especially true near the anterior end. Pope (1944: 172) mentioned a male *flaviventris* 1067 mm long which possessed traces of the juvenile spots. I have seen two specimens from Michigan that were 914 and 1001 mm long on which traces of ventral markings were quite noticeable anteriorly. Occasionally specimens of *paludicolus* also retain this juvenile ventral coloration anteriorly, though always faint as in the other subspecies.

*Abberrant head color.*—Occasional individuals are examined that have the supralabials, infralabials and sometimes the chin, variously colored, usually some shade of yellow, or even orange in some cases. Although occurring rarely, they are found throughout the range of the species, at least in the eastern portions of North America.

## Acknowledgements

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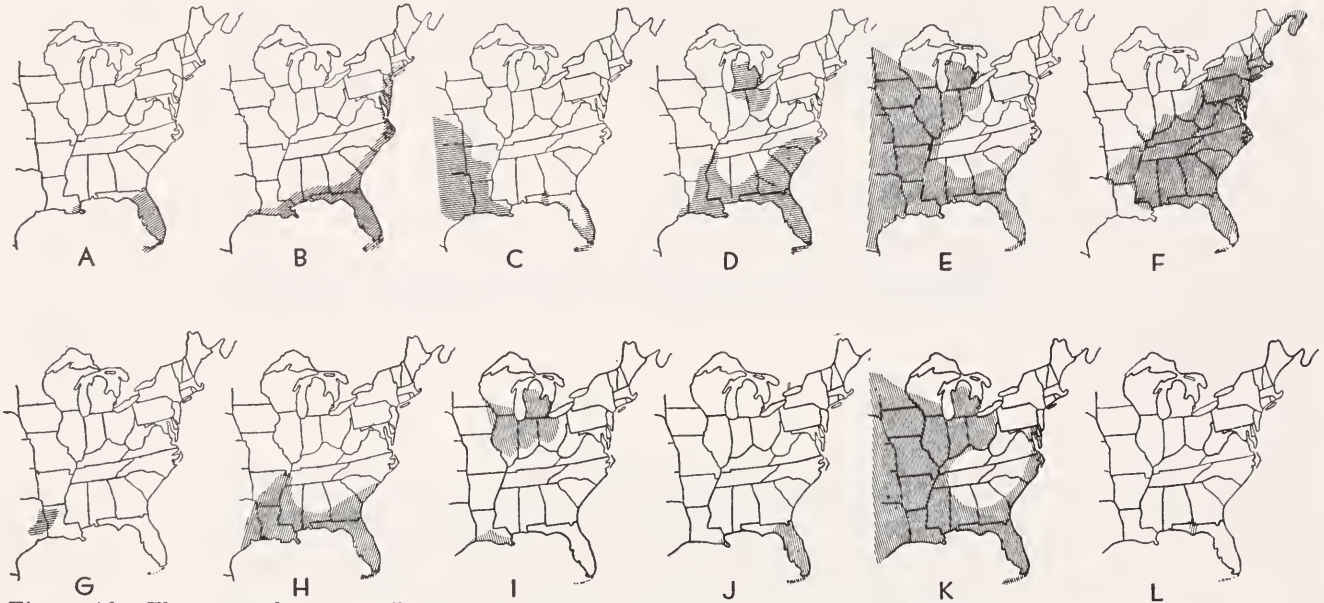


Figure 16. The generalized distribution of certain characters in *Coluber constrictor* of eastern United States: **A.** regions in which red-eyed juveniles may be found; **B.** areas in which red ventral spots may be found on juveniles; **C.** regions in which adult specimens may have brown on the supralabials; **D.** areas in which at least 10% of the specimens may have the loreal in contact with the first supralabial; **E.** regions in which hemipenial hooks are usually found; **F.** regions in which black-colored adults are found; **G.** regions in which speckled adults are found; **H.** areas in which adults may have black punctations on the ventral surface, caused by a burrowing mite (*Ophioptes* sp.); **I.** regions in which dark "postocular stripes" may be found; **J.** regions in which the ventral spots may be very much reduced, or absent entirely; **K.** areas in which full grown specimens usually have white chins; **L.** regions in which full grown specimens have brown or tan chins.

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## Summary

As now recognized, the genus *Coluber* includes four species. These are:

*Coluber oaxaca* (Jan) 1863: 63. A species known from a very few specimens. It has been recorded from the Mexican states of Oaxaca and Colima.

