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**SYSTEMATIC AND ECOLOGICAL RELATIONSHIPS  
OF THE WATER SNAKES *NATRIX SIPEDON*  
AND *N. FASCIATA* IN ALABAMA AND  
THE FLORIDA PANHANDLE**

By

TERRY D. SCHWANER<sup>1</sup> AND ROBERT H. MOUNT<sup>2</sup>

Recent studies on the systematics of the North American water snakes of the *Natrix sipedon-fasciata* complex have led to conflicting interpretations. Conant (1963:4) concluded that the *Natrix sipedon-fasciata* complex consists of two polytypic species, *N. sipedon* with three subspecies (*sipedon*, *insularum*, and *pleuralis*) and *N. fasciata* with six subspecies (*fasciata*, *clarki*, *compressicauda*, *confluens*, *pictiventris*, and *taeniata*). An additional subspecies, *N. sipedon williamengelsi*, was described recently (Conant and Lazell, 1973). The present study was undertaken to develop a further understanding of the relationships within the group, concentrating on populations in Alabama and the Florida Panhandle. Since Conant's works are the most recent concerning taxonomy of the group and have been generally accepted, his nomenclatural arrangement will be followed herein. Epithets, when used alone, refer to subspecies, except for *fasciata*, which refers to the species (*sensu* Conant). *N. f. fasciata* refers to the subspecies.

Conant (1963) based his division of the complex into two species on a study of *sipedon*, *pleuralis*, and *fasciata* in North Carolina and

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South Carolina, and on evidence of sympatric occurrence of populations of *pleuralis* and *fasciata* in other areas. He believed the intermediates that he found and those that other workers have reported are the result of hybridization between two species rather than intergradation between subspecies. He further stated that interbreed-

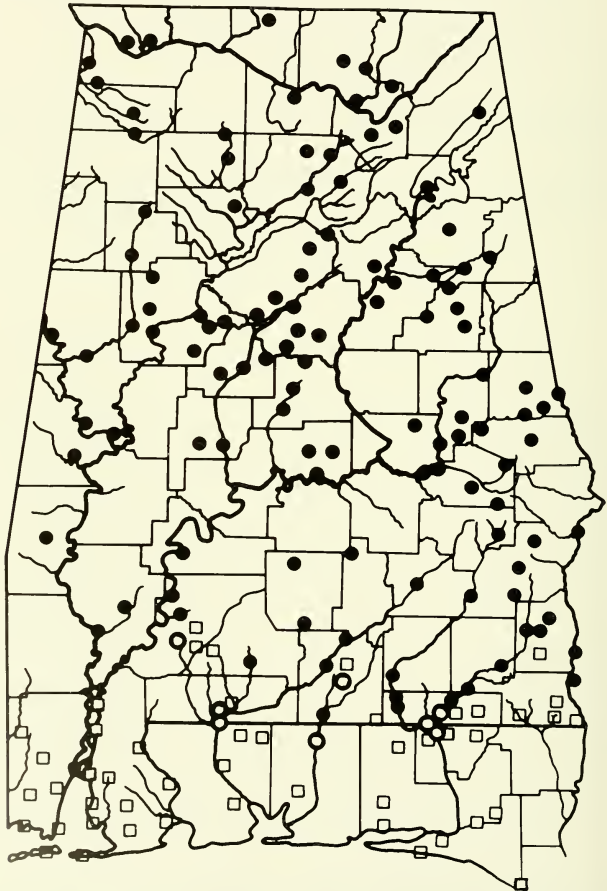


FIG. 1.—Localities from which snakes of the *Natrix sipedon-fasciata* complex were examined. Squares = *fasciata*; solid circles = *pleuralis*; hollow circles = localities from which *fasciata*, *pleuralis*, and intermediates were found.

ing between the two forms has produced hybrid swarms of sporadic occurrence in habitat that has been drastically altered by man along a narrow zone of sympatry (the Fall Line). He maintained that in relatively undisturbed areas the two forms are reproductively isolated from each other due to differences in habitat preference, and that interbreeding would not occur were it not for man's intervention. Conant and Lazell (1973:8) noted the occurrence of "hybrids" between *williamengelsi* and *fasciata*, and suggested that habitat disturbance due to hurricanes could have been responsible for the breakdown of reproductive barriers.

It has been reported that the range of *pleuralis* overlaps that of *confluens* throughout part of the Mississippi River Valley (Rhoads, 1895:376; Parker, 1939:84-85; Woodman, 1959:19). Clay (1936:218) could find no specimens intermediate between the two forms, but postulated that they do occur. Woodman (1959:19) stated that there was no evidence of intergradation between *pleuralis* and *confluens* in the highlands of Arkansas, although both were collected in the same river on the same day; however, only two specimens, one of each, were taken from the river. Smith (1961:261) suggested *confluens* influence in occasional specimens of *pleuralis* from southern Illinois. He noted that no specimens had been examined which were not clearly referable to either *pleuralis* or *confluens*. Anderson (1965:151) noted that the two forms appear to be ecologically separated in Missouri. Barbour (1971:300) stated that *confluens* was found only in extreme southwestern Kentucky and that it preferred large shallow bodies of water. He noted that *pleuralis* occurs in southwestern Kentucky, but prefers flowing water. Webb (1970:265, 271) indicated an overlap in the ranges of *pleuralis* and *confluens* in Oklahoma. Gordon (1952:117) reported *pleuralis* in the same drainage with *confluens* and *N. f. fasciata*. Neill (1946:256, 1954:85) also found *pleuralis* within the range of *N. f. fasciata* in Alabama, the Florida Panhandle, and Georgia. Neither of these workers found intermediates between the forms in question. Gordon suggested that future studies might "reveal distinct habitat differences which permit overlapping of the range."

In contrast, Viosca (1924:10) examined numerous intermediates between *Natrix sipedon* and *N. fasciata* from areas of North Carolina and South Carolina. Barbour (1943) named *Natrix sipedon engelsi* from one specimen from coastal North Carolina. That specimen and additional ones similar to it were considered by Robertson and Tyson (1950:142) to be intermediate between *sipedon* and *fasciata* in most characters. Cliburn (1957:198) synonymized *N. s. engelsi* with *N. f. fasciata*, finding the holotype closest to the latter subspecies. He noted considerable variation among *N. f. fasciata* in South Carolina and stated that this area was the "blend zone of northern and southern races" (Cliburn, 1957:198). (In his doctoral

dissertation Cliburn (1960:157) referred to the "blend zone of *fasciata* and (*N.*) *s. sipedon*" as coastal North Carolina. We believe the designation by Cliburn (1957) of the blend zone being "South Carolina" was a *lapsus*, since no other reference at that time or since indicated the presence of *N. s. sipedon* in South Carolina.)

Conant (1961:19) followed Cliburn's synonymy of *engelsi* with *N. f. fasciata*. However, Conant and Lazell (1973) named *Natrix sipedon williamengelsi* from the Outer Banks of North Carolina, indicating that the name *engelsi* was applied to a snake of the wrong species. They also reported "hybrids" between *williamengelsi* and *N. f. fasciata* in several areas of North Carolina. Smith's photograph (1961:260, Fig. 242) of "an adult *Natrix sipedon pleuralis*" from

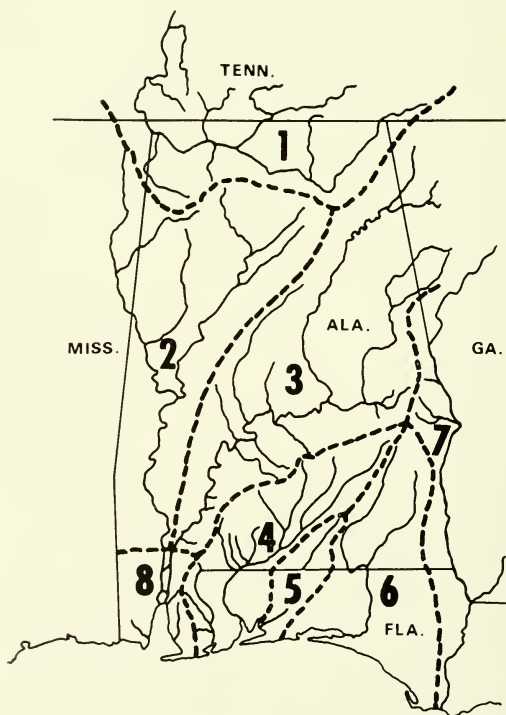


FIG. 2.—Drainages of the study area. (1) Tennessee R. (2) Warrior-Tombigbee R. (3) Alabama-Coosa-Tallapoosa R. (4) Escambia-Conecuh R. (5) Yellow R. (6) Choctawhatchee-Pea R. (7) Chattahoochee R. (8) Mobile Bay drainage.



Illinois very closely resembles, in dorsal pattern, one Alabama snake reported herein (see Fig. 21), intermediate between *pleuralis* and *fasciata*.

Conant (1963) collected snakes belonging to the *Natrix sipedon-fasciata* complex in the Carolinas and grouped them by overall color pattern, but did not attempt to determine the pattern of geographic variation in greater detail than that exhibited from above and below

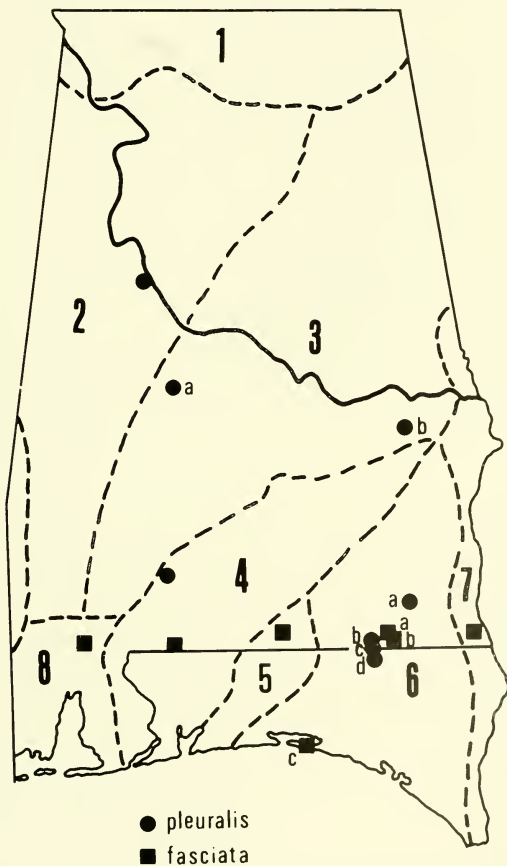


FIG. 3.—Localities for female snakes of the *Natrix sipedon-fasciata* complex from which broods were obtained. Broken lines indicate study area drainages in Fig. 2.

the Fall Line in these states. Attempts to analyze geographic variation within the *N. sipedon-fasciata* complex have been inconclusive due to small sample size (Boyles, 1952; Clay, 1936; Cliburn, 1957, 1960).

