American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2122 MARCH 8, 1963

Evidence for the Specific Status of the Water Snake *Natrix fasciata*

By Roger Conant[1]

No North American members of the genus *Natrix* have engendered more taxonomic confusion than those of the *Natrix sipedon-fasciata-erythrogaster* group. Widely overlapping ranges, marked similarities in details of scutellation, and an almost bewildering array of pattern and color variations long obscured their true relationships and made identifications difficult. They have been lumped together in various ways. For example, Boulenger (1893, pp. 242–244) listed all of them (and also *rhombifera*) as varieties of his composite species *Tropidonotus fasciatus*. Cope (1900, p. 966 *et seq.*) included them all as varieties of *Natrix fasciata*. Stejneger and Barbour, in their earlier check lists (1917, p. 96; 1923, p. 108; 1933, p. 117), designated *fasciata* as a race of *sipedon* and ignored *erythrogaster* except for a footnote. This footnote reads: "Apparent forms which are more or less uniformly rufescent are found in the ranges of both the subspecies *fasciata* and *sipedon*. To these the names of *Natrix sipedon erythrogaster* . . . have been given." In later editions (1939, p. 126; 1943, pp. 158–159) they accorded *erythrogaster* the status of a full species but retained a footnote (pp. 129 and 161 in the respective lists) referring again to rufescent individuals among the populations of *fasciata* and *sipedon*. By recognizing *erythrogaster* as distinct, they followed Taylor (1929, p. 58) and others whose action in removing this species from the complex was a major step in clarifying part of the confusion. Since then herpetologists have been

[1] Research Associate, Department of Herpetology, the American Museum of Natural History; Curator of Reptiles, Philadelphia Zoological Garden.

virtually unanimous in accepting *erythrogaster* as a full species, but *sipedon* and *fasciata* have remained linked together.

The most recent review of the group is by Clay (1938, pp. 173–182) whose key and synopsis were based in part on evidence he assembled while compiling a doctoral thesis completed in 1936, but which was never published. He listed *erythrogaster* (with subspecies *transversa*) as a full species, but considered all other members of the complex, plus the salt-marsh forms of *clarki* and *compressicauda*, as races of *sipedon*. Thus Clay's classification, which has been generally accepted for more than two decades, recognized no fewer than eight subspecies of *Natrix sipedon*, viz., *clarki*, *compressicauda*, *confluens*, *fasciata*, *insularum*, *pictiventris*, *pleuralis*, and *sipedon*. He included the salt-marsh forms because of the existence of specimens morphologically intermediate between them and certain other members of his *sipedon* group. [Two additions to the complex have been made subsequently. Carr and Goin (1942) resurrected the Cope (1895) name *taeniata* for an isolated Florida east coast population of salt-marsh snakes. Barbour (1943) described *Natrix sipedon engelsi* on the basis of a single specimen from the Shackleford Banks off the coast of North Carolina.]

Clay's conclusions, although based on a thorough and careful study of all material available to him at the time, can now be re-assessed, especially in the light of the many hundreds of specimens that have been collected subsequently. Under his arrangement some of the subspecies, although morphologically distinct, occur together in the same geographical areas, even side by side or under the same log or board in seemingly identical habitats. For example, I have taken *pleuralis* and *confluens* together at Reelfoot Lake in western Tennessee, and *confluens* and *clarki* together in several localities in Louisiana. Similar overlappings, reported by several herpetologists and detailed under the heading Sympatry below, are so numerous that I found it impossible, in the "Field Guide," clearly to delineate the ranges of the various races of *sipedon* on a single map and compromised by using three (Conant, 1958, maps 84, 85, and 87).

In view of the mass of new material that has accumulated, combined with the application of genetic concepts that were not employed by taxonomists during the early 1930's, it seems advisable to re-evaluate and reinterpret the *sipedon* complex. The present paper is concerned primarily with the relationship between *fasciata* and *sipedon*. The status of the salt-marsh forms, *clarki*, *compressicauda*, and *taeniata*, is reserved for a later publication, as are also several other facets of the *sipedon-fasciata* complex.

Although Clay was well aware of the overlapping ranges of several of

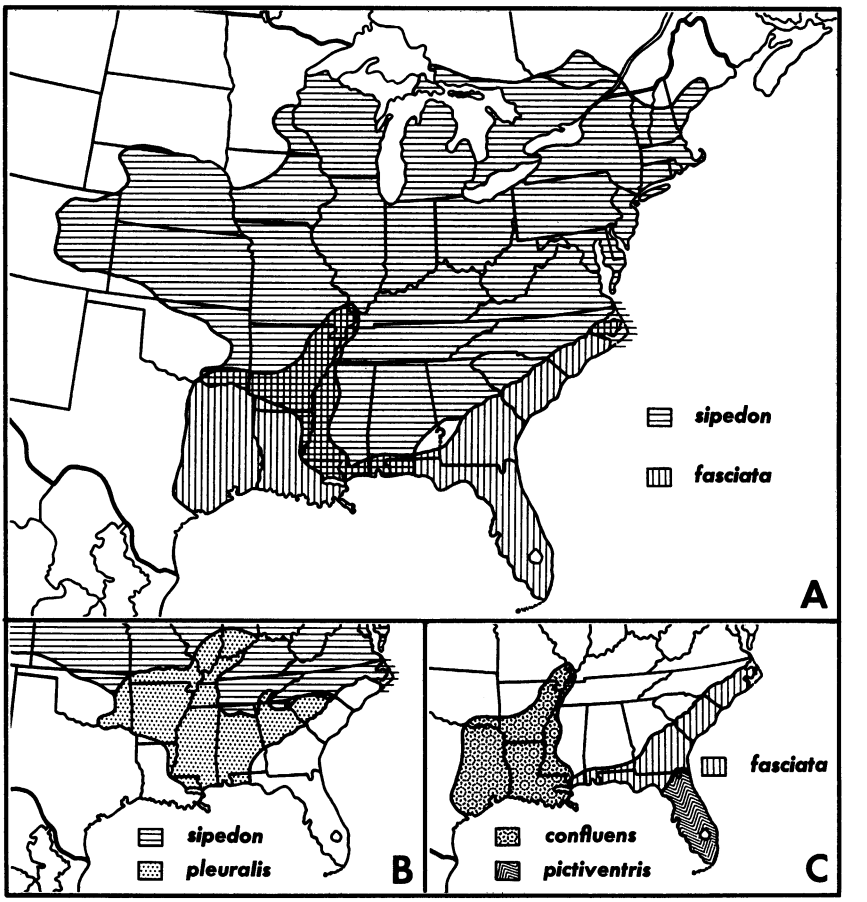


FIG. 1. General distribution of *Natrix sipedon* and *Natrix fasciata*, exclusive of the salt-marsh forms of the Gulf and Florida coasts. A. Ranges of the two species showing areas where sympatry occurs (cross hatching) in the Mississippi Valley, along the Gulf coast, and in northeastern North Carolina. B. Approximate ranges of the subspecies of *Natrix sipedon* in the southeastern states. C. Approximate ranges of the subspecies of *Natrix fasciata*.

the forms in his *sipedon* complex, he linked them all together on the basis of intergradation. He was able to demonstrate a broad area of intergradation between *sipedon* and *pleuralis* and lesser ones between *fasciata* and *confluens* and between *fasciata* and *pictiventris*. Further, in his thesis (MS, p. 132) Clay stated that "*pleuralis* intergrades with *fasciata*, at least in South Carolina," and, although he did not designate individual speci-

mens, he obviously interpreted some of his material as combining pattern characteristics of both forms (pp. 130, 133).

A preliminary review of the complex, which I made a few years ago, confirmed Clay's indications that intermediate specimens between *pleuralis* and *fasciata* do exist, and emphasis was therefore placed on the acquisition and examination of fresh material from the Southeast. Through the cooperation of several residents of the Carolinas, many collections were made in critical localities, and several gravid females were included whose young, born shortly afterward in captivity, provide useful data on pattern variations. In addition I have examined all specimens from the eastern Carolinas and extreme southeastern Virginia in a considerable number of museums, as well as many other specimens from sundry southeastern localities. Selected series were also seen from a number of other collections.

Examination of all this material, in excess of 1200 specimens, leads to the conclusion that "intergradation" between *pleuralis* on the one hand and *fasciata* on the other (in South Carolina and also in Georgia) can more properly be interpreted as hybridization, especially since the intermediate snakes are all from localities where ecological conditions have been profoundly disturbed by activities of mankind. Such an interpretation permits the removal of *Natrix fasciata* from the *sipedon* complex, makes it possible to recognize *fasciata* as a full species, and eliminates the inconsistency of overlapping ranges. The races of *sipedon* and *fasciata* would thus be as follows:

Natrix sipedon sipedon (Linnaeus)
Natrix sipedon pleuralis Cope
Natrix sipedon insularum Conant and Clay
Natrix fasciata fasciata (Linnaeus)
Natrix fasciata confluens Blanchard
Natrix fasciata pictiventris Cope[1]

The grouping of *confluens* and *pictiventris* as subspecies of *fasciata* is not a new concept, for Blanchard proposed such an arrangement in 1923. Pending a thorough study of the salt-marsh snakes, upon which, as indicated, I have already embarked, it appears advisable to retain them (*clarki*, *compressicauda*, and *taeniata*) as races of *fasciata*.

---

[1] To avoid possible future confusion, attention should here be called to an often overlooked synonym of the name *pictiventris*. Loennberg (1894, p. 331) proposed *Natrix fasciata atra* for a melanistic snake of this species from the St. Johns River not far from Lake Jessup (Florida), and, under the rule of priority, *atra* would take precedence over Cope's *Natrix fasciata pictiventris* of 1895. However, *atra* of Loennberg is preoccupied by *Natrix atra* Gosse (1851, p. 228), which was applied to a snake from Jamaica now known as *Alsophis ater*.