*Coluber spinalis* (Peters) 1866: 91. An Asiatic form of northern China and Mongolia.

*Coluber acuminatus* (Cope) 1899: 197. A fossil species which is reported from the Pleistocene of Montgomery County, Pennsylvania. Examination of the skulls of a few specimens of *Coluber constrictor* seems to indicate that there is reason to doubt the validity of the fossil species.

*Coluber constrictor* Linneaus 1758: 216. This is a polytypic species dispersed throughout most of North America. It is found as far north as Halifax, Canada, and as far south as the Florida Keys on the east coast. On the Pacific coast it occurs from British Columbia to extreme southern California. In middle North America it is found from North Dakota to southern Texas, and in the eastern Gulf Coastal Plain of Mexico to the state of Vera Cruz, thence to Guatemala.

Included in the species *Coluber constrictor* are eight races. These are:

*Coluber c. mormon* Baird and Girard 1852: 351. No intergradation is known between this race and its closest relative geographically (*flaviventris*), and is included as a subspecies because of its extreme similarity to other members of the group. Although *mormon* and *flaviventris* have been found within 130 miles of one another (Stuart, 1930: 44), large series will have to become available from suspected areas of intergradation before intermediate populations can be demonstrated. Undoubtedly such series will show that intergradation exists, at least in Montana, and probably along the Front Ranges of the Rocky Mountains in other states farther south.

It is distributed from southern British Columbia to extreme southern California and from the Pacific Coast to the Rocky Mountains. It seems absent from the Sonoran Physiographic Province of southeastern California and western Arizona.

*Coluber c. stejnegerianus* (Cope) 1895: 797. A subspecies of extreme southern Texas and Mexico, being found from Nueces County south in the Gulf Coastal Plain to Vera Cruz. *Coluber c. ortenburgeri* Stuart is referred to the synonymy list of this form, as there seems to be no reliable character with which to separate the two races, thus extending the range of *stejnegerianus* to Guatemala.

*Coluber c. flaviventris* Say 1823: 185. A subspecies of the Great Plains and Interior Lowlands as well as restricted portions of the Gulf Coastal Plain in eastern Texas and southern Louisiana. Its northern limits of distribution are from Montana to North Dakota, southern Minnesota and Lower Michigan. It extends westward as far as the Front Ranges of the Rocky Mountains and the Edwards Plateau in southern Texas. In the northern parts of its range its distribution has been shown to be correlated with the prairie provinces in both Ohio and Minnesota by Conant (1938: 50) and Breckenridge (1944: 116). Further collecting will probably show that this is true of the remainder of the northern parts of its range.

Specimens of this race, although so far reported only from Ontario in Canada (Mills, 1948: 10), will probably be found in the southern portions of Saskatchewan and Alberta. Intergradation between this race and *constrictor* is to be sought along the northern shore of Lake Erie in southern Ontario.

*Coluber c. constrictor* Linnaeus 1758: 216. This is a subspecies of the eastern forests. It does not seem to range above 4,000 feet elevation in the Appalachian Mountains. It is found from Halifax, Canada, south to the Fall Line; west to the Mississippi Lowlands and the unglaciated portions of Ohio. It seems absent from the non-coastal areas of Maine, the greater part of New Hampshire and Vermont and the Adirondack

Mountains. The distributional patterns of this race and *flaviventris* are nearly congruent with those of many other groups of snakes (Schmidt, 1938; Ruthven, 1908; Grobman, 1941; *et. al.*).

*Coluber c. priapus* Dunn and Wood 1939: 4. A lowland form of southern United States being found in the Atlantic and Gulf Coastal Plain from North Carolina to Lake Pontchartrain, Louisiana, and north in the Mississippi Lowlands to extreme southwestern Ohio. Considerable interdigitation seems to exist in Arkansas between this race and *flaviventris.* It is a syngeograph of many southeastern snakes, including *Farancia abacura, Agkistrodon piscivorus, Crotalus h. atricaudatus,* etc., as well as many frogs, such as *Rana grylio, Hyla cinerea,* etc.

*Coluber c. anthicus* (Cope) 1862: 238. A subspecies found in western Louisiana and eastern Texas.

*Coluber c. helvigularis* subsp. nov. This is a form inhabiting an area along the Appalachicola and Chipola Rivers in western Florida. *Lampropeltis g. goini* seems to have a somewhat equivalent range.