A detailed study of the systematic and ecological relationships between *pleuralis* and *fasciata* has never been attempted in Alabama. Boyles (1952) conducted a survey of Alabama *Natrix* and considered several DeKalb Co. specimens to be typical *pleuralis*. He found only a slight indication of *sipedon* influence in other *pleuralis* populations in northern Alabama. On the basis of one specimen from Chattahoochee State Park in Houston Co., Boyles (also Cliburn, 1957:196) reported genetic influence of *pictiventris*, a subspecies previously unreported from Alabama, in the southeastern part of the state. Subsequent studies of the relationship between *Natrix sipedon* and *N. fasciata* have been of a general nature and not specifically concerned with the situation in Alabama and the Florida Panhandle.

A preliminary examination of Alabama specimens of *Natrix sipedon* deposited in the Auburn University Museum revealed several intermediate individuals similar to those described by Conant (1963) as "hybrids" between *pleuralis* and *fasciata*. Some of these specimens, however, were from natural streams and other relatively undisturbed habitats. In addition, variation in many characters in these Alabama snakes indicated a complex relationship involving not only *pleuralis* and *N. f. fasciata*, but *pictiventris* and *confluens* as well.

#### ACKNOWLEDGMENTS

For loan of material we are indebted to the following institutions and their respective curators: Howard College (HC); Jacksonville State University (JSU); University of Alabama Herpetological Collection (UAHC); University of Michigan Museum of Zoology (UMMZ); private collection of Mr. Rhett Barnes (RB). Auburn University Museum specimen numbers are prefixed by the designation AUM. Specimens examined are listed in the appendix.

Others who contributed their time and effort to this study are R. M. Blaney, J. T. Collins, H. B. Cunningham, D. E. Davis, J. L. Dobie, J. L. Dusi, D. Dwyer, II, S. R. Edwards, R. E. Estridge, G. W. Folkerts, H. Harima, R. Jordan, Jr., R. Kirkland, and A. H. Savitzky. Lila Schwaner typed the final manuscript.

#### METHODS

More than 1000 snakes of the *Natrix sipedon-fasciata* complex were examined by the authors. Most specimens are from Alabama and the Florida Panhandle west of the Apalachicola R., here called

the study area (Fig. 1). Several specimens from peninsular Florida, Georgia, Illinois, Kentucky, Louisiana, Mississippi, North Carolina, South Carolina, and Tennessee were examined for comparative purposes. Statistical treatment was limited to specimens from the study area except for one series each from Wayne and Lincoln counties, Tennessee, which were included in the statistical analyses with the Alabama specimens from the Tennessee R. drainage.

Emphasis was placed on collecting specimens from the Lower

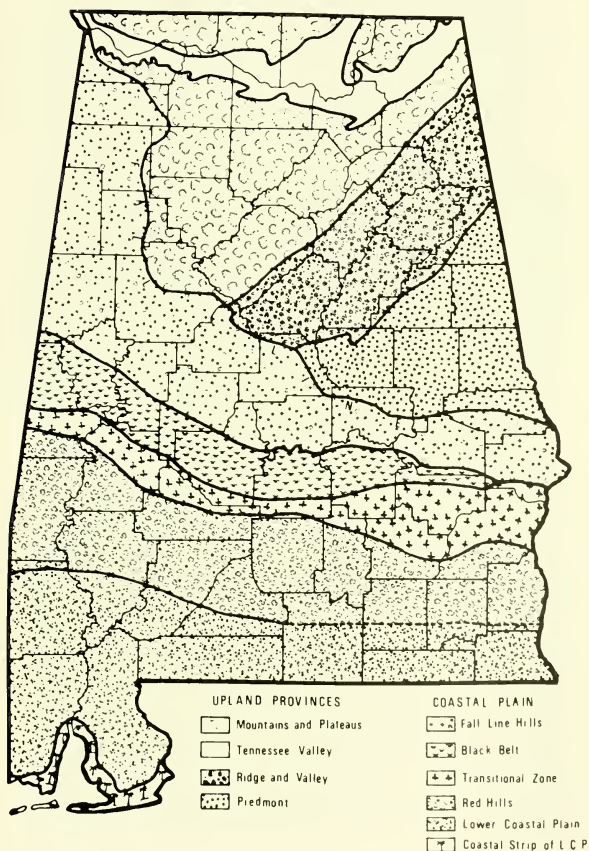


FIG. 4.—Physiographic provinces of Alabama.

Coastal Plain region of the study area, and efforts were made to collect specimens from streams as well as from ponds and lakes.

For presentation of data the study area was divided into the following stream drainage systems (Fig. 2): (1) Tennessee R. (2) Warrior-Tombigbee R. (3) Alabama-Coosa-Tallapoosa R. (4) Conecuh-Escambia R. (5) Yellow R. (6) Choctawhatchee-Pea R. (7) Chattahoochee R. (8) Mobile Bay area. Specimens from each drainage were sorted on the basis of color pattern as *pleuralis*, *fasciata*, or intermediates between the two.

Ventral scales were counted by the method of Dowling (1951: 98). Subcaudal scales were counted in pairs. Post-temporals were counted on both sides of the head. Dorsal scale rows were counted at the neck region, at midbody, and near the tail. At the neck region the row was counted diagonally backward from the level of the 5th

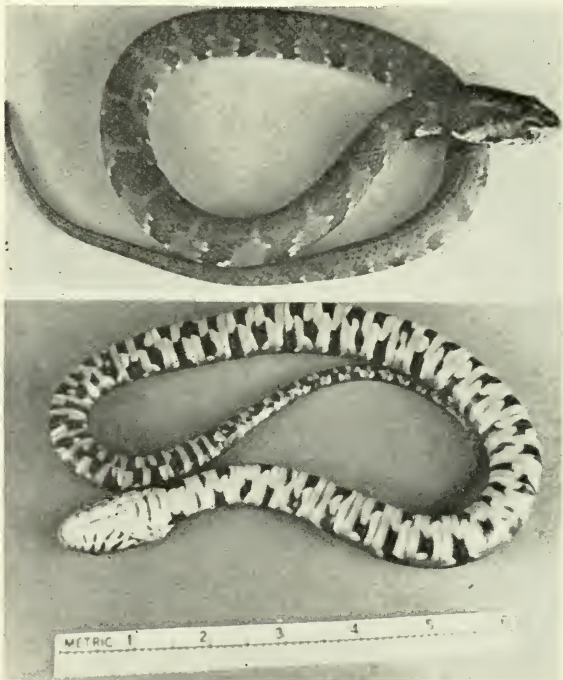


FIG. 5.—Dorsal and ventral aspects of an example of the patterned phase of *Natrix fasciata* from the study area (AUM 13458).

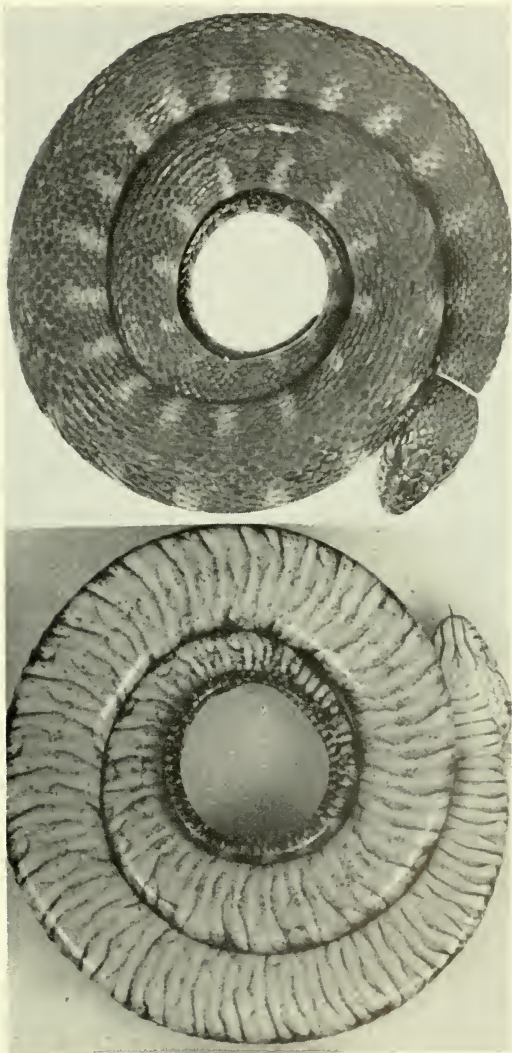


FIG. 6.—Dorsal and ventral aspects of an example of the melanistic phase of *Natrix fasciata fasciata*  $\times$  *pictiventris* from the study area (AUM 10337).

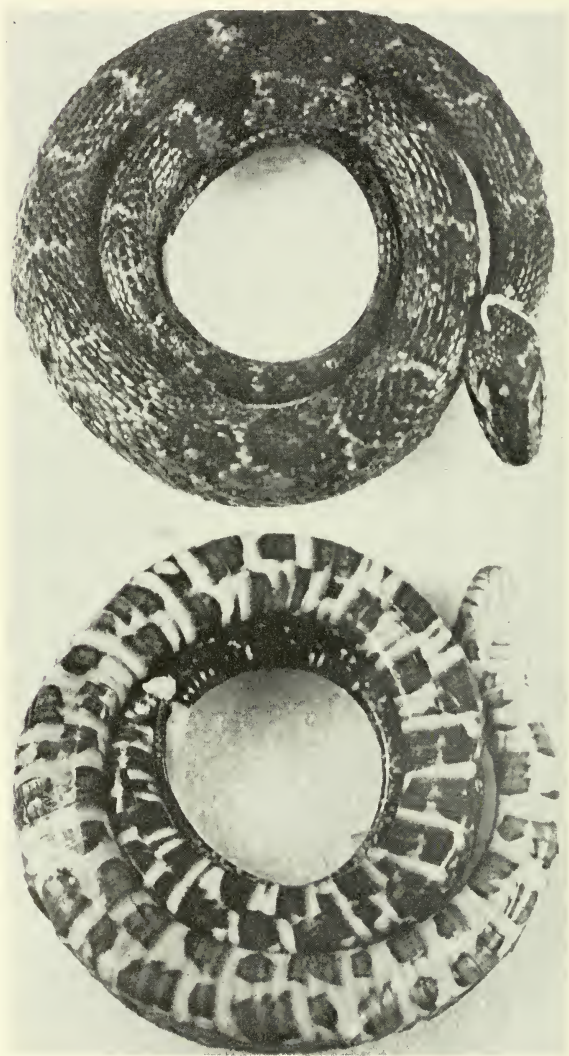


FIG. 7.—Dorsal and ventral aspects of an example of *Natrix fasciata fasciata* × *confluens* from Mobile Co., Alabama (AUM 2893).