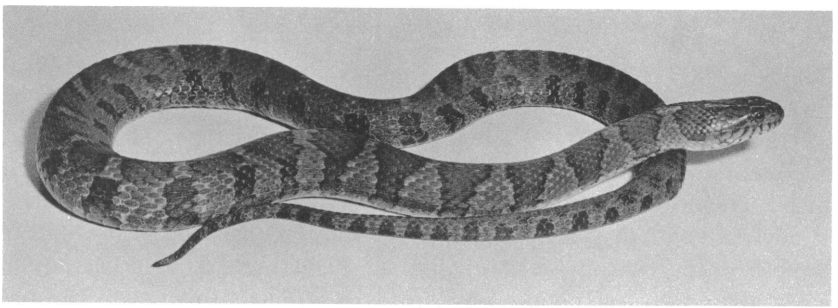
GEOGRAPHICAL RANGES

Figure 1A reveals a relatively large area from southern Illinois and southeastern Oklahoma to southern Alabama and the Florida panhandle wherein the range of the species *sipedon* overlaps the range of the species *fasciata*. Throughout most of this region the two maintain their identities, with no evidence of hybridization between them, even though specimens of one may be found in apparently identical habitats with individuals of the other. In general, *fasciata*, including all its races, is a species of the lowlands, occupying ponds, lakes, sloughs, ditches, small streams, and the environs of sluggish rivers, including their bottomland swamps. In contrast, *sipedon* in the southern states normally occurs in more upland habitats and is typically a species of rivers and streams, especially of the larger ones and those exhibiting appreciable gradient. In the more northerly and westerly portions of its range, where *fasciata* is absent, *sipedon* occupies virtually all fresh-water habitats (as well as brackish-water habitats in some areas; see below).

SYMPATRY

Although most populations of the species *sipedon* and the species *fasciata* are separated ecologically, an abundance of records indicates that they occur together in many localities. For example (as mentioned above) I have taken *pleuralis* and *confluens* at Reelfoot Lake, Tennessee, at the same place and only minutes apart on April 9, 1933. I also took both species at Reelfoot Lake again on March 30, 1934, but not together in the same microlocality. Parker (1939, pp. 84–85) reported both forms from Reelfoot Lake, and the Academy of Natural Sciences of Philadelphia has three specimens of *confluens* (A.N.S.P. Nos. 4477, 4479, 4480) and one of *pleuralis* (A.N.S.P. No. 4476) collected at Samburg, Reelfoot Lake, many years ago (Rhoads, 1895, p. 376). Parker (1948, p. 27) implied sympatry between the same two forms in Obion and Shelby counties, Tennessee, without citing specific localities. At Reelfoot Lake *confluens* is largely confined to the lake proper and its immediate environs, whereas *pleuralis* is most common in the smaller streams that traverse the nearby uplands before emptying into the lake, but the two definitely occur together and maintain their identities.

Gordon (1952) showed that *pleuralis* deeply invades the ranges of *confluens* and *fasciata* without evidence of intergradation, Neill (1954, p. 85) reported *pleuralis* from Okaloosa County, Florida, which is well within the range of *fasciata*, and Neill (1957, p. 47) also reported *fasciata* from within the range of *pleuralis* in Georgia.



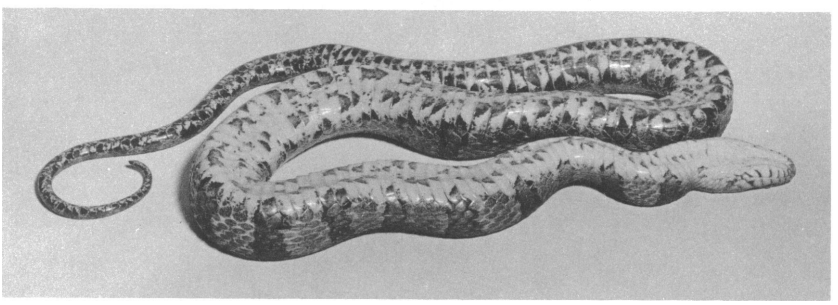
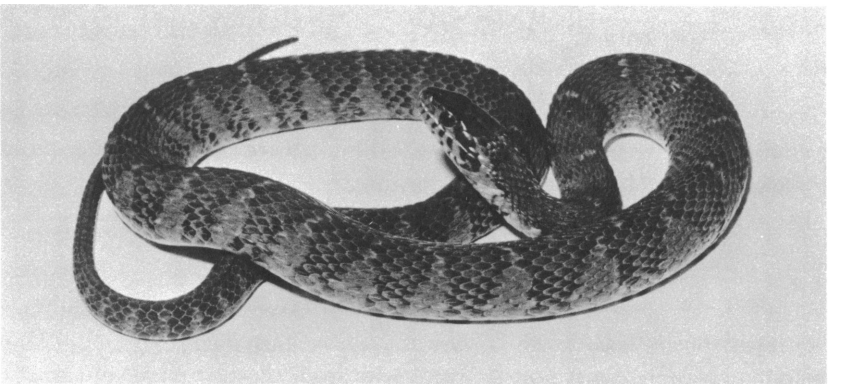


FIG. 2. *Natrix sipedon sipedon* (A.M.N.H. No. 85422); Tar River, Greenville, Pitt County, North Carolina; length, 1120 mm.; female. The dorsal pattern consists of dark cross bands anteriorly and alternating lateral and middorsal blotches posteriorly.

FIG. 3. *Natrix sipedon sipedon*, same snake as is shown in figure 2. View of under surfaces, showing basic pattern of dark half-moons.

Douglas A. Rossman and Earl Olson obtained *pleuralis* (A.M.N.H. No. 88317) and *confluens* (A.M.N.H. No. 88318) at Horseshoe Lake, Alexander County, Illinois, on September 30, 1956. Woodman (MS, p. 19) stated that *pleuralis* and *confluens* "were collected in the Black River, in the vicinity of Pocahontas, Randolph County, Arkansas" on the same day. The Tulane University collection includes three specimens of *confluens* and one of *pleuralis* (all four catalogued as T.U. No. 15958) that were taken together along the Bogue Chitto River at Enon, Washington Parish, Louisiana. C. Robert Shoop (personal communication) reports that during the course of three years of field work at Talisheek, St. Tammany Parish, Louisiana, he encountered many *confluens* and many *pleuralis* along Talisheek Creek, a tributary of the Pearl River. Robert G. Webb (personal communication) reports that *pleuralis* and *confluens* occur sympatrically at two Oklahoma localities: near Mountain Fork River, 15 miles southeast of Broken Bow, McCurtain County, and 4 miles east of



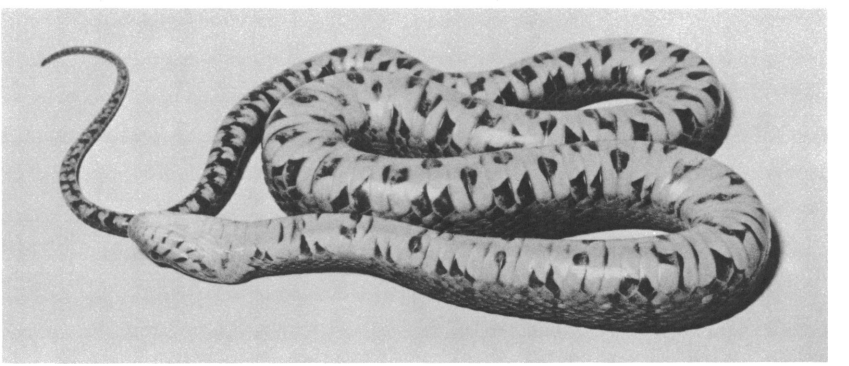


FIG. 4. *Natrix fasciata fasciata* (A.M.N.H. No. 79120); 3 miles south of New Bern, Craven County, North Carolina; length, 840 mm.; male. The dark dorsal cross bands are continuous throughout the length of the body, and there is a dark postocular stripe.

FIG. 5. *Natrix fasciata fasciata*, same snake as is shown in figure 4. View of under surfaces. The dark markings are chiefly triangular or squarish in shape.

Tuskahoma, Pushmataha County. J. William Cliburn collected a specimen each of *pleuralis* and *fasciata* × *confluens* (M.S.C. Nos. 55–54, A and B, respectively) along Red Creek, at Ramsey Springs, Stone County, Mississippi. Recently I have acquired evidence of sympatry between *sipedon* and *fasciata* in the Tar River drainage of North Carolina.

Probably I have overlooked other recorded cases in which representatives of the two species occur together, and doubtless there are numerous others that have been neither reported nor published.

Despite the many instances of sympatry, there is evidence of hybridization in at least a few localities, as is discussed below.

DIAGNOSTIC CHARACTERS

To avoid confusion and to point up dissimilarities at the species level, subspecific names (except in a few special cases) are omitted from the remainder of this text, and all populations are designated as either *sipedon* or *fasciata*. The approximate ranges of the pertinent races of the two species in the Southeastern United States are shown in figure 1 (B–C). Accurate delineation of the areas of intergradation between adjacent subspecies must await the examination of many more specimens, especially from critical areas. The present paper, although concerned with the species *sipedon* and *fasciata* as a whole, has been prepared in large part on the above-mentioned large series from the Carolinas and nearby

TABLE 1

CHIEF PATTERN CHARACTERISTICS OF *Natrix sipedon* AND *Natrix fasciata*[a]

Species	Dorsal Pattern	Ventral Pattern	Head Pattern
sipedon	Dark cross bands anteriorly, changing to alternating middorsal and lateral blotches usually at or before midbody (fig. 2)	Basically composed of dark half-moons with light, often reddish, centers; subject to great variation (fig. 3)	Virtually unicolored or vague and irregular. May approach *fasciata* pattern, especially near range of that species (fig. 6)
fasciata	Dark cross bands throughout length of body (fig. 4)	Dark squarish or triangular spots often accompanied by dark, wavy, cross lines (fig. 5)	Dark stripe from eye to angle of jaw (fig. 6)

[a] Based on population samples from North and South Carolina.

portions of the adjacent coastal states. All descriptions of patterns and summarizations of scale counts presented hereinafter (and listed in tables 1 to 3, inclusive) are based on material from this restricted region, unless otherwise indicated.