*Coluber c. paludicolus* Auffenberg and Babbitt 1953: 44. A race mainly confined to the Everglades of southern Florida. An outlying population occurs on Cape Canaveral, Brevard County, Florida. Geographical equivalents are found in such forms as *Seminatrix p. cyclas, Liodytes a. lineapiatus* and *Pseudobranchus s. belli.*

Three new subspecies have been proposed since Ortenburger's monograph, and even since the 5th Edition of the Checklist (Stejneger and Barbour, 1943). All of these are from Florida and are: *C. c. paludicolus* Auffenberg and Babbitt (1953), *C. c. helvigularis* subsp. nov. and *C. c. haasti* Bell (1952). The last named race does not seem worthy of subspecific designation. Of the five characters stated as being diagnostic of *haasti,* one is always found in typical specimens of *priapus* (black belly); one is occasionally found in both *priapus* and *haasti* (brown snouts); another is found in all specimens of *priapus* except the central and south-central Florida peninsular populations (black supralabials); and I consider the comparative luster and size extremely difficult to measure (there being considerable overlap), and of too small an average difference, if they exist at all, to warrant the erection of a new subspecies based on these characters alone. It also seems highly significant that of all of the characters which have been examined, the populations from the Middle and Lower Keys seem to have closer affinities to those from the northern parts of the peninsula than to those from any other portion of the southeast. In fact, the two populations seem practically identical, and I find it impossible to tell them apart on the basis of any character, or group of characters, which I have studied so far.

Three names have been revived from the synonymy of *C. c. flaviventris* since Ortenburger's monograph. These are *C. c. anthicus, C. c. foxi* and *C. c. stejnegerianus.* Two races (*anthicus* and *stejnegerianus*) seem worthy of this distinction. *Coluber c. foxi,* considered a synonym of *C. c. flaviventris* in this paper, may deserve subspecific designation if it is shown that the area of intergradation between the two populations exhibits an external, rather than an internal cline as suggested in this paper.

The variations found in the eastern races have been examined critically. Some of these were found to be correlated with either locality, sex, environment, or age.

Of the correlated variations, those concerned with geographic variation are most obvious. When plotted, they appear to be internal, external and ontogenetic clines or character gradients. Some of these have been summarized in figure 16 for easier reference and to show the varying limits of distribution from one character to the next.

*External Clines:*

*Length of the hemipenial spines.*—An examination of this character has indicated that the range of *C. c. priapus,* heretofore thought to be restricted to peninsular Florida, includes the Atlantic and Gulf Coastal Plains and the Mississippi Lowlands. *Coluber c. constrictor* is the only subspecies which does not possess an enlarged basal hemipenial spine which may be termed a hook.

*Coloration.*—The color of the temporals, gulars, supralabials, chin, and ventral and dorsal surfaces are examples of this type of cline. On the basis of the dorsal and ventral coloration the ranges of *C. c. constrictor* and *C. c. flaviventris* have been changed from those given by Ortenburger (1928). The eastern edge of the range of *flaviventris* has been placed farther westward in Arkansas and northeastern Louisiana. The southern edge of the range of this form in the states of Illinois and Indiana has been placed a little farther northward.

*Internal Clines:*

*Number of hemipenial spines.*—The number of spines on the hemipenis of male specimens, which may be termed hooks, is variable and seems to form a continuous gradient. A lower number of hooks are found in the eastern forms than in those from western United States. Although specimens of *Coluber c. flaviventris* normally have at least one hook, many specimens from the northern portions of the range of this form have basal spines which are not large enough to be termed hooks. Specimens which are intermediate in coloration between the races *flaviventris* and *constrictor* from central Ohio do not seem to be intermediate in this spinal character.

*Coloration of the young.*—Many colors suspected of being characteristic of populations from the Southeast have been shown to be character-gradients. These include the color of the dorsal and ventral surfaces and the number and size of the dorsal and ventral markings. The mean number of dorsal spots is highest in the West,