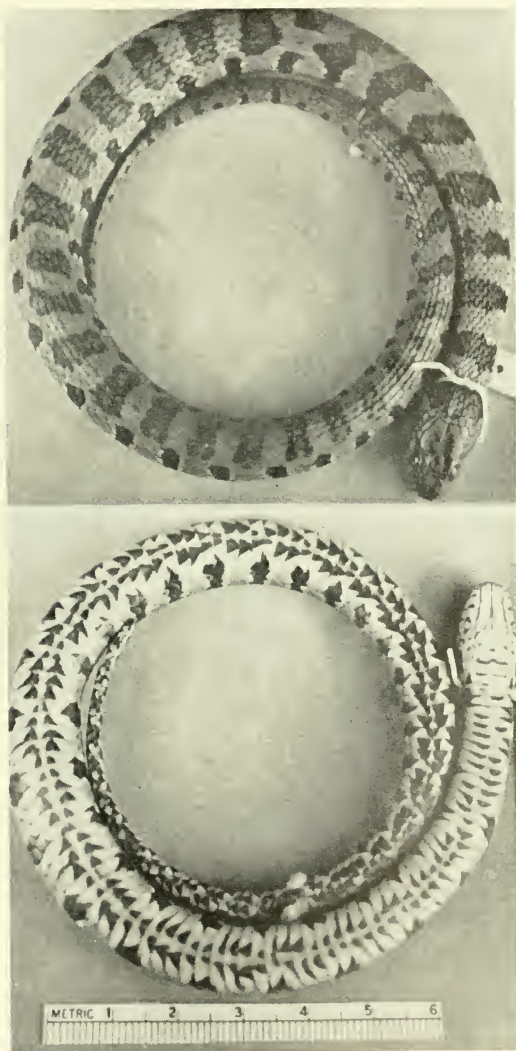


FIG. 8.—Dorsal and ventral aspects of an example of *Natrix sipedon pleuralis* from the study area (AUM 12680).

ventral scale. Midbody scale counts were counted diagonally backward from approximately midway between the head and vent. Posterior scale rows were counted diagonally forward from the level of the 5th ventral scale anterior to the vent. Upper labials, lower labials, preoculars, postoculars, and supraoculars were also counted on both sides of the head.

The ratio of tail length to total length was determined for preserved specimens having a complete tail and no bodily disfiguration. Body length was measured from the tip of the snout to the posterior margin of the anal scale. Tail length was measured from the posterior margin of the vent to the tip of the tail.

Counts were made for the total number of complete body bands, dorsal spots, or combination thereof, in the manner of Conant (1963:9). Melanism is common in some taxa of the *N. sipedon-fasciata* complex, and many specimens lacked discernible dorsal markings as a result of melanism. For this reason counts of lateral markings were also made from the rear of the head to the vent, inclusive. Counts were made for both left and right sides of the body and, if different, were averaged. The lateral bars extend onto the ventral plates. Cliburn (1957:195) noted that this extension of the dark lateral markings onto the venter involved varying numbers of ventral scales. In the specimens examined in the study area the average number of belly scutes touched or covered by these extensions ranged from one to approximately three and one half and the quantitative expression of this character on each snake was indicated accordingly for each drainage. Boyles' (1952:36) indication that pigmentation of the upper labials in *pleuralis* might be a valid character for separating it from *fasciata* was also examined for snakes in the study area.

Several characters were analyzed using a modification of the "hybrid index" of Anderson (1949). These characters were (1) dorsal pattern (2) ventral pattern (3) relative prominence of the postocular stripe (4) head shape (5) extent of light spotting along the edges of the lateral bands and (6) extent of serration of the lateral band edges. For each character each snake was given a numerical value ranging from 0 to 5. Zero indicated that the character was typically associated with *pleuralis*; 5 indicated typical *fasciata*. The numbers 1 through 4 were assigned to those snakes visually determined to reflect degrees of intermediacy. Values for each character were analyzed by drainages and presented graphically as means and ranges.

Several gravid female *Natrix* were collected from the study area (Fig. 3) and were maintained alive. Neonates produced by them were preserved, and data from the neonates were analyzed separately for most of the characters previously mentioned. The brood



was designated *pleuralis* or *fasciata* on the basis of the female's phenotype.

#### COLOR DESCRIPTIONS

Clay (1936:143) distinguished *N. f. fasciata* from *pleuralis* by its quadrate belly markings, completely banded dorsum, serrated edges of the bands, and dark postocular stripe. The characteristic markings of *pleuralis* include a belly pattern of paired half-moons on each ventral scale, forming two more-or-less parallel columns of semi-circles; a dorsal pattern of complete anterior bands with alternating dorsal and lateral blotches posteriorly; smooth edges on bands and blotches. There is no dark postocular stripe except in populations near the range of *fasciata*.

Coloration of *Natrix sipedon pleuralis* is similar to *sipedon*, except that in the latter the lateral bands are wider than the interspaces between them, the ventral pattern is less distinct, often appearing mottled, and the average number of complete anterior bands is lower than for *pleuralis* (Clay, 1936:126-127).

Ventral markings of *Natrix fasciata confluens*, as distinguished from *N. f. fasciata*, tend to form squarish blotches involving more than one scale, as opposed to smaller blotches in the latter, and by having fewer complete body bands than any other North American *Natrix* (Clay 1936:157, 159). *N. f. confluens* is reported to intergrade with *N. f. fasciata* in southern Mississippi (Cliburn 1957:201).

*Natrix fasciata pictiventris* is distinguished from *N. f. fasciata* chiefly by ventral pattern, which in *pictiventris* consists of dark, wavy, transverse lines at the anterior edge of each ventral scale, as opposed to quadrate markings in *N. f. fasciata* (Clay 1936:171). *N. f. pictiventris* is reported to intergrade with *N. f. fasciata* in the Florida Panhandle (Carr 1940:85), southeastern Georgia (Neill 1946:256), southeastern Alabama (Boyles 1952:45), and possibly in South Carolina (Conant 1963:10).

Boyles (1952:35-36) noted that the dark ground color of the head in specimens of *pleuralis* from above the Fall Line covered at least the first three upper labials on both sides of the head. He indicated that *pleuralis* from the Coastal Plain had yellowish pigment on all upper labials, similar in this respect to *fasciata*. He interpreted this as evidence of possible intergradation between *pleuralis* and *fasciata* in Alabama. Boyles emphasized, however, that his sample of snakes from below the Fall Line was small, and that his interpretation might not be correct.

#### RESULTS

##### ECOLOGICAL CONSIDERATIONS OF THE STUDY AREA

In North Carolina, South Carolina, and Georgia, the Fall Line

marks the approximate separation between the ranges of *Natrix fasciata* and *N. sipedon* (Neill, 1946:256; Conant, 1963:3). In these states the Coastal Plain is mostly flat to gently rolling with either sandy or loamy soil. Rock outcroppings are relatively scarce.

In Alabama, much of the Coastal Plain habitat is similar to some of that above the Fall Line (Fig. 4). The Fall Line Hills region, or Upper Coastal Plain, of Alabama is moderately hilly, and clay soils predominate in many areas. The Black Belt and Red Hills regions, and the transitional zone between these two, are characterized by predominantly heavy soils and rolling to hilly topography. The Red Hills region is especially hilly and includes the most deeply dissected terrain within the entire Coastal Plain Province. Many of its formations are rocky.

East of the Conecuh River, the Red Hills Province is less deeply dissected, but hilly terrain is still evident to the Chattahoochee River area. Topographically, the difference between the habitats of the Lower Coastal Plain and those of the Red Hills is roughly comparable to that between the Coastal Plain and the Piedmont in Georgia and South Carolina.

The headwaters of some Coastal Plain streams in Alabama have stretches of riffles and rapids. The bottoms of the stream beds are composed more of rock and gravel than of silt and sand. The streams are often narrow, with steep banks. Streambank vegetation is dominated by hardwood species.

As the streams flow out of the Red Hills Province and onto the Lower Coastal Plain, they tend to widen and become sluggish. Bottoms become increasingly sandy. Banks become more sloping and less densely wooded. Bald cypress (*Taxodium distichum*) increases in frequency along the banks. Floodplain occurs along some stretches. The Choctawhatchee, Pea, Yellow, and Conecuh-Escambia Rivers, among other Alabama streams, exhibit this transition.

Artificial farm ponds are fairly numerous in portions of the Red Hills region. Most have well-defined margins and are relatively deep. Low vegetation is usually confined to a narrow zone along the edges of these ponds. All of the artificial ponds visited during this study were created either by damming a small watercourse or by routing a spring into an impounded depression.

The Lower Coastal Plain within the study area has fewer artificial ponds. However, there are a number of natural, dish-shaped depressions, most of which are "lime sinks," in low-lying areas. These ponds are relatively shallow and have abundant emergent vegetation. In some years many of these ponds dry up in summer or fall.

#### GEOGRAPHIC VARIATION

Little sexual dimorphism is found in either *pleuralis* or *fasciata* from the study area. Males of both forms generally have a few

more subcaudal scales and have relatively longer tails than females (Table 1). The broods of both forms showed slightly higher mean values and narrower ranges for both characters than collected indi-

TABLE 1.—SEXUAL DIMORPHISM IN SUBCAUDAL COUNT AND TAIL LENGTH RATIO IN INDIVIDUALS AND BROODS OF *pleuralis* AND *fasciata* FROM THE STUDY AREA.

	Range	Adults Mean	n	Range	Broods Mean	n
<b>Subcaudals</b>						
<i>pleuralis</i>						
Males .....	51-85	75.0	125	70-88	78.0	74
Females .....	42-81	65.0	212	55-80	67.0	70
<i>fasciata</i>						
Males .....	51-88	75.8	28	68-86	80.0	72
Females .....	52-86	70.0	38	62-77	71.0	82
<b>Tail/Total Length</b>						
<i>pleuralis</i>						
Males .....	.23-.37	.27	73	.26-.30	.28	69
Females .....	.18-.28	.24	128	.23-.29	.26	63
<i>fasciata</i>						
Males .....	.24-.30	.27	17	.26-.31	.28	71
Females .....	.20-.28	.25	30	.23-.28	.26	74

viduals. Females of both forms averaged slightly higher ventral scale counts than males (see Figs. 33 and 34).

Variation among the members of the *Natrix sipedon-fasciata* complex in the study area occurs in (1) dorsal pattern, (2) ventral pattern, (3) head pattern, (4) head shape, (5) relative tail length and (6) scutellation of head, tail, and body.

*Dorsal pattern.*—Conant (1963) mentioned finding two color phases in *fasciata* populations from North Carolina and South Carolina, a melanistic phase and a red or yellow phase in which the dark pigment was absent. Specimens tentatively identified as *fasciata* from the study area also exhibited two color phases, a patterned phase in which dorsal and lateral markings were visible (Fig. 5) and a distinct melanistic phase, shown by some adults, in which only lateral markings were visible (Fig. 6). Some of the older individuals of the patterned phase were very dark, especially those from Drainage 8; submerging these individuals in fluid (Conant 1963:9) revealed traces of bands that could be counted. On the other hand, individuals of the melanistic phase were uniformly black except for pink or red bars on the sides. Immersing these specimens in liquid did not reveal any additional pattern.

Among the specimens examined, the melanistic pattern seems to accompany aging, in agreement with Conant's (1963:8) findings. Three gravid *fasciata* from southeastern Alabama, and one from Dougherty Co., Georgia, all with melanistic patterns, gave birth in

captivity, and all neonates had banded patterns. A careful examination of the melanistic individuals, especially a consideration of belly patterns in relation to lateral markings, shows that the light red or pink bars on the sides of old individuals are homologous to the lateral portion of the dark black or brown bands on the young. A determination of the size at which the pattern begins to change and the proportion of individuals showing such pattern reversal awaits additional specimens of intermediate size.