The chief pattern characteristics of *Natrix sipedon* are compared with those of *Natrix fasciata* in table 1 and figures 2 to 6, inclusive. Except in areas where hybridization occurs, well-marked specimens can be assigned to *sipedon* or *fasciata* with ease, as I have proved to my own satisfaction while sorting newly borrowed museum collections bearing numbered tags but no labels that indicate localities. Difficulties may arise among specimens that have their pattern details obscured by dark pigment. There is a marked tendency for snakes of both species to darken with age and to assume a uniform, or nearly uniform, appearance. This is

especially true in *fasciata*, many adults of which exhibit a dorsum that is completely melanistic or relieved only by small areas of red or brown on the lower sides of the body; the venters in such animals usually also are black in part, at least beneath the tail. The amount of dark pigment may vary locally. In many populations two color phases may almost be recognized, a reddish or yellowish one, in which black pigment is at a minimum, and a black one in which there is an abundance of melanin. Submerging snakes in liquid will often reveal unsuspected traces of pat-

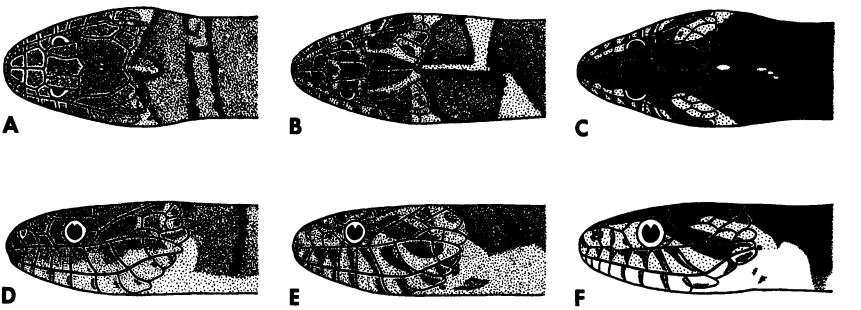


FIG. 6. Head patterns in *Natrix sipedon* and *Natrix fasciata*, semidiagrammatic dorsal (upper row) and lateral views. A, D. *Natrix sipedon sipedon* (A.M.N.H. No. 85424) from Silver Lake, near Wilson, Wilson County, North Carolina; head-body length, 735 mm.; total length, 944+ mm.; female. B, E. *Natrix sipedon sipedon* (C.M. No. 23600), Dismal Swamp, Norfolk County, Virginia; head-body length, 737 mm., total length, 947 mm.; female. C, F. *Natrix fasciata fasciata* (A.M.N.H. No. 85408) from near Carolina Beach, New Hanover County, North Carolina; head-body length, 719 mm., total length, 935 mm.; female.

tern, particularly among dark individuals or those preserved a short time prior to ecdysis. Some of the more important variations from the norm are as follows:

DORSAL PATTERN: Rarely *sipedon* may be cross-banded to or nearly to the tail and thus resemble *fasciata*. More commonly the cross banding of *fasciata* may break up into dorsal and lateral segments near the tail, or a few alternating blotches may appear near midbody or elsewhere. Variation in the number of dark dorsal markings on the body is shown in table 2. In *fasciata* all cross bands were counted from the rear of the head to the last cross band anterior to the anus, inclusive; counts in *sipedon* were made in similar fashion, except that cross bands were counted anteriorly and middorsal blotches posteriorly.

In both species there is a strong tendency for the dark markings on the sides of the body to be outlined by light pigment that is paler than the

adjacent ground color. In most *sipedon* and numerous *fasciata* the edges of the light outlining, when the latter is present, are relatively smooth, but in many *fasciata* they are highly irregular, and individual scales or portions of scales may be uniformly white, cream, or tan, thus imparting a somewhat random light spotted appearance to the sides of the body (fig. 7A). Such irregular spotting is common in the Florida subspecies (*Natrix fasciata pictiventris*), but northward through the range of the subspecies *fasciata* it appears to occur less and less frequently (clinally?). A suggestion of lateral dark spotting often appears in *fasciata* because of the presence of "shadow" spots between the dark cross bands, each centered

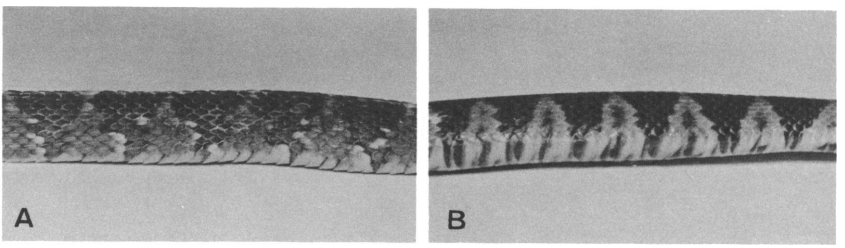


FIG. 7. Lateral patterns in *Natrix fasciata fasciata*. A. Random light spots on a snake (A.M.N.H. No. 88071) from 2 miles south of Bloomingdale, Chatham County, Georgia; length, 577 mm.; male. B. Dark "shadow" spots centered in areas of ground color on a newly born snake (A.M.N.H. No. 85412.10) whose mother was collected at Greenville, Pitt County, North Carolina; length, 240 mm.; male.

in an area of ground color (fig. 7B). Such "shadow" spots are usually most prominent in young specimens in which the development of dark pigment, associated with advancing age, is not yet strongly apparent.

VENTRAL PATTERN: Although dark half-moons, often reddish in color and outlined by darker pigment, form the basic ventral pattern in *sipedon* (fig. 3), there are many variations. In many specimens the half-moons lose their characteristic shape and run together, especially toward the rear of the body. In some individuals they are virtually absent and may be replaced by dark stippling. In many such specimens the central portion of the belly may be unicolored (yellow, orange, or pink in life). In *fasciata* (fig. 5) the squarish or subtriangular dark markings are usually prominent except in very dark or very light specimens, but they are almost always discernible on at least part of the belly.

HEAD PATTERN: In *fasciata* there normally is a prominent dark (often black) stripe from the eye to the angle of the mouth, and this is rendered conspicuous by a light stripe bordering its upper edge (fig. 6F). The dark

stripe may be weak or virtually absent, however, particularly in very young snakes. Specimens of *sipedon* from many parts of the South, but especially from the outer edge of the Piedmont in the Carolinas and from the vicinity of the Dismal Swamp area of Virginia and North Carolina, show evidence of convergence toward *fasciata* in having head patterns that include a dark postocular element strongly suggesting the dark stripe of *fasciata* (fig. 6E). In *sipedon* the temporal region normally is well stippled or clouded with dark pigment (fig. 6D), imparting a virtually uniform appearance to the side of the head, but in many specimens from the above areas the dark pigmentation is not uniform, being darkest from

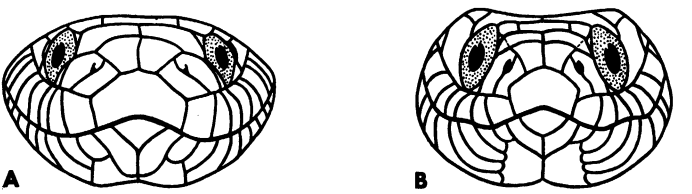


FIG. 8. Head-on views (semidiagrammatic) of *Natrix sipedon sipedon* (left) and *Natrix fasciata fasciata* (right). The canthus rostralis is considerably sharper and the head is proportionately narrower in *fasciata*. Same snakes as are shown in figure 6A and C, respectively.

the eye to the angle of the mouth and palest on the temporals and adjacent scales. The presence of such pigmentation (in both the subspecies *sipedon* and *pleuralis*) was previously interpreted as evidence of intergradation between those forms and *fasciata* (Clay, MS, p. 130; Conant, 1943b, p. 86).

HEAD SHAPE: The canthus rostralis, although difficult to evaluate without direct comparison of live or carefully preserved specimens of similar dimensions, is more pronounced in *fasciata* than in *sipedon*. The plane of the side of the head, anterior to the eyes, meets the dorsal surface at a perceptible angle in *fasciata*, whereas in *sipedon* the angle is less pronounced or replaced by a rounding off from one surface to the other (fig. 8). The dissimilarity is also clearly evident in two illustrations in Cope's work on the crocodilians, lizards, and snakes of North America (1900, figs. 250, 251). The difference in head shape is apparent in skulls of the two species; the prefrontal bone, anterolaterad to its articulation with the frontal, turns downward at a sharper angle in *fasciata* than in *sipedon*.