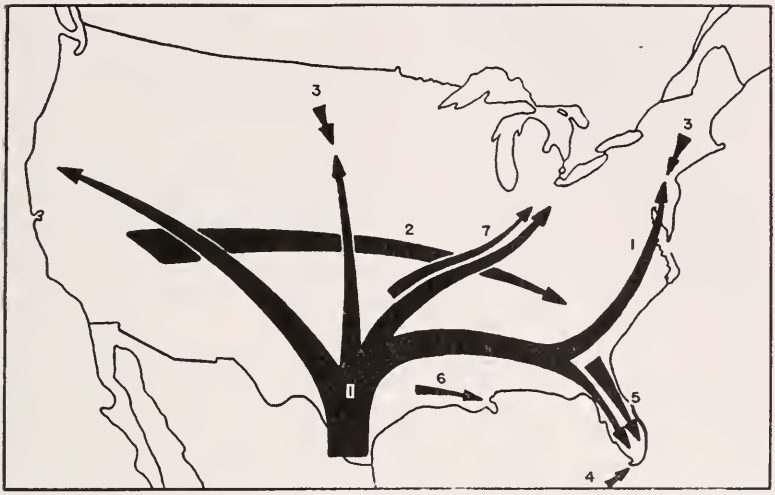


Figure 17. Generalized directions for the major internal geoclines which are evident in the morphological variations of *Coluber constrictor*. **1.** A primary focal point, represented by the race *C. c. stejnegerianus*, is the basis for many clines running in northerly directions, such as the internal clines represented by the number of ventral and caudal scales, the point of reduction of the dorsal scale rows, and adult size. Most of these characters increase in value or degree as one moves away from southern Texas. **2.** A very broad and generalized cline from western to the eastern portions of North America, which seems to terminate in southeastern United States. The characters involved in this cline are the general increase in the number of some of the teeth, the number of hemipenial spines, and the changing shape of the premaxillary bone. **3.** An obvious reversed cline is found in the extreme northern portions of the range of this species, at least in central and eastern United States. This internal cline deals with the number of ventrals and caudals, and the point of reduction of dorsal scale rows. This is a reversal of cline number 1. **4.** Another reversed cline is found from the Lower to the Upper Keys of Florida. It is represented by the increase of ventrals, caudals, point of reduction of the dorsal scale rows, larger size (?), and the gradual change from brown to reddish eyes in the adults, as well as an increase of red colors in the juveniles on both dorsal and ventral surfaces. **5.** A cline from the continental portions of the southern Coastal Plain into peninsular Florida, terminating in the extreme southern tip of the mainland. It is represented by the increase in the frequency of a loreal-first supralabial contact, increase in the number of ventrals and caudals, more posterior reduction of the dorsal scales, a gradual change from brownish to red eyes, larger size, and decrease of number of dorsal and ventral spots in the juveniles, as well as a change of color in these markings. **6.** A cline from *flaviventris* from the Great Plains and Coastal Prairies of Texas along the Coastal Prairies of Louisiana into the delta region. It is represented by an increase in the reddish colors on the ventral surface of juveniles, the decrease of ventral markings in number and size, and the increase of darkly colored temporals in adults. **7.** An internal cline from the populations of *flaviventris* of the Great Plains northeastward into the Steppe Peninsula, represented by the increase of the number and size of juvenile belly markings, and the increase of the frequency of darkly-colored temporals.

where the spots are smallest, and lowest in the East, where they are largest. The number and size of the ventral markings are largest and most numerous in the northern latitudes, and smallest and least numerous in the southern latitudes.

*Scutellation.*—The mean number of both ventral and caudal scales for various localities have been shown to be internal clines. The lowest mean numbers of ventral and caudal scales are found in the western races, while the highest are found in peninsular Florida and the greater part of the glaciated regions of North America. The highest mean number of ventrals and caudals is found in the south Florida race, *paludicolus.* The lowest number occurs in the southeastern Texas and Mexican Gulf Coast race, *stejnegerianus.* The mean number of ventral and caudal scales of populations from Florida show fair correlation with the physiographic divisions of the state; the geologically "older" portions of the state having significantly lower mean counts than do those from the geologically "newer", and lower coastal areas. The northern portions of these peninsular physiographic areas tend to have lower mean counts than do the southern portions, though the differences are not statistically significant. However, significant differences occur between specimens from northern, southern and the Keys areas of Florida. The coastal areas of Georgia and South Carolina have higher mean counts than do populations from the Piedmont and Appalachian Mountain Provinces of these two states.

A high percentage of the specimens from southern United States possess a contact between the loreal and first supralabial. However, these percentages vary with locality and the character is a good example of geographically variable dimorphism. This contact occurs infrequently in specimens from Michigan, Ohio and Illinois, but in at least 10% of the specimens from south of the Fall Line. It occurs in about 60% of the specimens from southern Florida.