Within the study area, the melanistic phase seems restricted to individuals from extreme southern Alabama and the Florida Panhandle westward into Covington Co., Alabama, and Santa Rosa Co., Florida. It appears to be characteristic of most adults from southeastern Alabama and the eastern portion of the Florida Panhandle, and characterizes many specimens from southern Georgia, southern South Carolina, and peninsular Florida.

The dorsal color of some *pleuralis* and a few *fasciata* from the study area is unusually light, with dark reddish brown markings on a lighter tan or pink ground color. The dorsal blotches of such *pleuralis* appear transversely divided, their centers and lateral edges being approximately the same hue as adjacent ground color. In *fasciata* of this light type, the coloration is simply of reddish brown bands on a lighter, pinkish background; occasionally the middorsal portions of the bands may be indistinct, imparting a unicolor appearance to the dorsum. Such specimens constitute a "rufescent phase," which evidently is not derived with age. Thirty percent of neonates in *pleuralis*-like broods from Drainage 6 had this pattern and a few were found in the *fasciata* brood from Drainage 5. Specimens of *pleuralis* displaying this color pattern were found only in the southern half of Alabama.

Some specimens of *fasciata* from southwestern Alabama show influence of *confluens* in their dorsal patterns (Fig. 7). The body bands are wider dorsally and fewer in number than in populations of *fasciata* to the east, and the anteriormost bands are diagonal. The extension of the lateral bands onto the venter involves more than one ventral scale in many of these specimens. Many specimens from near the Gulf Coast are very dark.

Although *pleuralis* from within the study area are usually patterned anteriorly with complete transverse bands and posteriorly with alternating dorsal and lateral blotches (Fig. 8), a number of specimens were completely banded throughout, as in *fasciata*. This is not a "rare" occurrence in *pleuralis* as was stated by Conant (1963:9). Boyles (1952:33) found the completely banded condition in 10% of the *pleuralis* he examined. However, he did not clearly indicate whether he considered these specimens to be intergrades. Completely banded *pleuralis* in the present study often came from localities far removed from *fasciata* populations, occurring most

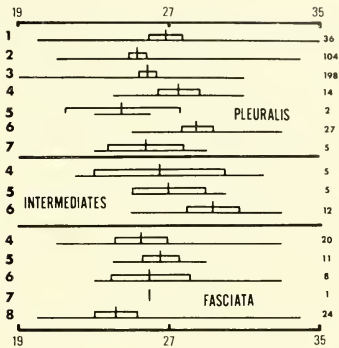


FIG. 9.—Variation in number of dorsal bands, blotches, or combination thereof, in individuals of the *Natrix sipedon-fasciata* complex from the study area. Numbers at top and bottom = total range for the character; numbers at left = drainages (see Fig. 2); numbers at right = sample size. Horizontal lines of Dice diagrams = ranges; vertical lines = means; rectangular boxes = two standard errors on either side of mean.

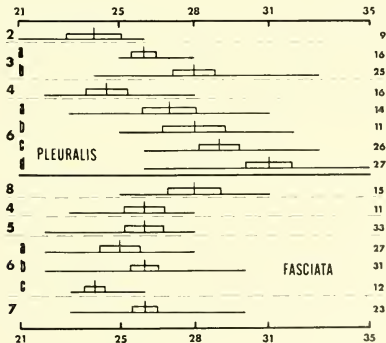


FIG. 10.—Variation in number of dorsal bands, blotches, or combination thereof, in broods of the *Natrix sipedon-fasciata* complex from females collected from the study area. Numbers at left refer to brood localities in Fig. 3. Refer to Fig. 9 for further explanation of symbols.

frequently in Tuscaloosa, Marshall, Madison, and Bibb counties. Clay (1936) indicated this condition sometimes occurred within the range of *pleuralis*. Although complete bandedness is characteristic of *fasciata* (except in the salt marsh subspecies), Cliburn (1957:193) stated that the presence of this trait in *pleuralis*-like individuals did

not indicate interbreeding with *fasciata* unless it was simultaneously linked with characteristics of the ventral pattern that also resembled *fasciata*. Our observations agree with Cliburn's.

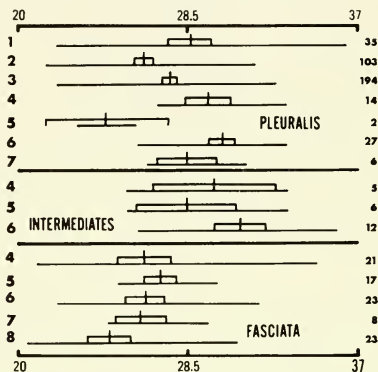


FIG. 11.—Variation in average number of lateral markings in individuals of the *Natrix sipedon-fasciata* complex from the study area. Refer to Fig. 9 for explanation of symbols.

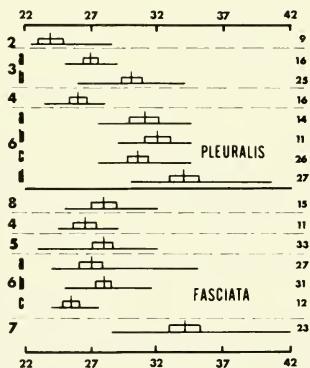


FIG. 12.—Variation in average number of lateral markings in broods of the *Natrix sipedon-fasciata* complex in females from the study area. Refer to Figs. 3 and 9 for explanation of symbols.

Woodman (1959:17, Table 2) showed that the number of complete anterior bands in *pleuralis* populations increases from Arkansas to Louisiana and Mississippi. The mean number for 24 Mississippi specimens was 16. She believed this increase indicated intergrada-

tion between *pleuralis* and *fasciata* populations in the southeast. For 397 *pleuralis* from throughout the study area, however, the mean number of anterior bands was only 10, and there appeared to be no geographic variation in the character.

Clay (1936:97) stated that the northernmost subspecies, *Natrix sipedon sipedon*, averages more than 30 dorsal markings and *pleuralis* less than 30. *Natrix fasciata confluens*, whose range lies generally to the west and southwest of *pleuralis*, has the lowest number of dorsal markings (10 to 20) and *pictiventris*, to the southeast, has the greatest average number of any member of the *N. sipedon-fasciata* complex, 32 to 34. Geographic variation in the number of dorsal and lateral markings in snakes from the study area is somewhat confusing (Figs. 9-12). In *pleuralis* the averages for lateral markings in the west and southwest are generally low ( $\bar{x} = 25$  for Drainage 2); in eastern and southeastern Alabama the averages are generally high ( $\bar{x} = 31$  for Drainage 6). *Natrix fasciata* populations in southern Alabama, however, remain more or less constant from west to east in the number of bands exhibited.

The edges of the dark bands in *pleuralis* are typically smooth, as are the edges of the posterior blotches. In *fasciata* the edges of the bands are typically serrated, because the band color tends to follow the outlines of individual scales rather than bisecting them as in *pleuralis*. Although in most of its range *pleuralis* has smooth-edged bands, many specimens from Drainage 6, including many

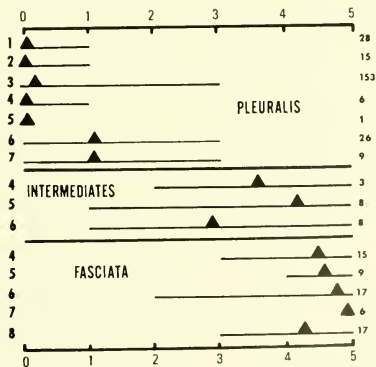


FIG. 13.—Variation in degree of serration of the edges of lateral markings of individuals of the *Natrix sipedon-fasciata* complex from the study area. Numbers at left refer to drainage areas (see Fig. 2); numbers at right = sample sizes. Numbers at top and bottom are character scores used in the hybrid index (see text). Horizontal lines indicate ranges and apices of triangles indicate means for the character.

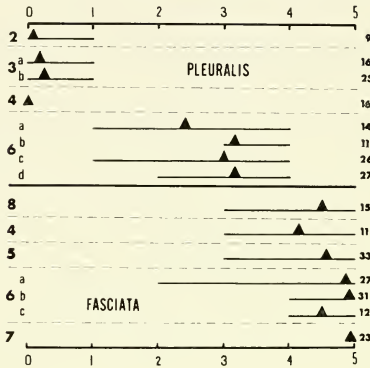


FIG. 14.—Variation in degree of serration of the edges of the lateral markings of broods of the *Natrix sipedon-fasciata* complex from females from the study area. Refer to Figs. 3 and 13 for explanation of symbols.

within the broods from females taken there, have bands of varying degree of serration (Figs. 13 and 14).

Light spotting along the edges of the lateral markings, often involving entire scales, is characteristic of *pictiventris*. Conant (1963:10) indicated that light spotting becomes more frequent in *fasciata* populations from North Carolina southward toward the range of *pictiventris* in Florida, and that the trend may be clinal. Broods of *fasciata* from Drainages 5 and 6 strongly show this character, as do broods of *pleuralis* from Drainage 6 (Fig. 16). A slight intensification in the expression of this character was noted in adult *pleuralis* in the southeast portion of the study area (Fig. 15).

*Ventral pattern.*—The ventral pattern of *fasciata* from the study area ranges from bold, rectangular markings confluent with the lateral bands of the dorsum to vermicular markings at the anterior edge of each ventral scale. The ground color ranges from yellow to white. Typically, the quadrate markings involve only one ventral scale; however, in populations from Drainage 8 they often involve from two to four ventral scales. Eastward across Alabama and the Florida Panhandle there is a gradual though definite change from quadrate spots to the irregular transverse lines typical of *pictiventris*.

Considerable individual variation occurs in the ventral pattern of most populations of *pleuralis* in the study area, but there are some notable geographic trends. In north and central Alabama the paired columns of semicircular spots are usually indistinct, either absent from the anterior ventrals or fused posteriorly. The dorsal ground color encroaches on the lateral edges of the ventral scutes in the



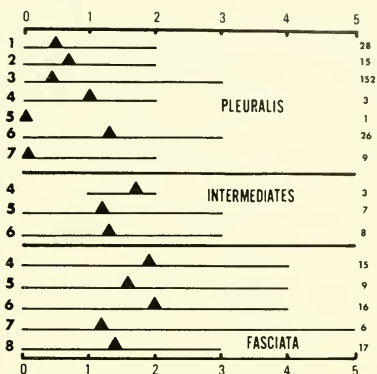


FIG. 15.—Variation in the amount of light spotting of the lateral markings of individuals of the *Natrix sipedon-fasciata* complex from the study area. Refer to Fig. 13 for explanation of symbols.