SCUTELLATION: In many features of scutellation the counts for *sipedon* are virtually identical with those for *fasciata*. This is true of the supra-

TABLE 2

VARIATION IN VENTRAL AND SUBCAUDAL COUNTS, NUMBER OF DARK DORSAL MARKINGS ON BODY, AND TAIL LENGTH PROPORTIONS IN *Natrix sipedon*, *Natrix fasciata*, AND HYBRIDS BETWEEN THEM, ALL CHIEFLY FROM NORTH AND SOUTH CAROLINA

Subject and Species	Sex	Number of Specimens	Mean	Range
Ventrals				
Natrix sipedon				
North Carolina (*sipedon*)[a]	♂	94	132.5 ± 0.25	(127–140)
	♀	112	133.8 ± 0.24	(128–142)[b]
South Carolina (*pleuralis*)[c]	♂	55	131.4 ± 0.28	(127–135)
	♀	45	132.0 ± 0.35	(128–136)
Hybrids	♂	5	129.4 ± 1.21	(126–133)
	♀	10	129.1 ± 0.95	(125–134)
Natrix fasciata[d]	♂	206	128.2 ± 0.20	(121–136)
	♀	256	128.8 ± 0.17	(121–136)
Subcaudals				
Natrix sipedon				
North Carolina (*sipedon*)[a]	♂	85	75.0 ± 0.29	(69–82)
	♀	90	64.4 ± 0.32	(58–72)
South Carolina (*pleuralis*)[c]	♂	52	77.8 ± 0.40	(69–84)
	♀	39	68.2 ± 0.50	(62–74)
Hybrids	♂	4	77.8 ± 2.14	(73–83)
	♀	6	70.7 ± 1.22	(65–73)
Natrix fasciata[d]	♂	189	78.9 ± 0.26	(70–86)
	♀	204	69.5 ± 0.26	(61–78)

TABLE 2—(*Continued*)

Subject and Species	Sex	Number of Specimens	Mean	Range
Dorsal markings				
Natrix sipedon				
North Carolina (*sipedon*)[a]	♂ and ♀	204	30.5 ± 0.18	(24–38)
South Carolina (*pleuralis*)[c]	♂ and ♀	101	30.0 ± 0.10	(22–37)
Hybrids	♂ and ♀	15	28.3 ± 1.10	(21–38)
Natrix fasciata[d]	♂ and ♀	439	29.5 ± 0.19	(22–39)
Tail length/total length				
Natrix sipedon				
North Carolina (*sipedon*)[a]	♂	85	26.9% ± 0.09	(25–28)
	♀	88	24.1% ± 0.08	(22–26)
South Carolina (*pleuralis*)[c]	♂	49	28.3% ± 0.12	(26–30)
	♀	35	25.5% ± 0.20	(22–28)
Hybrids	♂	4	28.0% ± 0.71	(26–29)
	♀	6	24.7% ± 0.74	(24–25)
Natrix fasciata[d]	♂	180	27.7% ± 0.08	(25–32)
	♀	196	25.1% ± 0.10	(21–28)

[a] Subspecies *sipedon;* snakes from the Norfolk-Dismal Swamp region of Virginia are included.
[b] An aberrant specimen with 118 ventrals is omitted.
[c] Subspecies *pleuralis:* a few snakes from Augusta, Georgia, and Richmond County, North Carolina, are included.
[d] Includes a few snakes from the Savannah River drainage of Georgia.

TABLE 3

VARIATION IN THE NUMBER OF SCALE ROWS, POSTOCULAR SCALES, AND THE SECOND ROW OF TEMPORAL SCALES IN *Natrix sipedon*, *Natrix fasciata*, AND HYBRIDS BETWEEN THEM, ALL CHIEFLY FROM NORTH AND SOUTH CAROLINA

	Natrix sipedon			
	North Carolina (*sipedon*)[b]	South Carolina (*pleuralis*)[c]	Hybrids	*Natrix fasciata*[a]
Scale rows				
Neck				
21 rows	13.3% (28)[d]	26.2% (26)	20.0% (3)	37.6% (176)
23 rows	75.5% (158)	63.6% (63)	66.6% (10)	55.1% (258)
Maximum				
23 rows	80.6% (167)	87.8% (87)	100.0% (15)	91.5% (422)
24 and 25 rows	19.3% (40)	11.1% (11)	—	5.4% (25)
Postoculars				
2 scales	0.9% (4)	1.5% (3)	—	27.0% (253)
3 scales	98.5% (420)	87.0% (194)	100.0% (30)	72.1% (674)
Temporals (2d row)				
2 scales	45.1% (192)	45.2% (90)	3.3% (1)	18.9% (178)
3 scales	54.3% (231)	54.7% (109)	96.6% (29)	80.6% (758)

[a] Includes a few snakes from the Savannah River drainage of Georgia.

[b] Subspecies *sipedon;* snakes from the Norfolk-Dismal Swamp region of Virginia are included.

[c] Subspecies *pleuralis;* a few snakes from Augusta, Georgia, and Richmond County, North Carolina, are included.

[d] Figures in parentheses indicate sizes of samples.

labials, which in almost all specimens are eight in number; the preoculars in almost all number one; and the anterior temporals, also in almost all, also number one. The infralabials are 10 in number in 83.5 per cent to 92.1 per cent of all the samples tested. Variations in the number of ventrals and subcaudals (both separated by sexes) are shown in table 2, and the ranges and means for the ventrals are portrayed graphically in figure 9. Other counts that indicate significant differences between the two species, including those for the postoculars, the second row of temporals, and the number of scale rows (on the neck and the maximum number in the mid-body region) appear in table 3.

HYBRIDIZATION

Through a large part of the Southeast, *sipedon* and *fasciata* are allopatric, with *fasciata* virtually confined to the Coastal Plain and *sipedon* occurring only on the Piedmont and westward into the Appalachians (fig. 1A).

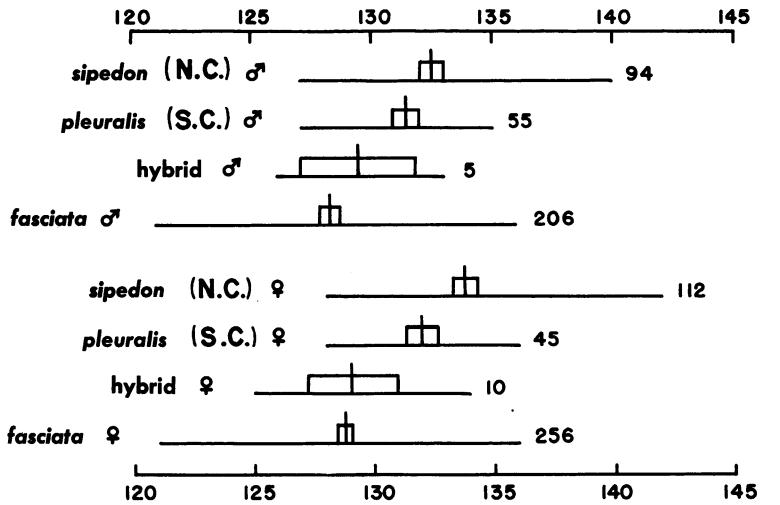


FIG. 9. Ventral scales among *Natrix sipedon*, *Natrix fasciata*, and hybrids between them, all chiefly from North and South Carolina. The horizontal bar indicates the range of variation in each sample; the vertical bar, the mean; and the rectangle, two standard errors of the mean on each side of the mean. The populations are labeled in accordance with the various subspecies; data are derived from table 2. The number of specimens comprising each sample is indicated for the individual graphs.

The ranges of both, for a considerable distance in the Carolinas and Georgia, meet along a narrow zone approximating the Fall Line, and it is precisely within this zone that evidence of hybridization has been found. Such hybridization is demonstrable in only a few localities, however; elsewhere along the zone of contact the two species apparently maintain their identities.

The places where hybrids[1] occur are discussed in detail below, and the population samples from them are compared with samples of *fasciata* and *sipedon* from adjacent regions. This breakdown in isolating mechanisms may be sporadic, but the possibility must not be overlooked that allopatric hybridization may be involved, perhaps fitting the hypothetical

[1] The words "hybrid" and "hybridization," appearing here and elsewhere in this paper, are employed with reservations. There is no definite proof of the hybrid origin of any specimens. In no case are both parents known, but the intermediate nature of the pattern and other characteristics that are evident in a number of specimens is such as to leave little doubt that they are the products of interspecific matings. Rather than to qualify every reference to these terms with such weasel words as "apparent," "seeming," or "supposed," I simply use "hybrid" and "hybridization."

case outlined by Mayr, Linsley, and Usinger (1953, p. 102), "where two species remain as distinct species over most of their range but form complete hybrid populations in a few areas." These authors further state: "This happens particularly in regions in which the natural ecological balance has been badly disturbed in recent years by human interference. It is recommended that such forms be treated as full species in spite of the occasional free hybridization under the stated conditions."

Evidence of hybridization is available from or near the following localities in close proximity to the Fall Line: Cheraw and Columbia, South Carolina, and Augusta, Georgia. Potential hybridization is also indicated in Everett Pond, Richmond County, North Carolina. Population samples from each area are discussed separately, beginning with Columbia from which by far the largest is at hand.

Vicinity of Columbia, South Carolina

Approximate collecting stations for this general area are plotted on the map (fig. 10), which embraces parts of Richland and Lexington counties, South Carolina.

Fairwold Pond: Twenty-three adult and subadult specimens are available from a small pond where a dam formerly impounded a tributary of Crane Creek. This pond, approximately 5 miles north of Columbia, is adjacent to Carmel Street of the Fairwold community and about ½ mile south of the South Carolina State Hospital for Negroes (Fort Jackson North quadrangle, United States Geological Survey, 1953). The dam was constructed in 1953 to create a "minnow pond," but was breached two years later by flood waters following a heavy rain. It was repaired but destroyed again in 1957. Since then only remnants of the pond remain (fig. 11), represented principally by a pondlet approximately 40 by 30 feet and with a maximum depth of about 3 feet. The main bed of the former pond is covered with tall marsh grasses through which small rivulets run toward the stream that averages 4 feet in width and 1 foot in depth.