The point of reduction of the dorsal scale formula has been found to vary geographically and represents an internal cline. It varies in direct proportion to the total number of mean ventral scales, and is contained in that number from 1.6-1.8 times, regardless of locality.

*Osteology.*—The shape of the premaxillary bone has been found to vary geographically as an internal cline. In the western subspecies the two posterior processes are shorter and in a horizontal plane, whereas in the eastern races, and especially in *priapus* and *paludicolus,* they are in a vertical plane, and longer.

*Dentition.*—The number of teeth also varies geographically, and in general the means are lower in the western races than in the eastern forms.

*Dimorphism:*

*Scutellation.*—The contact of the first supralabial and loreal has already been mentioned as a dimorphic character, but it also varies geographically as an internal cline.

*Sexual dimorphism.*—Dimorphism of this nature is indicated in

the number of caudals, though not statistically significant. Very slight differences in the mean numbers of ventrals and supralabials, mentioned by Ortenburger as being sexually dimorphic characters, are shown to be non-significant. Associated with the number of caudals is the relative length of the tail, and as in the caudals, the differences in length are probably not statistically significant.

*Environmentally produced characters.*—Small black punctations on the ventral and lower lateral surfaces of adults have been shown to be caused by a small burrowing mite (*Ophioptes* sp., near *tropicalis* Ewing). Although seemingly restricted to the Mississippi Lowlands and the Coastal Plain, the character does not have obvious taxonomic significance.

Variations in the following characters have been found to be uncorrelated with environment, age, sex or locality: dorsal scales, number of scales between the chin shields, number of supralabials, infralabials, postoculars, preoculars, loreals and temporal scales. Variations in the ontogenetic color change from a blotched pattern of the juvenile to the uniform coloration of the adult do not seem correlated with locality.

## References Cited


Allen, E. R. and R. Slatten 1945. A herpetological collection from the vicinity of Key West, Florida. *Herpetologica*, 3(1): 25-26.

Anderson, P. 1942. Missouri amphibians and reptiles. *Bull. Chicago Acad. Sci.*, 6: 203-220.

Atkinson, D. A. 1901. The reptiles of Allegheny County, Pennsylvania. *Ann. Carnegie Mus.*, 1: 145-157.

Auffenberg, W. 1949. The racer, *Coluber c. stejnegerianus* (Cope), in Texas. *Herpetologica*, 5(4): 53-58.

---------- 1955. The status of the fossil snake *Coluber acuminatus* (Cope): *Copeia*, 1955 (in press).

Auffenberg, W. and L. H. Babbitt 1953. A new subspecies of *Coluber constrictor* from Florida. *Copeia*, 1953 (1): 44.

Babbitt, L. H. 1932. Remarks on Connecticut herpetology. *Bull. Boston Soc. Nat. Hist.*, (63): 23-28.

Baird, S. F. and C. Girard 1853. *Catalogue of North American Reptiles in the Museum of the Smithsonian Institution. Part I,—Serpents.* Smithsonian Inst., Wash., D. C., pp. 1-172.

Bell, L. N. 1952. A new subspecies of the racer *Coluber constrictor*. *Herpetologica*, 8(2): 21.

Blair, W. F. and T. H. Hubbell 1938. The biotic districts of Oklahoma. *Amer. Midl. Nat.*, 20(2): 425-454.

Blanchard, F. N. 1924. A collection of amphibians and reptiles from southeastern Missouri and southern Illinois. *Pap. Mich. Acad. Sci. Arts and Letters*, 4: 533-541.

Bogert, C. M. 1947. The status of the genus *Leptodrymus* Amaral, with comments on modification of Colubrid premaxillae. *Amer. Mus. Novitates*, No. 1952: 1-14.

Bogert, C. M. and R. B. Cowles 1947. Moisture loss in relation to habitat selection in some Florida reptiles. *Amer. Mus. Novitates*, No. 1858: 1-32.

Boulenger, G. A. 1893. *Catalogue of the Snakes in the British Museum*, London. 1: pp. 1-448.

BRANSON, E. B. 1904. The snakes of Kansas. *Kans. Univ. Sci. Bull.*, 2(12): 353-430.

BRECKENRIDGE, W. J. 1944. *The Reptiles and Amphibians of Minnesota.* Univ. Minn. Press, Minneapolis, pp. 1-202.