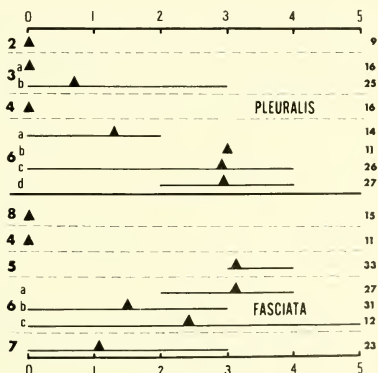


FIG. 16.—Variation in the amount of light spotting of the lateral markings in broods of the *Natrix sipedon-fasciata* complex in females from the study area. Refer to Figs. 3 and 13 for explanation of symbols.

form of a fine stippling. In many individuals the half moons are replaced by the stippling almost to the mid-ventral line. The venters of some snakes, especially those from Macon County, have fine, reddish stippling along the medial portion of the belly, and no other maculations. In general appearance some of these ventral patterns approach those characteristic of the northern form, *sipedon*. How-

ever, none of the specimens examined have lateral bars wider than the lateral interspaces. In a few specimens from northeastern Alabama, the dark bands and light interspaces are of equal width, but in none of these do the ventral pattern (or other features of pattern)

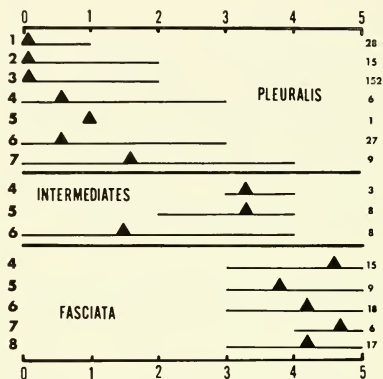


FIG. 17.—Variation in the ventral pattern of individuals of the *Natrix sipedon-fasciata* complex from the study area. Refer to Fig. 13 for explanation of symbols.

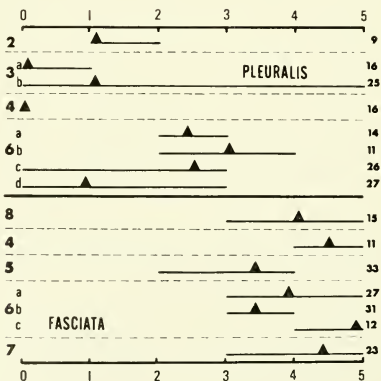


FIG. 18.—Variation in the ventral pattern of broods from females of the *Natrix sipedon-fasciata* complex from the study area. Refer to Figs. 3 and 13 for explanation of symbols.

differ noticeably from typical *pleuralis* in other parts of the study area.

Many *pleuralis* from southern Alabama exhibit bold patterns of paired half moons against an otherwise immaculate yellow or white background. Others, especially from the southeastern portion, have half moons that are either fused medially to form a single column of spots, or elongated and connected at midventer to form irregular, transverse lines at the anterior edges of the ventral scales. Character scores of ventral patterns of *pleuralis* and *fasciata* from the study area show that *pleuralis* populations increase in range and mean toward those of *fasciata* populations in the Lower Coastal Plain stream drainages (Fig. 17). Intermediacy relative to the two is particularly evident in broods from Drainages 4 and 6 (Fig. 18).

The brood of a female from the Choctawhatchee R. near the Alabama-Florida boundary identified as *pleuralis* with a somewhat obscure ventral pattern (Fig. 19) included individuals having dorsal, ventral, and head patterns of both *fasciata* and *pleuralis*, and others with various combinations of these patterns (Fig. 20). The ventral patterns on many consisted of transverse wavy lines.

A gravid female from Drainage 4, resembling *fasciata* in most respects but with suggestions of *pleuralis* influence in the color pattern (Fig. 21), gave birth to a brood whose dorsal, ventral, and head patterns are clearly intermediate between *fasciata* and *pleuralis* (Fig. 22). Ventral markings consist of rectangles confluent with the lateral bands, paired semicircles or trapezoids in the center of each ventral scale, or various combinations thereof.

The number of ventral scales involved in each lateral band extension in *pleuralis* decreases clinally from northern to southern Alabama, and approaches the condition exhibited by *fasciata* (Fig. 23); analysis in broods (Fig. 24) seems to indicate genetic influence of *fasciata*.

*Head pattern and shape.*—In *pleuralis* the incidence of a dark postocular stripe, and its relative prominence in the snakes possessing it, generally increase from north to south (Fig. 25). This is also true of *pleuralis* broods from the study area (Fig. 26). A dark postocular stripe is characteristic of *fasciata* (Conant 1963:8).

The yellowish coloration on the first three upper labials, as well as on the remainder, was equally apparent in *pleuralis* from above and below the Fall Line. There appears to be no evidence that this character can separate *pleuralis* and *fasciata* in the study area, as suggested by Boyles (1952).

Conant (1963:11) stated that in *fasciata* “. . . the plane of the side of the head anterior to the eyes, meets the dorsal surface at a perceptible angle, . . .” producing a distinct canthus rostralis. He noted that in *pleuralis* this angle is not so sharp, imparting a rounded

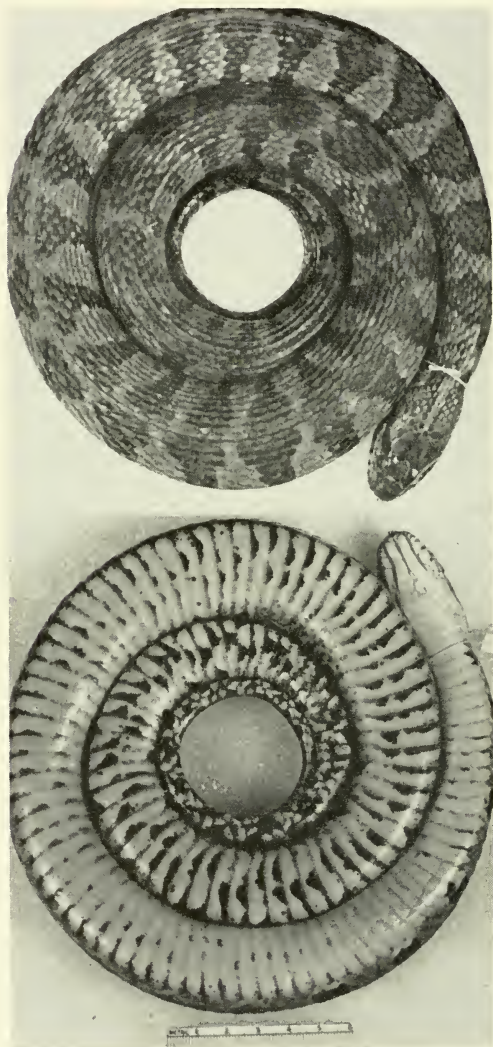


FIG. 19.—Dorsal and ventral aspects of the ♀ parent (AUM 10738) of a brood (AUM 10739-66) from Geneva Co., Alabama, intermediate between *Natrix sipedon pleuralis* and *Natrix fasciata fasciata* × *pictiventris*.

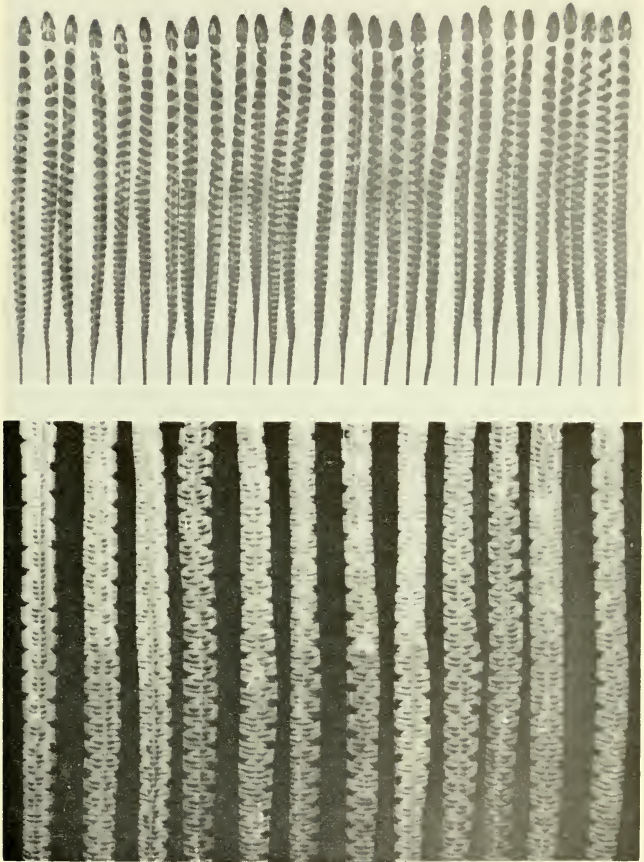


FIG. 20.—Dorsal and ventral aspects of a brood (AUM 10739-66) from Geneva Co., Alabama.

appearance to the snout and head. We concur with Conant's interpretation to the extent that the angular head is usually associated with specimens having the *fasciata* color pattern. However, in many of our specimens referable to *pleuralis* on the basis of color pattern, the head shape is that which Conant ascribed to *fasciata*. Such snakes become increasingly frequent in areas supporting *fasciata*

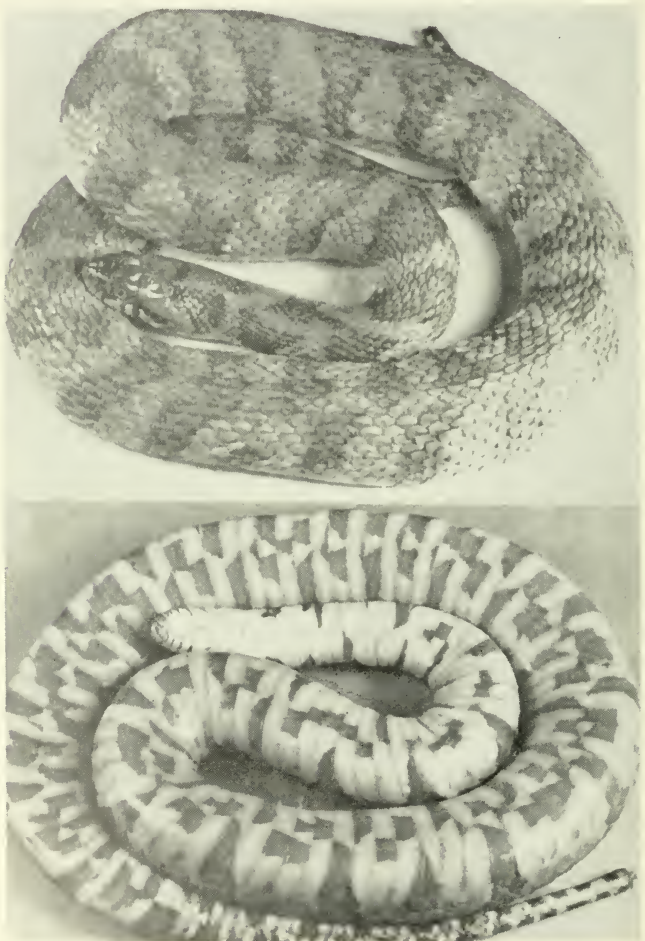


FIG. 21.—Dorsal and ventral aspects of the ♀ parent (AUM 12857) of a brood (AUM 13420–57) from Escambia Co., Alabama, intermediate between *Natrix sipedon pleuralis* and *Natrix fasciata fasciata*.