Color pattern variation in this group of 23 specimens (A.M.N.H. Nos. 88011–88033) is extreme. An attempt was made to score the characteristics of each specimen, weighting them heavily on the basis of dorsal and ventral patterns and head markings and lightly on the presence of random light spots along the edges of the dark lateral markings and the shape of the canthus rostralis. Three specimens (two males and one female) are virtually indistinguishable from *fasciata* from Coastal Plain localities; 12 (six males and six females) fall within (or almost within) the range of

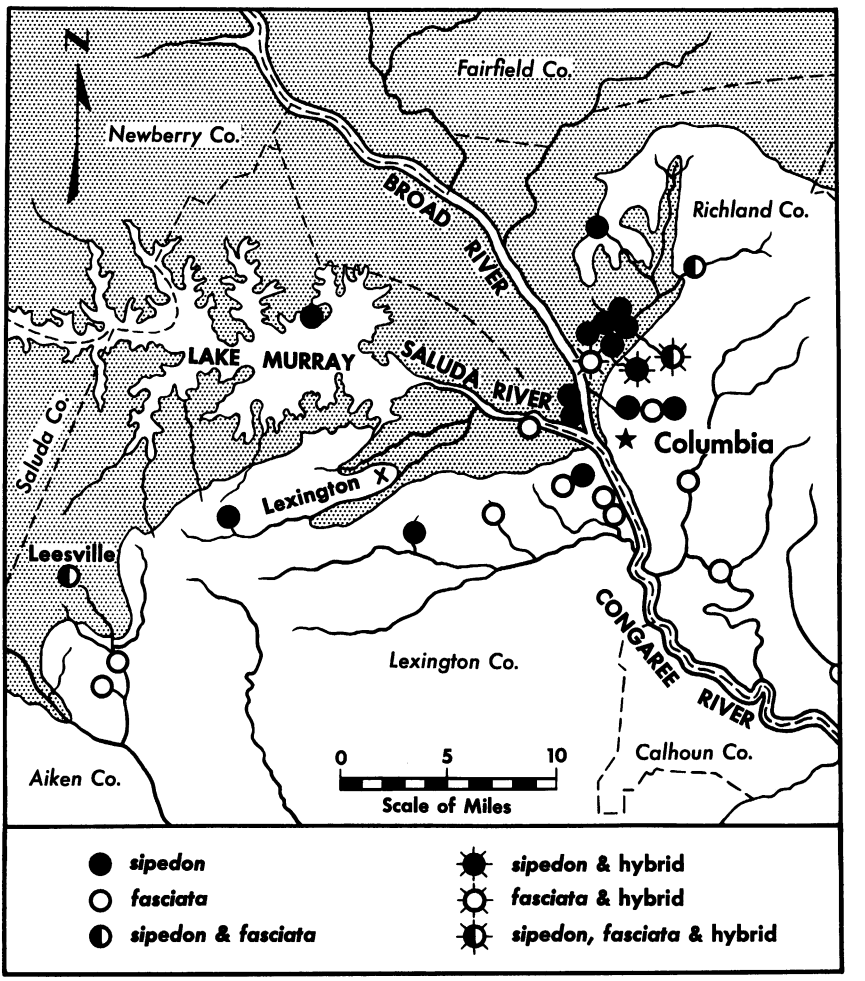


FIG. 10. Localities for snakes of the *Natrix sipedon-fasciata* complex in the vicinity of Columbia, South Carolina. The forms occurring in this area are *Natrix sipedon pleuralis* and *Natrix fasciata fasciata*. The Piedmont is indicated by stippling; the Coastal Plain is unpatterned. The boundary between them, the Fall Line, is adapted from plate 2 in Cooke (1936). All localities plotted on this map and the map shown in figure 13 are based on specimens examined during the course of the present study.

variation of *sipedon* (subspecies *pleuralis*); the remaining eight (two males and six females) are intermediate in a variety of ways and are interpreted as hybrids. For example, one has the dorsal pattern and light lateral spots

FIG. 11. Remnant of former pond near the Fairwold community, Richland County, South Carolina, a collecting station for *Natrix sipedon pleuralis*, *Natrix fasciata fasciata*, and hybrids between them.

of *fasciata*, the belly pattern and canthus shape of *sipedon*, and head markings that are intermediate. Another shows all characters of *sipedon* except for the dorsal pattern which is strongly that of *fasciata*. Another has the head markings and canthus shape of *sipedon*, the light spots of *fasciata*, and intermediate dorsal and ventral patterns. No two of the eight hybrids have the same combination of characters. Even among several of the specimens that checked out as either *fasciata* or *sipedon*, on the basis of the five characters enumerated, subtleties in patterns can be detected that indicate contamination by the other species. The wide range of variation among these snakes strongly suggests introgressive hybridization.[1]

Another sample is available from approximately 300 yards farther upstream, where state highway No. 555 crosses the stream. Two adult females (A.M.N.H. Nos. 88040, 88041) score 100 per cent for *sipedon*, and

[1] The receipt of additional material from Fairwold Pond subsequent to the completion of this paper virtually confirms introgression and strongly indicates the advisability of acquiring more samples from this locality and compiling hybrid indices such as those outlined by Anderson (1949, pp. 88–90). These will be incorporated in a future study.

a young female and an adult male (A.M.N.H. Nos. 88007, 88008) score 100 per cent for *fasciata.* In addition to these four specimens, a litter of 25 apparently full-term young (A.M.N.H. No. 88009) was removed from a large female snake found dead on the highway during August, 1959. With few exceptions these exhibit *fasciata* characteristics only; all have the postocular dark stripe well defined and bear the basic ventral markings of *fasciata,* although these markings are exceptionally large and dark and often tend to be paired. In 20 snakes there are dark cross bands from head to base of tail; in four the cross bands change to alternating dorsal and lateral blotches at or anterior to midbody, as in *sipedon;* in one the pattern is essentially cross-banded, but two lateral spots appear on the left side and three on the right near midbody. Unfortunately, the mother snake was "beyond preservation," according to the collector, and her pattern characteristics are unknown. Although this litter of young is from near a locality where hybridization can be demonstrated, the range of variation in dorsal patterns is no greater than in another litter of 25 young of *fasciata* (A.M.N.H. No. 88001) from Poinsett State Park, Sumter County, South Carolina, among which five have alternating dorsal and lateral blotches posteriorly as in *sipedon.*

DREAM LAKE: This pond, situated about 3 miles north of Columbia and 1 mile north of Eau Claire, was created in 1939 by the construction of a dam across another tributary of Crane Creek and was widely used as a public swimming area for a few years after World War II. A second pond a short distance northwest along the same stream (Columbia North quadrangle, United States Geological Survey, 1948) is now dry, and Dream Lake has been partially drained so that its southern half is boggy and covered by only a few inches of water. Among six specimens from this locality (A.M.N.H. Nos. 88034–88039), scored in similar fashion, three (one male and two females) are *sipedon* and three (one male and two females) are hybrids. The influence of *fasciata* is strong in two of the latter, but there are no specimens clearly assignable to *fasciata.*

OTHER LOCALITIES NEAR COLUMBIA: At least one additional hybrid is available from the Columbia area. A male with a total length of 668 mm. from Crane Creek at its confluence with the Broad River, 2 miles north of Columbia (A.M.N.H. No. 88010), has a peculiar dorsal pattern: the cross bands change to alternating dorsal and lateral blotches, as in *sipedon,* but the dorsal spots on the posterior half of the body are poorly defined; dark pigment is almost entirely absent except in the middorsal area at the anterior and posterior tip of each blotch. There is a profusion of light spots along the edges of the dark lateral markings, as in many *fasciata.* There are no distinct stripes on the head; the belly is chiefly

half-mooned, but some of the dark markings suggest those of *fasciata.* (Another snake from this same locality has all the characteristics of *fasciata.*)

Two additional snakes may also be hybrids, but I choose the conservative approach and refer them to *fasciata.* Both closely resemble that species, but they have aberrant dorsal patterns that barely fall within the range of variation of *fasciata* as exhibited by a considerable series of specimens from the Coastal Plain. These are a juvenile male (U.S.C.R.C. No. 292) and a subadult female (Ch.M. No. 31.219.15), both from

FIG. 12. Gravel pit situated on the Fall Line near Cheraw, Chesterfield County, South Carolina, a collecting station for *Natrix fasciata fasciata* and hybrids between that form and *Natrix sipedon pleuralis.*

Columbia. In addition to other pattern irregularities, the dorsum is abnormal in both in having irregular dorsal and lateral blotches posteriorly. Mention also should be made of a snake, an adult male *fasciata* (U.S.C.R.C. No. 293) from 22 miles southeast of Columbia, which shows an essentially *fasciata* dorsum but has 14 alternating lateral blotches on the posterior part of the body, on the right side only.

Including all the above, plus many other snakes not specifically mentioned, a total of 140 specimens of the *sipedon-fasciata* complex is available from Columbia and vicinity. Among these, 72 are identifiable as *Natrix sipedon,* 56 as *Natrix fasciata,* and 12 as hybrids between the two species. Most of the last-mentioned are from two demes, living in Fairwold Pond and Dream Lake, respectively, where habitat conditions have been considerably disturbed by human activities. Other snakes from the general area exhibit aberrant patterns.