BRIMLEY, C. S. 1942. Reptiles and amphibians of North Carolina. *Carolina Tips*, No. 21: [No pagination].

BROWN, B. C. 1950. An annotated check list of the reptiles and amphibians of Texas. *Baylor Univ. Studies*, pp. 1-257.

BURGER, W. L., JR. 1948. *Farancia abacura reinwardtii* in Oklahoma. *Copeia*, 1948 (2): 133.

BURT, C. E. 1935. Further records of the ecology and distribution of amphibians and reptiles in the middlewest. *Amer. Midl. Nat.*, 311-336.

BURT, C. E. and M. D. BURT 1929. A collection of reptiles and amphibians from the Mississippi Valley with field observations. *Amer. Mus. Novitates*, No. 381: 1-14.

BURT, C. E. and W. L. HOYLE 1934. Additional records of the reptiles of the central prairie regions of the United States. *Trans. Kans. Acad. Sci.*, 37: 193-216.

CAGLE, F. R. 1941. A key to the reptiles and amphibians of Illinois. *Mus. Nat. and Soc. Sci., Southern Ill. Normal Univ., Contrib.* No. 5: 1-32.

_____ 1942. Herpetological fauna of Jackson and Union Counties, Illinois. *Amer. Midl. Nat.*, 28(1): 164-200.

CARR, A. F., JR. 1940. A contribution to the herpetology of Florida. *Univ. Fla. Publ., Biol. Sci. Series*, 3(1): 1-118.

CONANT, R. 1930. Field notes on a collecting trip. *Bull. Antivenin Inst. Amer.*, 4(3): 60-64.

_____ 1938. Reptiles of Ohio. *Amer. Midl. Nat.*, 20(1): 1-200.

_____ 1942. Notes on the young of three recently described snakes with comments on their relationship. *Bull. Chicago Acad. Sci.*, 6(10): 194-198.

COOKE, C. W. 1939. Scenery of Florida interpreted by a geologist. *Fla. Geol. Bull.*, 17: 1-118.

_____ 1945. Geology of Florida. *Fla. Geol. Bull.*, 29: 1-339.

COPE, E. D. 1862. Notes upon some reptiles of the Old World. *Proc. Acad. Nat. Sci. Phila.*, 14: 337-344.

_____ 1899. Vertebrate remains from Port Kennedy bone deposit. *Jour. Acad. Nat. Sci. Phila.*, (2nd ser.), 11: 193-267.

_____ 1900. Crocodilians, lizards and snakes of North America. *U. S. Nat. Mus. Rept.*, 1898: 153-1270.

DELLINGER, S. C. and J. D. BLACK 1938. Herpetology of Arkansas. Part One, the Reptiles. *Occ. Pap. Univ. Ark. Mus.*, No. 1: 1-47.

DITMARS, R. L. 1907. *The Reptile Book.* Doubleday Page and Co., New York, pp. 1-472.

_____ 1936. *The Reptiles of North America.* Garden City Publ. Co., N. Y., pp. 1-477.

_____ 1939. *A Field Book of North American Snakes.* Doubleday Doran and Co., New York, pp. 1-305.

DOWLING, H. G. 1950. Studies of the black swamp snake, *Seminatrix pygaea* (Cope), with descriptions of two new subspecies. *Misc. Publ. Mus. Zool. Univ. Mich.*, No. 76: 1-38.

---------- 1951. A proposed method of expressing scale reduction in snakes. *Copeia*, 1951 (2): 131-133.

DUMÉRIL, A. M. C., G. BIBRON and A. DUMÉRIL 1854. *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*, 7(1): 1-780. Librairie Encyclopédique de Roret, Paris.

DUMÉRIL, A. and F. BOCOURT 1870. Études sur les reptiles et les batraciens. *Mission scientifique au Mexique et dans l'Amérique Centrale* [Paris], 3(3): 1-1012.

DUNN, E. R. and C. WOOD 1939. Notes on eastern snakes of the genus *Coluber*. *Notulae Naturae*, No. 5: 1-4.

ECKEL, E. C. and F. C. PAULMIER 1902. Catalogue of New York reptiles and batrachians. *N. Y. State Mus. Bull.*, 51: 356-414.

ELLIS, M. M. and J. HENDERSON 1913. The amphibia and reptilia of Colorado. *Univ. Col. Studies*, 10(2): 35-129.