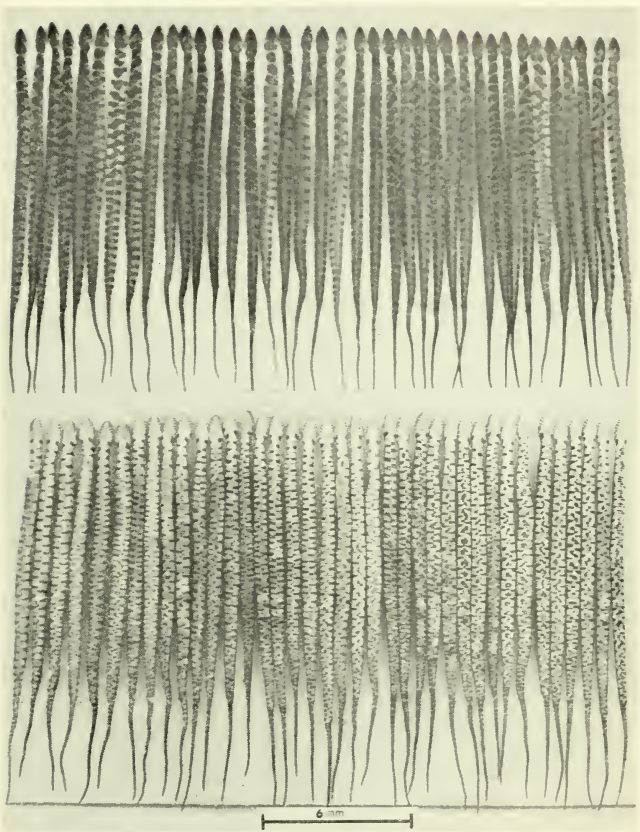


FIG. 22.—Dorsal and ventral aspects of a brood (AUM 13420-57) from Escambia Co., Alabama.

populations (Fig. 27). Some individuals in broods of *pleuralis* from Drainage 6 also exhibit a sharp canthus rostralis (Fig. 28).

*Scutellation and relative tail length.*—In most aspects of head scutellation, variation was insignificant. Conant (1963:14) indicated a difference in the number of posterior temporal scales between *pleuralis* and *fasciata* from North Carolina and South Carolina.

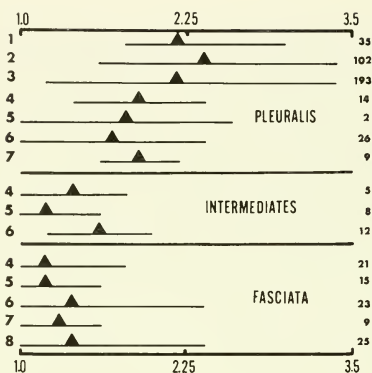


FIG. 23.—Variation in number of ventral scales touched by the lateral band extensions in individuals of the *Natrix sipedon-fasciata* complex from the study area. Numbers at top and bottom indicate number of scales; numbers to left = drainage areas (Fig. 2); numbers at right = sample size. Horizontal lines = ranges; apices of triangles = means.

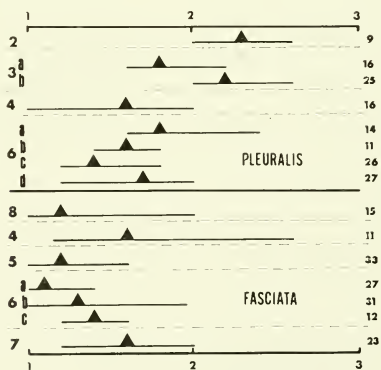


FIG. 24.—Variation in number of ventral scales touched by the lateral band extensions in broods of the *Natrix sipedon-fasciata* complex from females from the study area. Numbers at left refer to brood localities in Fig. 3. Refer to Fig. 23 for explanation of symbols.



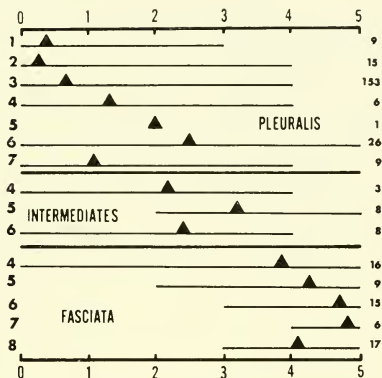


FIG. 25.—Variation in the incidence and relative prominence of the dark postocular stripe in individuals of the *Natrix sipedon-fasciata* complex from the study area. Refer to Fig. 13 for explanation of symbols.

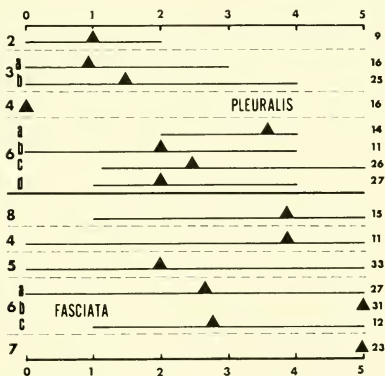


FIG. 26.—Variation in the incidence and relative prominence of the dark postocular stripe in broods of the *Natrix sipedon-fasciata* complex in females from the study area. Refer to Figs. 3 and 13 for explanation of symbols.

Variation in this character in snakes from the study area is modest, and there is little geographic variation in either form. Apparently there is a difference in the mean number of posterior temporal scales between *pleuralis* and *fasciata*; however, when analyzed by stream drainages the character is too variable to separate populations in the study area.

Variation in anterior and midbody scale rows for adult indi-

viduals and broods is likewise modest. Evidently, a relationship similar to that exhibited by posterior temporals exists for dorsal scale row counts in *pleuralis* and *fasciata* in the study area.

Specimens of *pleuralis*, *fasciata*, and their apparent intermediates from the drainages of the study area show little geographic variation in either subcaudal count or relative tail length (Figs. 29 and 30). However, broods of both *fasciata* and *pleuralis* from the southern drainages, especially those of Drainage 6, show greater sexual dimorphism than adults of either form (Figs. 31 and 32). This could be due to allometric growth; however, Clay (1936:133) indicated that populations of both forms from southern areas exhibited greater sexual dimorphism in these two characters than those from more northerly areas, apparently because in the south the number of subcaudals increases in males only. Cliburn (1960:144) disagreed with Clay on the geographic significance of caudal sexual dimorphism in *Natrix*; he indicated, however, that the greatest sexual difference in these two characters in any form within the *N. sipedon-fasciata* complex occurs in *pictiventris* (Cliburn 1960:148-149; Cliburn 1957:196).

Sexual dimorphism was also present in ventral scale counts. Females had slightly higher average counts than males in most drainages in the study area. Mean ventral scale counts within the *N. sipedon-fasciata* complex tend to vary clinally, with individuals in the northern portion of the range having the greatest numbers (Clay 1936:108, 132, 161). Conant (1963:15) found a significant difference in the number of ventral scales between *pleuralis* and *fasciata*

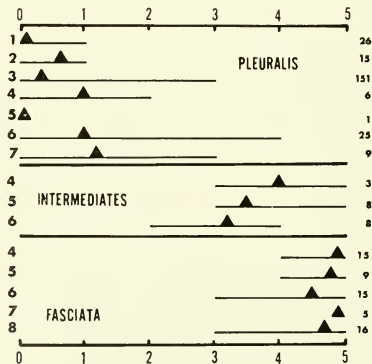


FIG. 27.—Variation in head shape of individuals of the *Natrix sipedon-fasciata* complex from the study area. Refer to Fig. 13 for explanation of symbols.

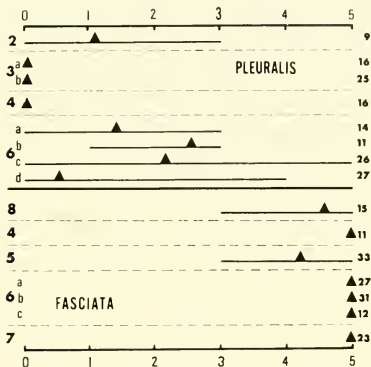


FIG. 28.—Variation in head shape of broods of the *Natrix sipedon-fasciata* complex from females from the study area. Refer to Figs. 3 and 13 for explanation of symbols.

in North Carolina and South Carolina. The “hybrids” between the two had intermediate counts. A similar relationship among *pleuralis*, *fasciata*, and the color pattern intermediates was found in the study area. In *pleuralis* (sexes combined) ventral count ranged from 120 to 150 ( $\bar{x} = 131.2$ ,  $n = 395$ ); in *fasciata*, 120 to 134 ( $\bar{x} = 127.0$ ,  $n = 99$ ); and in the color pattern intermediates, 125 to 132 ( $\bar{x} = 128.7$ ,  $n = 33$ ).

When variation in this character is examined by drainages the relationship proves to be more complex (Fig. 33). In *pleuralis*, the highest mean counts are in Drainages 1 and 2. Those from Drainages 4–7 possess ventral counts similar to those designated as intermediates, and have counts not appreciably higher than those in most *fasciata* from all drainages. For *pleuralis*, the means from Drainage 3 lie between those of Drainages 1 and 2, collectively, and those of Drainages 4–7. Specimens of *fasciata* from Drainage 5 average lower counts than those of *fasciata* from other areas. The data on broods show roughly the same pattern of variation (Fig. 34). The ranges for this character for many specimens of *pleuralis* and *fasciata* from the southeastern portion of the study area are small and are well within those previously reported for *pictiventris* (Clay 1936:178; Cliburn 1960:146).

#### DISCUSSION

The pattern of phenetic geographic variation in snakes of the *Natrix sipedon-fasciata* complex in the study area is complex and involves genetic interchange between at least 4 described taxa (Fig. 35). *Natrix sipedon pleuralis* is the most widespread form in the

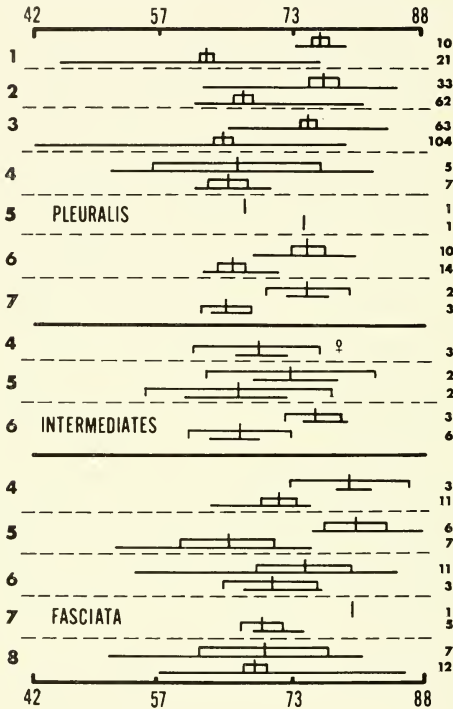


FIG. 29.—Variation in subcaudal counts in individuals of the *Natrix sipedon-fasciata* complex from the study area. Top Dice diagrams for each area are for males, bottom diagrams for females. Refer to Fig. 9 for further explanation of symbols.

study area. It occurs in abundance in both streams and impoundments northward from the boundary between the Red Hills and Lower Coastal Plain provinces. In the Tennessee R. and upper Tombigbee-Warrior R. drainages, the high ventral counts suggest genetic influence of *N. sipedon sipedon*, as does the tendency for the lateral band widths to equal widths of lateral interspaces. In other characters there is little indication of such influence, and we do not consider these populations intergradient.