Vicinity of Cheraw, South Carolina

Among four adult and subadult water snakes from a mile northwest of Cheraw, Chesterfield County, South Carolina, two are *fasciata* and two are hybrids. These were taken in gravel pits partially filled with water (fig. 12) at a locality that is almost exactly on the Fall Line. The two hybrids (U.S.C.R.C. Nos. 423, 424; both females, 812 and 570+ mm. in total length) have essentially the dorsal patterns of *fasciata*, but in one there are two lateral blotches on one side of the body and one on the other, and in the second there are eight blotches on the left and two on the right; the ventral markings are within the range of variation of *fasciata*. The heads are mottled with dusky pigment, and dark postocular stripes are lacking. In one (U.S.C.R.C. No. 423) there is a fairly well-defined, pale, V-shaped area, with apex pointing forward, that involves the most posterior portions of the parietals and temporals.

A *fasciata* (Ch.M. No. 56.70.2, male, 600+ mm.) from nearby (2 miles northwest of Cheraw) has an aberrant pattern that consists of widely separated dorsal blotches arranged in two rows, with the blotches chiefly opposite one another in pairs. The general effect is as though the cross bands had been split down the back by a middorsal stripe of the ground color. All other characters are like those of *fasciata*.

A number of other specimens from the general vicinity of Cheraw are at hand, and a few of these deserve comment. Among them is an adult female 992+ mm. long (A.M.N.H. No. 85929, from the Everett Mill Pond, 4 miles north of Wallace, Marlboro County) and a series of 17 young that were removed after her death. These are not full-term, for the hemipenes are still extruded in the males, and in some the scales are imperfect so that accurate counts are not possible. The essential details of the dorsal patterns are, however, clearly visible in all. Four of the young are cross-banded throughout the length of the body; in eight the cross bands change to alternating dorsal and lateral blotches, as in *sipedon;* in five there are numerous alternating lateral blotches near midbody or other irregularities that produce patterns more or less intermediate between the two main types. All have the dark postocular stripe, and most have the belly pattern of *fasciata*, but there are suggestions of half-moons in some. The mother has the characters of *fasciata*, and she is thus classified, even though her dorsal markings are irregular.

There are 50 specimens of *fasciata* from the Cheraw Fish Hatcheries, 6 miles south of Cheraw, and, of these, six are adults and the remainder are samples from three litters of young. There is an additional adult from below the dam at Cheraw Lake, Cheraw State Park, about the same dis-

tance south of the town. In all these, the pattern characteristics are those of *fasciata* with two exceptions, both of which involve dorsal patterns. In two of the juveniles (A.M.N.H. No. 85899 and U.S.C.R.C. No. 417) there is a shift from cross bands to blotches as in *sipedon*. In numerous others, however, many of the cross bands are diagonal in position or fork into two parts on one side of the body.

Three adult snakes from the Anderson Mill Pond, 3 miles southeast of Wallace, Marlboro County, are good *fasciata*.

Among 79 specimens available from the Cheraw area, including those from Richmond County, North Carolina (see below), two are *sipedon*, 58 are *fasciata* or close to that form, and the remaining 19 are intermediate. The last-named include several young from a mill pond and two adult hybrids from a series of gravel pits.

Everett Pond, North Carolina

This locality, near the Great Pee Dee River in Richmond County, North Carolina (10 miles southwest of Rockingham), and known locally as the Everett Hunting Club Pond, should not be confused with the Everett Mill Pond in Marlboro County, South Carolina. From the North Carolina Everett Pond there are three adult specimens, one each of *sipedon* and *fasciata* and one that, although probably within the range of variation of *fasciata*, requires some comment. This snake (Ch.M. No. 56.90.10) is a large female, 940 mm. in total length. Although its pattern is essentially cross-banded, alternating lateral blotches appear irregularly, three on the left side of the body and about seven on the right. Both the head pattern and belly pattern are closest to those of *fasciata*, but elements of both are suggestive of *sipedon*. I cannot conservatively designate this specimen as a hybrid, but it is close to and may indeed be one. Perhaps the significant thing about this locality is the presence of both *sipedon* and *fasciata* in the same pond. Further collecting may reveal the presence of hybrids. There is an additional specimen of *sipedon* (U.S.C.R.C. No. 428) from Marks Creek a short distance below the outlet of the pond.

Augusta, Georgia

A young male (U.S.N.M. No. 8790), from Augusta, Richmond County, Georgia, measuring 266 mm. in total length, is a hybrid on the basis of having cross bands from head to anus and a postocular stripe (as in *fasciata*) and a profusion of bold, paired half-moons on the belly (as in *sipedon*). The two "intermediate" specimens reported by Neill (1946, p.

256) from Richmond County probably also are hybrids. Both *sipedon* and *fasciata* are abundant in the Augusta region, with *sipedon* (*pleuralis*) occurring in the Piedmont and *fasciata* on the Coastal Plain (Neill, *loc. cit.*).

Sympatry at Other Fall Line Localities

Other localities along the Fall Line from which specimens of both *sipedon* and *fasciata*, but no hybrids, are at hand include the vicinity of Leesville, Lexington County, South Carolina, and Southern Pines, Moore County, North Carolina (also Everett Pond, North Carolina, as stated above). A large adult female (U.M.M.Z. No. 84144) from 3½ miles northeast of Gilbert, Lexington County, South Carolina, has an irregular dorsal pattern in which the cross bands change to alternating blotches and then resume as cross bands again; all its other pattern characteristics are strongly those of *sipedon*, however, and it is so designated.

HYBRIDIZATION IN OTHER AREAS

Hybridization occurs in South Carolina and Georgia (and probably also in North Carolina) along the Fall Line, which marks the common boundary of the ranges of the two species involved. There is also evidence of genic introgression by *fasciata* (although clear-cut hybrid specimens are lacking) in another area near the edge of the Coastal Plain, but far removed from the Carolinas. This is in southern Illinois a relatively short distance north of the northernmost limit of the range of *fasciata* in the Mississippi Valley, the two species there being represented by *Natrix sipedon pleuralis* and *Natrix fasciata confluens*, respectively. The only known locality for *fasciata* in Illinois, at Horseshoe Lake, Alexander County, is close to the southernmost tip of the state. But *sipedon* is statewide in distribution (Smith, 1961, pp. 262–263). Pattern characteristics of *fasciata* appear in several population samples of *sipedon* from the following places: ½ mile south of Energy, Williamson County (I.N.H.S. No. 5060); 4 miles south of Energy, Williamson County (I.N.H.S. Nos. 6808–6811); and 2 miles west of Jonesboro, Union County (I.N.H.S. No. 6023). These localities are roughly 45 and 40 miles north-northeast, and 20 miles north, of Horseshoe Lake, respectively.

All six of these snakes are closest to *sipedon*. There are half-moons on the bellies of all, chiefly arranged in pairs, and the canthus rostralis is blunt in all except one. Three have dorsal patterns consisting of cross bands anteriorly that change to alternating blotches posteriorly, but in

two the cross bands continue to the tail, and in another they begin to alternate virtually at the anal region. The head is unicolored in one, but among the others there are indications of a head pattern resembling the type seen in the Carolinas and Virginia (fig. 6E) and which is probably best interpreted as convergence. One has well-defined "shadow" spots on the lower sides of the body, and another has traces of them. Smith's illustration of *Natrix sipedon pleuralis* (1961, p. 260) from Union County, Illinois, depicts a snake that is apparently cross-banded throughout its length.

The presence of pattern characteristics of *fasciata* in these Illinois populations of *sipedon* may represent introgression from either of two sources: (1) currently unknown populations of *fasciata* from localities lying to the north or northeast of Horseshoe Lake; or (2) from populations that formerly occurred in the general area. Habitats suitable for *fasciata* in southern Illinois are now probably limited to river flood plains. Such may not have been the case, at least during part of the post-Pleistocene period. Smith (1957, pp. 209–210) reviewed the evidence indicating that many southern animals were more widely distributed at northern latitudes during the Climatic Optimum than they are at present. *Natrix fasciata* may well have been among their number. If so, the presence of *fasciata* characters among demes of *sipedon* from localities to the north and northeast of the existing range might be interpreted as "relict" in the sense that contributions from *fasciata* have survived in the gene pools down to the present time.

Cliburn (1957, p. 193) reported intermediate specimens from both Mississippi and Louisiana, and personal examination has confirmed the hybrid nature of three of his four snakes from Forrest County, Mississippi. The fourth one, which he designated as J.W.C. No. 18–42 (now M.S.C. No. 53–1021), has all the characters of *sipedon*, and I would so identify it, but the virtual absence of melanophores on the belly results in a pale pattern somewhat resembling that of *fasciata*. Cliburn (*loc. cit.*) also mentioned a "blend" between the two species in the vicinity of Baton Rouge, Louisiana. I have seen four of the five snakes on which he based this statement (L.S.U.M.Z. No. 2883 cannot now be found). Among these one from Wakefield, West Feliciana Parish (L.S.U.M.Z. No. 2863), is a rather pale (faded?) *sipedon*. In the other three (L.S.U.M.Z. Nos. 4822, 5816, and 6110, all from south or southeast of Clinton, East Feliciana Parish) the characters of *fasciata* predominate. The ventral markings are large and squarish, the canthus rostralis is sharp, and traces of dark head stripes are evident in two. On the other hand, the dorsal patterns are peculiar. There is little indication of markings in the middorsal area, and

the only strongly dark pattern elements consist largely of narrow, vertical bars on the lower sides of the body. The largest specimen (L.S.U.M.Z. No. 6110), when submerged in fluid, shows indications of broad dark markings like those typically seen in *fasciata* (subspecies *confluens*). In all three snakes the black pigment is much reduced, which, in combination with the fact that the snakes have "shed in the bottle," makes a careful analysis of the patterns difficult, if not impossible. The dark lateral markings in the two smaller snakes (L.S.U.M.Z. Nos. 4822 and 5816) are strongly suggestive of those seen in some specimens of *sipedon*, but they number 16 and 17 and thus fall within the range of *fasciata* (*confluens*). I am inclined to view all three of these specimens as aberrant *fasciata* but am willing to admit that some *sipedon* influence may be present.