ETHERIDGE, R. E. 1952. The southern range of the racer *Coluber constrictor stejnegerianus* (Cope), with remarks on the Guatemalan species *Coluber ortenburgeri* Stuart. *Copeia*, 1952 (3): 189-190.

FOX, W. 1948. Effect of temperature on development of scutellation in the gartersnake, *Thamnophis e. atratus*. *Copeia*, 1948 (4): 252-262.

GROBMAN, A. B. 1941. A contribution to the knowledge of variation in *Opheodrys vernalis* (Harlan), with the description of a new subspecies. *Misc. Publ. Mus. Zool. Univ. Mich.*, No. 50: 1-37.

GÜNTHER, A. C. L. G. 1850. *Catalogue of the Colubrine Snakes in the British Museum*. London., pp. 1-281.

GUTHRIE, J. E. 1926. The snakes of Iowa. *Bull. Iowa St. Agric. Exper. Sta.*, No. 239: 1-192.

HOLBROOK, J. E. 1842. *North American Herpetology*, (2nd ed), 3: 1-128, J. Dobson Co., Philadelphia.

HUBBS, C. L. 1922a. Variations in the number of vertebrae and other meristic characters of fishes correlated with the temperature of the water during development. *Amer. Nat.*, 56: 360-372.

---------- 1922b. Seasonal variation in the number of vertebrae of fishes. *Papers Mich. Acad. Sci., Arts & Lttrs.* 2: 207-214.

---------- 1940. Increased number and delayed development of scales in abnormal suckers. *Papers Mich. Acad. Sci., Arts & Lttrs.* 26: 229-237.

HUXLEY, J. 1943. *Evolution, the Modern Synthesis*. Harper Brothers, New York, pp. 1-645.

INGER, R. F. and P. L. CLARK 1943. Partition of the genus *Coluber*. *Copeia*, 1943 (3): 141-145.

JAN, G. 1863. *Elenco Sistematico degli Ofidi, Descritti e Desegnati per L'Iconografia Generale*. Lombardi, Milano, pp. 1-143.

---------- 1867. *Iconographie Generale des Ophidiens*. liv. 22, pls. 1-3, Paris.

JORDAN, D. S. 1893. *Temperature and Vertebrae: A Study in Evolution, Being a Discussion of the Relations of the Number of Vertebrae among Fishes to the Temperature of the Water and to the Character of the Struggle for Existence*. Wilder Quarter-Century Book, Ithaca, pp. 13-36.

KELLY, H. A. 1936. Snakes of Maryland. *Nat. Hist. Soc. Maryland*, pp. 1-103.

KING, F. W. 1932. Herpetological records and notes from the vicinity of Tuscon, Arizona, July and August. *Copeia*, 1932 (4): 175-177.

KLAUBER, L. M. 1940. Two new subspecies of *Phyllorhynchus*, the leaf-nosed snakes, with notes on the genus. *Trans. San Diego Soc. Nat. Hist.*, 9: 192-214.

LINNAEUS, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentis Synonymis, Locis*, 10th. ed. Laurentii, Holiae, 1: 1-824.

LINSDALE, J. M. 1940. Amphibians and reptiles in Nevada. *Proc. Amer. Acad. Arts and Sci.*, 73(8): 197-257.

LOENNBERG, E. 1894. Notes on the reptiles and batrachians collected in Florida in 1892 and 1893. *Proc. U. S. Nat. Mus.*, 17: 317-339.

LUETH, F. X. 1941. *Manual of Illinois Snakes.* Ill. Dept. Cons., Springfield, pp. 1-48.

MACNEILL, F. S. 1951. Pleistocene shore lines in Florida and Georgia. *Geol. Surv. Prof. Paper 221-F.*, pp. 95-107.

MCCAULEY, R. H., JR. 1945. *The Reptiles of Maryland and the District of Columbia.*, publ. by Author, Baltimore, pp. 1-194.

MILLS, R. C. 1948. A checklist of the amphibians and reptiles of Canada. *Herpetologica*, 4(2): 1-15.

MITTLEMAN, M. B. 1947. Miscellaneous notes on Indiana amphibians and reptiles. *Amer. Midl. Nat.*, 38(2): 466-484.

MULAIK, S. and D. MULAIK 1942. A neglected species of *Coluber*. *Copeia*, 1942 (1): 13-15.