In the Lower Coastal Plain, populations of unadulterated *pleuralis* are scarce. Individuals referable to that form are found in some of the major streams and their tributaries and in some ponds that lie close to large streams. Other individuals from such locali-

ties, however, show some influence of *fasciata*, and still others are more similar to *fasciata* than to *pleuralis*. Specifically, snakes with apparent *pleuralis* influence were found in the Lower Coastal Plain at the following places within the study area: Chattahoochee R. to Columbia, Houston Co., Alabama (the southernmost locality on this river from which specimens were examined); several localities on the Choctawhatchee R. south to approximately 3 mi. S Alabama-Florida boundary; two localities on the Yellow R., the southernmost 5 mi. S Alabama-Florida boundary; Shoal R. at U.S. Hwy. 90, Okaloosa Co., Florida; several localities in the Conecuh-Escambia R. south to the level of Flomaton, Escambia Co., Alabama; Buck Pond, Conecuh National Forest, a lime sink pond located less than a mile from Pond Ck., a tributary to the Yellow R., Covington Co., Alabama; Vanity Fair Lake, Monroeville, a small impoundment created around 1960 by damming a tributary to Big Escambia Ck., Monroe Co., Alabama; and Martin's Catfish Ponds at Keego, Escambia Co., Alabama. The Keego locality is about one mile from the Conecuh R.

Individuals of *fasciata* with no apparent *pleuralis* influence were found in ponds and small streams within the Lower Coastal Plain and in all the major streams of this province except the Chattahoochee R. In Alabama, populations in the Lower Coastal Plain as far east as the eastern boundary of the Mobile Bay drainage (see Fig. 35) show influence of *confluens*. This influence is manifested in populations away from the coast in the tendency of ventral extensions of lateral bands to involve more than one, and usually between 2 and 4, ventral scales. Populations near the coast show *confluens* influence not only in ventral markings but also in a tendency for reduction in number of body bands. The ventral pattern of *fasciata* is strongly influenced by *confluens* in southwestern Alabama. *Natrix fasciata clarki* occurs along the coast within the study area, but apparently has little influence on populations except in the immediate vicinity of coastal marshes.

The distinctive melanistic phase of *fasciata*, described above, was first recognized by Loennburg (1894:331), who proposed assigning a trinomial (*Natrix fasciata atra*) to snakes with this pattern. Conant (1963:4) explained that *atra* was preoccupied by *Natrix atra*, which was subsequently referred to another genus (*Alsophis*). Loennburg's *atra* has since been assumed to be a color variant of Cope's (1895:677) *Natrix fasciata pictiventris* (Clay 1936:170; Conant 1963:4). Moreover, no author has ever assigned any geographic significance to these melanistic snakes. Wilfred T. Neill (personal communication) believes the melanistic phase to be typical of *fasciata* from the Apalachicola region of Florida. Our data indicate the phase is characteristic of most *fasciata* in southeastern Alabama, adjacent areas of the Florida Panhandle, and

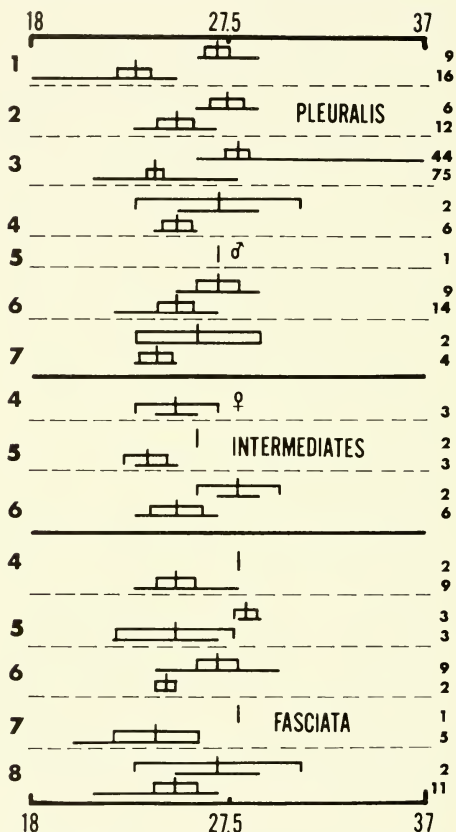


FIG. 30.—Variation in relative tail length of individuals of the *Natrix sipedon-fasciata* complex from the study area. Top Dice diagrams for each area are for males, bottom diagrams for females. Refer to Fig. 9 for further explanation of symbols.

southwestern Georgia. Since these snakes usually have ventral patterns that are vermicular or *pictiventris*-like, we also consider them to be color variants of *pictiventris*, but note that there may be geographic significance in the occurrences of the phase.

Boyles (1952) and Cliburn (1957) reported *pictiventris* influence in populations from Houston Co., in southeastern Alabama. We detected *pictiventris* influence in the form of vermicular mark-

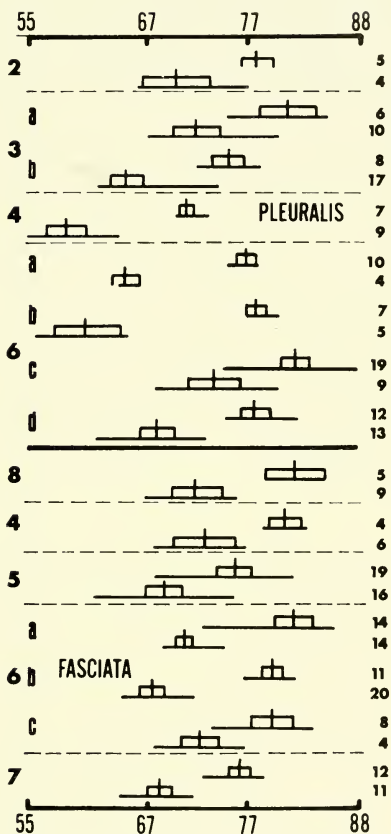


FIG. 31.—Variation in subcaudal count in broods of the *Natrix sipedon-fasciata* complex from females from the study area. Top Dice diagrams for each area are for males, bottom diagrams for females. Refer to Figs. 3 and 9 for further explanation of symbols.

ings on the venter and in the occurrence of melanism in populations as far west as Monroe Co. and Escambia Co., Alabama, and Santa Rosa Co., Florida, points that lie near the easternmost extent of *confluens* influence. There is some question, then, whether typical *N. f. fasciata* occurs in Alabama. Nearly all the populations sampled

show influence of at least one of the three forms, *pictiventris*, *confluens*, or *pleuralis*. Cliburn (1957:196) questioned the taxonomic validity of the form *N. f. fasciata*. He contended that the holotype of *N. f. fasciata* was collected from a zone of intergradation and noted extensive variation in topotypic material. Thus, it is with considerable reservation that we recognize occurrence of *N. f. fasciata* in Alabama.

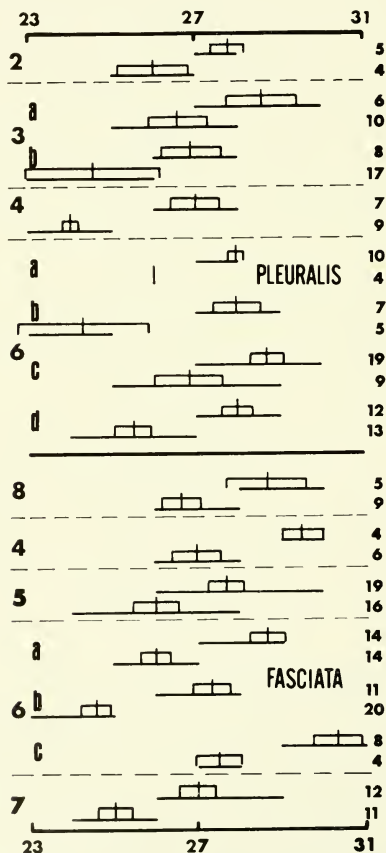


FIG. 32.—Variation in relative tail length in broods of the *Natrix sipedon-fasciata* complex from females from the study area. Top Dice diagrams for each area are for males, bottom diagrams for females. Refer to Figs. 3 and 9 for further explanation of symbols.



The nature of gene exchange between *Natrix sipedon* and *N. fasciata* is, according to Conant (1963:15), one of sporadic inter-specific hybridization or possibly "allopatric hybridization." Allopatric hybridization, as defined by Mayr (1969:397) is "hybridization between two allopatric populations (species or subspecies) along a well defined contact zone." Conant implies that if allopatric hybridization occurs between *N. sipedon* and *N. fasciata* it has resulted from human interference in recent years. In that case nominal forms should be treated as full species (Mayr 1969:194).

In the area involved in the present study, the situation appears different. "Sporadic hybridization" is certainly not the case. We were unable to find any place where *pleuralis* and *fasciata* occurred together without the presence of intermediate individuals. The situation in Drainage 6 where many specimens of *pleuralis*-like, *fasciata*-like, and intermediate snakes were taken, is exemplary. Many, if not most, of the *pleuralis*-like snakes from the Lower Coastal Plain segments of the Choctawhatchee and Pea rivers, showed some influence of *fasciata*. The brood from a *pleuralis*-like snake (AUM 10738) from the Choctawhatchee R. near Geneva, Alabama, was obviously of mixed parentage. Within this brood almost any combination of *pleuralis* and *fasciata* characteristics could be detected. The sex ratio in this brood was approximately 1:1, and there were no apparent deformities among the siblings or in any intermediate snake examined during this study.

Serration of the lateral bands, light spotting on the edges of the lateral markings, the relative prominence of a postocular stripe, and head shape in *pleuralis*-like specimens from the study area suggest influence of *fasciata*. And, ventral scale counts, number of ventral scutes touched by the extension of the lateral bands, and the noticeable sexual dimorphism in *pleuralis*-like snakes from Drainage 6 indicate *fasciata* influence. Trends in the number of dorsal markings in *pleuralis* from the study area suggest influence of *confluens* from the west and of *pictiventris* from the southeast. The *fasciata* populations in southern Alabama, however, remain more-or-less constant in this character from west to east.

Conversely, a *fasciata* from the Choctawhatchee R. near Geneva, Alabama, showed no perceptible influence of *pleuralis*. Two typical *fasciata* were collected in East Pittman Ck. near its junction with the Choctawhatchee R. approximately 3 mi. below the Alabama-Florida boundary, Holmes Co., Florida. Ponds within Drainage 6 support either *fasciata* or *pleuralis*, but we were unable to find the two together, or obvious intermediates between them, in any of these ponds. When hybrid indices for snakes from Drainage 6 were plotted, regardless of habitat, a bimodal distribution was obtained (Fig. 36A). However, indices for snakes collected from the river habitats in Drainage 6 showed a unimodal distribution (Fig. 36B).