Further investigation will undoubtedly reveal other instances of hybridization, probably from a number of localities. Whether they represent introgression or the occasional production of non-viable hybrids may eventually be ascertained by experimental procedures, but the ophiologist in this respect is at a distinct disadvantage compared with his colleagues who study fishes and anurans. Not only is the developmental period longer, but the eggs cannot be fertilized externally or under controlled conditions. Also there is the problem of obtaining virgin females or those known to be free of viable sperm retained from previous matings.

ALLOPATRY AND SYMPATRY IN NORTH CAROLINA

As indicated, no hybrids have yet been found near or along the Fall Line in North Carolina. South of the Tar River and Pamlico Sound the mainland distribution of the two species is similar to that prevailing farther south, with *fasciata* confined to the Coastal Plain and with *sipedon* on the Piedmont and in the mountains. North of this area they occur sympatrically in fresh-water localities in or near the Tar River near Greenville, Pitt County, and probably also in the vicinity of Lake Phelps in Washington or Tyrrell County. Only *sipedon* occurs north of Albemarle Sound. (Refer to figs. 1A and 13.)

From Greenville and vicinity the following material is available: *Natrix fasciata* (A.M.N.H. Nos. 85405, 85406, 85409–85415, 85423), 10 adults, including three large females that gave birth to litters of 36, 27, and 17 young, respectively; *Natrix sipedon* (A.M.N.H. No. 85422), an adult female that gave birth to a litter of 22 young, and (N.C.S.M. No. 58.5.7) a subadult male. A comparison of these 114 snakes with one another reveals no evidence of hybridization.

Many specimens of *fasciata* have been seen from the eastward-projecting peninsula between Pamlico and Albemarle sounds, and the species apparently is abundant throughout the fresh-water lakes, streams, and swamps of the region. The single *sipedon* from this area (A.M.N.H. No. 43427) is from Lake Phelps; its pattern is typical, and neither it nor any *fasciata* from fresh-water localities on the peninsula show any indications of hybridization.

Specimens of *sipedon* from Vultare, Northampton County (A.M.N.H. No. 85427), and from Winton (A.M.N.H. No. 44924) and the Chowan River at Petty Shore, near Tunis (A.M.N.H. No. 85426), both in Hertford County, as well as many specimens from the Dismal Swamp region in both North Carolina and Virginia and eastward to the coast, show strong indications of convergence toward *fasciata* in their head patterns (fig. 6E), yet on the basis of other characteristics all are readily assignable to *sipedon.*

Werler and McCallion (1951, p. 251) state that most specimens from the Seashore State Park, Princess Anne County, Virginia, "lack lateral blotches and possess dorsal blotches which extend to the ventrals for the entire length of the body." Werler saw many water snakes while stationed in Princess Anne County during the early 1940's, but, among the small sample of five that I have examined from the Park, three are blotched posteriorly and two are cross-banded to the anus. Among 39 snakes from the Dismal Swamp area and eastward to the ocean, including the five from the Seashore State Park, only four are cross-banded throughout. The change from cross bands to alternating blotches occurs farther back on the body in this geographical region, however, than in samples from some other areas. For example, among the 39 specimens the number of cross bands varies from six to 33 (mean 15.8), whereas among 83 specimens from Nash County, North Carolina, the corresponding figures are five to 25 (mean 10.8). Available data on dorsal patterns in *sipedon* indicate, however, that the average point of change from cross bands to alternating blotches varies in local populations.

Natrix sipedon, which is characteristically a species of the Piedmont and the mountains in other parts of the two Carolinas, invades the Coastal Plain in northeastern North Carolina. It occurs sympatrically with *fasciata* in at least two localities, and completely replaces the latter species north of Albemarle Sound even in habitats that are extremely similar to those in which *fasciata* occurs abundantly a short distance farther south. The eastward displacement of the range of *sipedon* takes place in a region where the transition from the Piedmont to the Coastal Plain is not clearly defined. According to Fenneman (1938, p. 129), "The location of the Fall Line is . . . confused in the Carolinas by the fact that many streams,

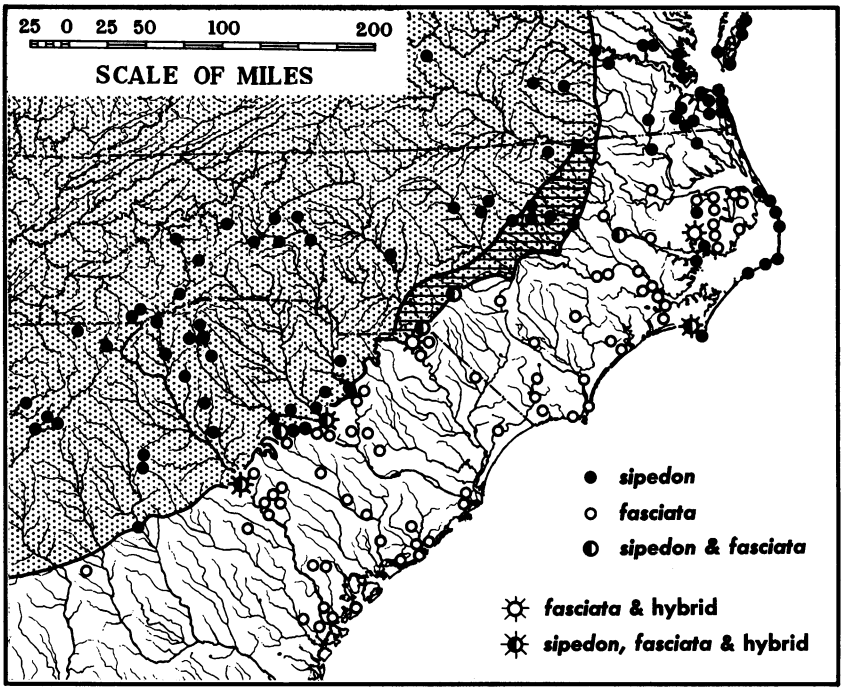


FIG. 13. Localities for snakes of the *Natrix sipedon-fasciata* complex in North and South Carolina and adjacent portions of Virginia and Georgia. (For additional Georgia localities, see Neill, 1946 and 1957.) The forms occurring in this area are *Natrix sipedon sipedon*, *Natrix sipedon pleuralis*, and *Natrix fasciata fasciata* (see fig. 1 for general distribution of the several subspecies). The Piedmont is indicated by stippling; the Coastal Plain is unpatterned. The position of the Fall Line, the boundary between them, is adapted from the following sources: North Carolina (Stuckey and Steel, 1953, fig. 1, and personal communication from Stuckey); South Carolina (Cooke, 1936, pl. 2); Virginia and Georgia (Fenneman, 1938, pls. 2, 3). Hatching indicates the Fall Line "zone" in North Carolina. Base map from the Museum of Zoology, University of Michigan.

the Roanoke, Tar, Neuse, Cape Fear, Peedee, and others, have their channels on crystalline rock and interspersed with rapids for 20 miles after entering the Coastal Plain."

Jasper L. Stuckey, North Carolina State Geologist, states (personal communication) that "the Fall Line in North Carolina is not a true line but a zone 25 to 30 miles wide." The Fall Line "zone" shown in figure 13 was drawn on the basis of information supplied by Stuckey and supplements figure 1 in Stuckey and Steel (1953). [Although the Fall Line through South Carolina, shown in both figs. 10 and 13, is adapted from

Cooke (1936, pl. 2), Horace G. Richards (personal communication) points out that a Fall Line "zone" is also involved in that state. Cooke's map (*loc. cit.*) shows many disconformities, with disjunct areas of Coastal Plain sediments occurring within the Piedmont, including Leesville from which both *sipedon* and *fasciata* are reported, and disjunct portions of the Piedmont within the Coastal Plain, including Red Bank from which a single specimen of *sipedon* is available.]

Rocky streams with gradient are common habitats of *sipedon*, but not of *fasciata*. *Natrix sipedon* is the characteristic species of the Fall Line "zone," and it has invaded the Coastal Plain for a considerable distance along the Tar River. Whether it has established itself in the face of competition from the apparently more abundant *fasciata* or whether its presence at Greenville is the result of flooding along the Tar River is not clear. Nor is it certain, from the small sample of *sipedon* available (a female and her litter plus a subadult male), whether genetic isolation is complete in this area. Further intensive collecting in the rivers that traverse the region may shed light on this problem. In this connection mention should be made of two specimens of *sipedon* (U.S.N.M. Nos. 8987a–b) allegedly from Kinston, Lenoir County, North Carolina. The presence of other obviously upland material in the United States National Museum from this same locality (Conant, 1943a, p. 17), and ascribed to the same collector, suggests that Kinston may have been the point of shipment of specimens rather than their actual origin. In any event this dubious locality is not shown on the map (fig. 13).

ANIMALS WITH SIMILAR DISTRIBUTIONS

The virtually exclusive ranges of *Natrix sipedon* and *Natrix fasciata* on opposite sides of the Fall Line through a large part of the Carolinas and Georgia are paralleled by the ranges of several pairs of amphibians. On the specific level are *Bufo americanus* and *Bufo terrestris*, *Pseudacris triseriata* and *Pseudacris nigrita*, and (much less clear cut) *Acris crepitans* and *Acris gryllus*. Subspecies pairs include (a) *Desmognathus fuscus fuscus* and *Desmognathus fuscus auriculatus* and (b) *Diemictylus viridescens viridescens* and *Diemictylus viridescens dorsalis* (with *louisianensis*).