ORTENBURGER, A. I. 1926. A report of the amphibians and reptiles of Oklahoma. *Proc. Okla. Acad. Sci.*, 6: 89-100.

---------- 1927. A key to the snakes of Oklahoma. *Proc. Okla. Acad. Sci.*, 6(1): 197-218.

---------- 1928. The whipsnakes and racers, genera *Masticophis* and *Coluber*. *Mem. Univ. Mich. Mus.*, 1: 1-247.

---------- 1930a. Reptiles and amphibians from Pawnee County, Oklahoma. *Copeia*, 1930 (3): 94-95.

---------- 1930b. A key to the lizards and snakes of Oklahoma. *Publ. Univ. Okla. Biol. Surv.*, 2(4): 209-239.

PERKINS, C. B. 1949. A key to the snakes of the United States (2nd ed.). *Bull. Zool. Soc. San Diego*, No. 24: 1-79.

PETERS, W. 1866. Mitteilung über neue amphibien und fische. *Monatsber. Akad. Wiss. Berlin*, 1866: 86-96.

POPE, C. H. 1944. *Amphibians and Reptiles of the Chicago Area.* Chicago Nat. Hist. Mus., Chicago, pp. 1-275.

RODDY, H. J. 1923. *Reptiles of Lancaster County, and the State of Pennsylvania.* Dept. Nat. Hist., Franklin and Marshall Coll., pp. 1-53.

RUTHVEN, A. G. 1908. The faunal affinities of the prairie region of central North America. *Amer. Nat.*, 42: 388-393.

SAY, T. 1823. *Account of An Expedition from Pittsburgh to the Rocky Mountains Under the Command of Major S. H. Long.* H. C. Peary and I. Lea, Philadelphia, 2: 1-442.

SCHMIDT, K. P. 1938. Herpetological evidence for the postglacial eastward extension of the steppe in North America. *Ecology*, 19(3): 396-407.

---------- 1953. *A Check List of North American Amphibians and Reptiles* (6th ed.) Amer. Soc. Ichthy. and Herp., Chicago, pp. 1-280.

SCHULTZ, L. P. 1926. Temperature-controlled variation in the golden shiner, *Notemegonus crysoleucas*. *Papers Mich. Acad. Sci. Arts & Lttrs.*, 7: 417-429.

SMITH, H. M. and A. B. LEONARD 1934. Distributional records of reptiles and amphibians in Oklahoma. *Amer. Midl. Nat.*, 15: 190-196.

STEJNEGER, L. and T. BARBOUR 1917. *A Check List of North American Amphibians and Reptiles* (1st. ed.), Harvard Univ. Press, Cambridge, pp. 1-125.

---------- 1943. A Check list of North American amphibians and reptiles (5th ed.), *Bull. Mus. Comp. Zool.*, 93(1): 1-260.

STRECKER, J. K. 1908. Reptiles and batrachians of McLennan County, Texas. *Proc. Biol. Soc. Wash.*, 21: 69-85.

---------- 1915. Reptiles and amphibians of Texas. *Baylor Bull.*, 18(4): 1-82.

STRECKER, J. K. and W. J. WILLIAMS 1927. Herpetological records from the vicinity of San Marcos, Texas, with distributional data on the amphibians and reptiles of the Edwards Plateau region and central Texas. *Contrib. Baylor Univ. Mus.*, No. 12: 1-16.

STUART, L. C. 1930. An extension of the range of *Coluber constrictor mormon* (Baird and Girard). Copeia, 1930 (2): 44.

---------- 1934. Studies on neotropical Colubrinae. IV. An apparently new species of *Coluber* from Guatemala. *Occ. Papers Mus. Zool. Univ. Mich.*, No. 284: 1-4.

TÅNING, A. V. 1952. Experimental study of meristic characters in fishes. *Biol. Rev.*, 27: 169-193.

TAYLOR, E. H. 1935. Arkansas amphibians and reptiles in the Kansas University Museum. *Univ. Kans. Sci. Bull.*, 22(10): 207-218.

TRAPIDO, H. 1944. The snakes of the genus *Storeria*. *Amer. Midl. Nat.*, 31(1): 1-84.

YARROW, H. C. and H. W. HENSHAW 1878. Report upon the reptiles and batrachians collected by the expedition of 1875, 1876, 1877 in California, Arizona and Nevada. *Ann. Rept. Chief Eng., Surv. West 100th. Merid.*, App. L. of App. NN., Washington, pp. 1-233.