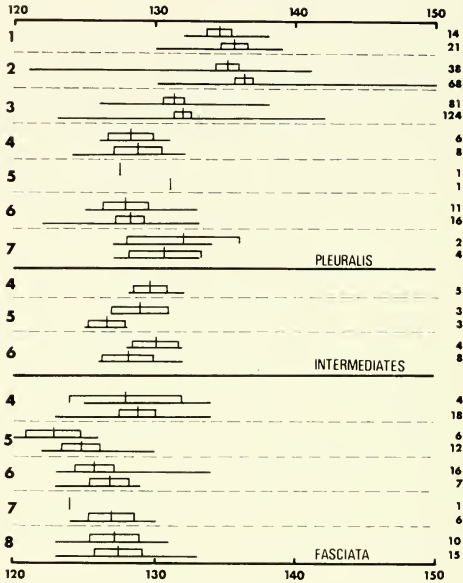


FIG. 33.—Variation in ventral scale number in individuals of the *Natrix sipedon-fasciata* complex from the study area. Top Dice diagrams for each area are for males, bottom diagrams for females. Refer to Fig. 9 for further explanation of symbols.

The relationship between *fasciata* and *pleuralis* within the Lower Coastal Plain thus appears to be one of an abundant lowland form, *Natrix fasciata*, interbreeding with *N. sipedon pleuralis*. *Natrix fasciata* maintains its specific integrity in most landlocked ponds and in the lower reaches of the large rivers. It interbreeds with *N. s. pleuralis* in the major streams, or most portions thereof, in the lowermost reaches of their tributaries, and in some ponds readily accessible from these streams.

Ecological preference for streams conceivably exists for *Natrix sipedon pleuralis*-like individuals in lowland situations. *Natrix fasciata*, however, moves readily overland from one aquatic habitat to another. Holman and Hill (1961:499) reported mass overland migration of *pictiventris* in Alachua Co., Florida, apparently in response to drought. There is nothing to suggest that *fasciata* does not thrive in streams; however, ecological studies on possible competition between *pleuralis* and *fasciata* are needed. We suggest that the apparent scarcity of "good" *fasciata* in large streams within the

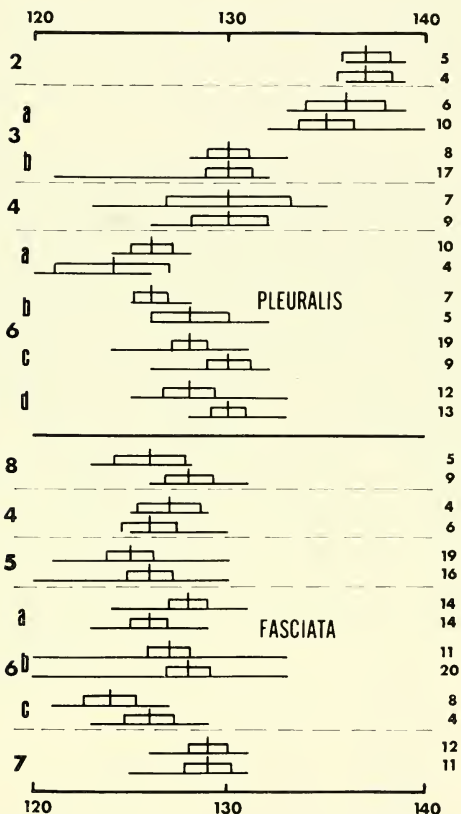


FIG. 34.—Variation in ventral scale number in broods of the *Natrix sipedon-fasciata* complex from females from the study area. Top Dice diagrams are for males, bottom diagrams for females. Refer to Figs. 3 and 9 for further explanation of symbols.

Lower Coastal Plain of the study area is due to the swamping effect of gene flow from *pleuralis* coming down these streams. These conditions prevailed long before man's influence.

The relationship between *Natrix sipedon* and *N. fasciata* in the study area appears, in our opinion, to be one of secondary intergradation, involving a "strong steepening of character gradients where two separately differentiated populations have reestablished

contact" (Mayr 1969:411). Smith (1969:255) argues that this type of relationship constitutes parapatry, a term "restricted in application to those geographically juxtaposed taxa which have not achieved genetic independence one of the other, and thus in effect is limited to subspecies." Gilbert (1961:182) has established 11 criteria to be used in determining whether a given case of inter-

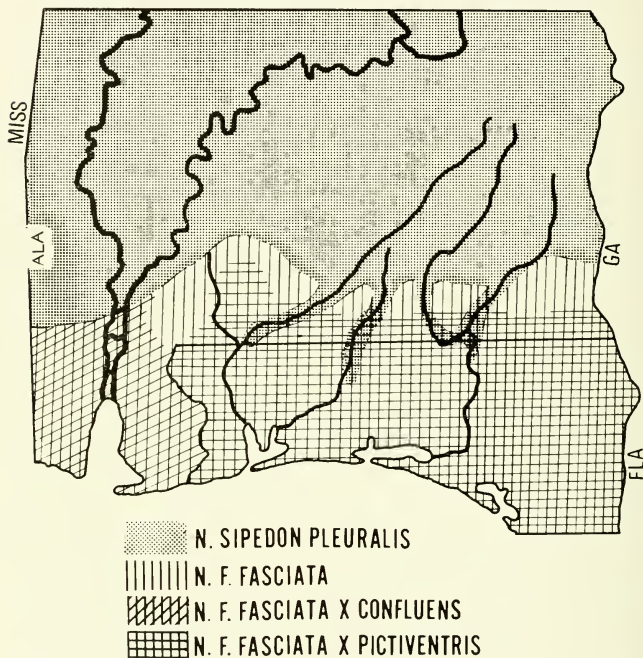


FIG. 35.—Distributional relationship of snakes of the *Natrix sipedon-fasciata* complex in the study area.

breeding involves interspecific hybridization or intersubspecific intergradation. Applying his criteria to characteristics of the *pleuralis-fasciata* relationship in the study area, the first seven indicate intergradation, the last one indicates hybridization, and the remaining three were inapplicable to our data.

#### CONCLUSIONS

*Natrix fasciata* ssp. and *N. sipedon pleuralis* interbreed extensively, although irregularly, in the Lower Coastal Plain of Alabama

and in the Florida Panhandle. Interbreeding occurs in the large streams rising north of the Lower Coastal Plain and in lakes, ponds, and oxbows in the immediate vicinity of these streams. The nature of the relationship between these snakes in the study area more closely resembles secondary intergradation between subspecies than interspecific hybridization. Analyses of stream populations in other critical areas, such as along the Fall Line in Georgia and South Carolina, are needed to determine if similar relationships between the two exist elsewhere.

Influence from *pictiventris* is evident from the Apalachicola-Chattahoochee R. drainage westward nearly to the Mobile Bay area, where *confluens* influence from the west becomes detectable. *N. f. fasciata* is recognized with reservation as predominating in many populations in the south central portion of the study area.

The melanistic phase of *Natrix fasciata*, as described herein, is found westward to the limit of the area influenced by *pictiventris*, and appears to have arisen within that form.

Finally, we think the present study has provided as much argument against the specific status of *fasciata* as has been proposed for its specific status by Conant (1963). However, knowledge of the relationship between the two forms throughout their ranges is not furthered by a change in taxonomic status at this time. We agree with Carr and Crenshaw (1957) that "when a trinomial is used, if it means anything at all, it means that a situation has been pretty well worked out, is understood, and is nothing to worry about." This is certainly not the case for snakes of the *Natrix sipedon-fasciata* complex, and we intend to address the still perplexing relationship between *N. sipedon* and *N. fasciata* in future studies.

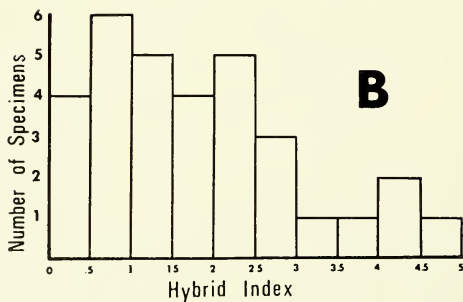
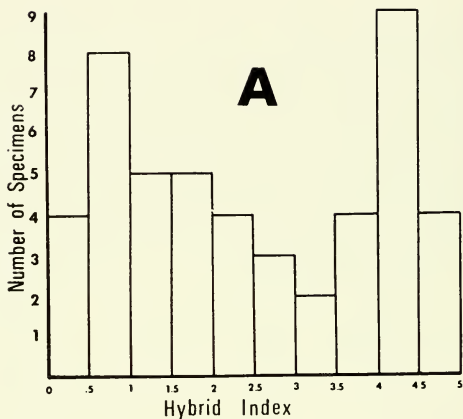


FIG. 36.—Hybrid indices (including scores for degree of serration of lateral markings, light spotting of lateral markings, ventral pattern, relative prominence of postocular stripe, head shape) for snakes of the *Natrix sipedon-fasciata* complex from (A) both pond and stream habitats, and (B) only stream habitats, in Drainage 6.

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## APPENDIX

## SPECIMENS EXAMINED

ALABAMA: Autauga Co., 6; Baldwin Co., 38; Barbour Co., 9; Bibb Co., 11; Blount Co., 5; Butler Co., 4; Bullock Co., 1; Calhoun Co., 14; Chambers Co., 7; Chilton Co., 6; Choctaw Co., 1; Clarke Co., 3; Clay Co., 10; Cleburne Co., 3; Coffee Co., 1; Colbert Co., 3; Conecuh Co., 3; Covington Co., 57; Crenshaw Co., 1; Cullman Co., 2; Dale Co., 29; DeKalb Co., 2; Elmore Co., 65; Etowah Co., 2; Fayette Co., 12; Franklin Co., 1; Geneva Co., 131; Green Co., 7; Henry Co., 5; Houston Co., 6; Jackson Co., 1; Jefferson Co., 11; Lawrence Co., 2; Lauderdale Co., 5; Lee Co., 54; Limestone Co., 1; Lowndes Co., 1; Macon Co., 36; Madison Co., 9; Marion Co., 7; Marshall Co., 3; Mobile Co., 20; Monroe Co., 21; Montgomery Co., 1; Morgan Co., 1; Perry Co., 21; Pickens Co., 3; Pike Co., 3; Russell Co., 3; Shelby Co., 30; St. Clair Co., 1; Sumter Co., 1; Talladega Co., 8; Tallapoosa Co., 6; Tuscaloosa Co., 48; Walker Co., 4; Wilcox Co., 2.

FLORIDA: Alachua Co., 11; Bay Co., 1; Brevard Co., 3; Dade Co., 6; Escambia Co., 1; Holmes Co., 8; Jackson Co., 1; Levy Co., 1; Liberty Co., 1; Marion Co., 8; Okloosa Co., 3; Orange Co., 3; Palm Beach Co., 1; Santa Rosa Co., 5; Walton Co., 15; Washington Co., 3.

GEORGIA: Charlton Co., 1; Clinch Co., 1; Decatur Co., 1; Dougherty Co., 35; Georgetown Co., 1; Mitchell Co., 1; Screven Co., 3.

ILLINOIS: Jackson Co., 1; Sangamon Co., 1.

LOUISIANA: Tangipahoa Parish, 1; St. Tammany Parish, 1.

MISSISSIPPI: Green Co., 1; Marion Co., 3; Hancock Co., 6.

NORTH CAROLINA: Clay Co., 1; Madison Co., 1.

SOUTH CAROLINA: Georgetown Co., 4.

TENNESSEE: Lincoln Co., 1; Sevier Co., 1; Wayne Co., 8.





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