There is no modern detailed review of the two species of *Bufo*, but a study of all available material, plus the careful plotting of locality records, may well demonstrate a distributional pattern similar to that of the two species of *Natrix*, with hybridization perhaps occurring in scattered localities along the common boundary of their ranges.

Several authors (Schwartz, 1957; Crenshaw and Blair, 1959; and

Batts, 1960) have discussed the specific status and distributions of the two species of *Pseudacris* in the Southeast, but thus far there is no detailed map for *nigrita* that includes its entire range, and there is no definitive work that thoroughly explores the problem of genetic isolation in such sympatric populations as are known.

The overlap in the ranges of the two cricket frogs (*Acris*) is so great that no satisfactory comparison can be made, yet *crepitans* is essentially an upland form, at least in the Carolinas, whereas *gryllus* is essentially a species of the Coastal Plain. How extensively each of these two frogs has invaded the range of the other since disturbance of the region by the human species probably will never be known.

In the case of the salamanders, allied races occur on opposite sides of the Fall Line zone.

There are comparable distributions among the fishes. For example, among the swamp darters of the subgenus *Hololepis* (genus *Etheostoma*), the species *collis* and *saludae* are restricted to the Piedmont and *fusiforme* and *serriferum* to the Coastal Plain (Collette, 1962, figs. 3 and 8).

Coastal Plain animals of a great many species have their ranges terminating at or near the Fall Line, but only a relatively few Piedmont-inhabiting species reach their terminus along the same boundary.

There is a striking parallel in the taxonomic history of three sets of triple reptile siblings, including the water snakes, all of which inhabit the Southeast and all of which consist of three distinct species that long masqueraded as one. These are: (1) *Natrix erythrogaster*, *Natrix fasciata*, and *Natrix sipedon;* (2) *Eumeces fasciatus*, *Eumeces inexpectatus*, and *Eumeces laticeps* (Taylor, 1935, p. 220); and (3) *Ophisaurus attenuatus*, *Ophisaurus compressus*, and *Ophisaurus ventralis* (McConkey, 1954, p. 133).

BRACKISH-WATER POPULATIONS

The presence of water snakes in brackish habitats on the coastal islands of North Carolina has been demonstrable at least since July, 1905, when a specimen now in the North Carolina State Museum was collected at Cape Hatteras. Others, taken from time to time, received little attention until Barbour (1943) described *Natrix sipedon engelsi* on the basis of a single specimen from Mullet Pond at the western end of the offshore Shackleford Banks. This locality is approximately 2 miles south-southeast of Beaufort, Carteret County. More recently, during a surge of biological interest in the fauna of the Outer Banks, many water snakes have been taken, and more than 70 are now available for examination. These represent localities on Roanoke, "Bodie," "Pea," Hatteras, and Ocracoke Islands and the

Core and Shackleford Banks. Also at hand are specimens from three brackish localities on the mainland side of Pamlico Sound, viz., from Ponzer and 7 miles west of Swanquarter, both in Hyde County, and Oyster Creek near Lowland, Pamlico County. There is also a specimen from a small woodland pool taken at Lennoxville Point, Carteret County, within a few yards of salt water along the shore. An analysis of patterns in this material reveals another interesting facet of the *sipedon-fasciata* complex.

With two exceptions, all *Natrix* population samples seen from brackish-water localities in North Carolina are readily identifiable as *sipedon.* The exceptions involve snakes from Ponzer, which is at the head of the Pungo River estuary, and those from and near the Shackleford Banks. An adult female (A.M.N.H. No. 88077) from Ponzer, measuring nearly a meter in length but with part of the tail missing, gave birth to 24 young (A.M.N.H. Nos. 88078–88101) on August 29, 1961. The mother appears to exhibit all the characters of *fasciata,* although she has such an abundance of black pigment that much of her pattern is obscured. The young are variable. The dorsum is cross-banded from the head to the base of the tail (as in *fasciata*) in 10 of the young; the cross bands are replaced posteriorly by alternating dorsal and lateral blotches (as in *sipedon*) in 11; in the remaining three there are lateral blotches at scattered places along the body. The dark markings on the venter vary, but they tend strongly toward those in *fasciata;* only four of the 24 young have belly markings that approach those of *sipedon.* The head patterns run the gamut from the sharply defined dark postocular stripe seen in many *fasciata* to the mottled head pattern that occurs in *sipedon.* Scoring was arbitrary, but, after all pattern characters were considered, 10 of the young were placed closest to *sipedon,* seven closest to *fasciata,* and seven were considered intermediate. I interpret the result of this scoring as evidence of hybridization between *sipedon* and *fasciata* (*fasciata* introgression in gene pools of *sipedon*?).

The deme from Mullet Pond on the Shackleford Banks is represented by seven adults and three litters of young. Among these the holotype of *engelsi* (M.C.Z. No. 46688) is cross-banded throughout the length of the body, and its head and belly markings are also like those of *fasciata.* It was chiefly for this reason that I placed *engelsi* in the synonymy of *fasciata* (Conant, 1961, p. 19). Several snakes from this island are identifiable as *fasciata,* but others show variations comparable with those reported above among the litter of young from Ponzer. It is possible that the Shackleford Banks were originally populated solely by *Natrix sipedon,* but, if so, their gene pool is now evidently being diluted by contributions from *fasciata* populations from the mainland. Engels (1952, p. 739) commented upon

the opportunities for fortuitous introduction of terrestrial vertebrates on the Shackleford Banks. A semiaquatic animal like *Natrix fasciata* would have even greater opportunity of being transported from the mainland, and, under the influence of the strong, storm-induced currents that occasionally sweep westward along the northern side of the island (Engels, 1952, p. 720), specimens of *fasciata* may occasionally make landfalls near Mullet Pond. Snakes from all the brackish-water localities tend to be dark in coloration, but those from the Shackleford Banks are especially so.

The influence of *sipedon* is also evident on the nearby mainland, for the snake taken near the shore at Lennoxville Point (W.L.E. No. 1337) also appears to be a hybrid between *sipedon* and *fasciata.*

The water snakes that inhabit the Outer Banks have a strong tolerance for salt water. Engels (1942, p. 290) pointed out that all of Ocracoke Island, with the exception of the highest dunes, is inundated during severe storms. He also (1952, p. 704) stated that there were no fresh-water ponds on the Shackleford Banks and commented on the salinity of Mullet Pond, which was a bay on the north shore of the island until a few years ago. John B. Funderburg (personal communication) states that the first *Natrix* he collected on the Outer Banks were "shot in salt-water canals with seaside sparrows singing all around, and the snakes were crawling in *Spartina alterniflora* marsh with horse mussels, oysters, barnacles, blue crabs, and other salt-water species all about them with no sign of fresh-water life anywhere."

Fresh-water ponds, artificially created at the Pea Island Refuge on Hatteras Island, are inhabited by *Natrix sipedon*, and these snakes also live in other ponds of the Outer Banks which at times are fresh or nearly fresh depending on the interrelation of heavy rains and high tides.

These observations and other preliminary studies made on the brackish-water populations warrant the following tentative conclusions: (1) *Natrix sipedon* ranges southward along the chain of the Outer Banks at least to the Core Banks and probably to the Shackleford Banks. (2) It also ranges south along the inner (mainland) side of Pamlico Sound. (3) It maintains its identity in most brackish-water habitats but occasionally hybridizes with *fasciata* where their distributions are contiguous, as at Ponzer and Lennoxville Point, on the mainland, and in Mullet Pond, on the Shackleford Banks. (4) *Natrix sipedon* has not invaded fresh-water habitats on the Coastal Plain in the Carolinas except in the extreme northernmost portion of the range of *Natrix fasciata* (as indicated by specimens from Greenville and Lake Phelps) and other areas farther north.

More satisfactory conclusions must await: (1) detailed studies of the specimens already at hand; (2) a search for additional material, especially

from the western perimeter of Pamlico Sound; (3) testing of the chloride content of water from actual habitats; and (4) determination of salinity tolerances among living samples of brackish-water *sipedon* and fresh-water *fasciata* and *sipedon*. I am pursuing such studies as rapidly as time will permit, and their results should aid in answering the following pertinent questions:

Is a relict population involved, possibly representing a form that was widespread before the subsidence of Pamlico Sound? If so, is it entitled to subspecific recognition, as Robertson and Tyson (1950, p. 142) suggest?

Or is *sipedon* a recent invader from the north? Has it moved southward along the island chain from a mainland base in the vicinity of Currituck Sound? At least two other vertebrates have similar distributions on the islands; the song sparrow occurs southward to Ocracoke but not beyond (Engels, 1952, p. 733), and the muskrat is absent from islands south of Cape Hatteras (*ibid.*, p. 735).

What is the status of salt-tolerant populations of *sipedon* that occur farther north? Werler and McCallion (1951, p. 251) report this snake from brackish habitats in Princess Anne County, Virginia, and the species occurs in estuaries of Chesapeake Bay and on some of the barrier beach islands of the Delmarva Peninsula.

DISCUSSION

Obviously, from the above, I subscribe to the following criteria for determining whether two dissimilar populations differ at the specific or subspecific level: (a) Intergradation between subspecies is involved when the ranges of two allopatric forms are geographically contiguous and there is a clear transition from one to the other through series of individuals that are intermediate in most respects between the two forms involved. (b) Hybridization between species is indicated when intermediate individuals are of sporadic occurrence, or if they vary widely in their resemblance to one or the other of the parent species. (c) Wide geographic overlap, with few or no intermediates, is indicative of difference at the species level.

In a review of the data presented in this paper, the following facts can be marshaled as evidence for elevating *Natrix fasciata* to specific status:

1. *Natrix sipedon* and *Natrix fasciata* are sympatric through a considerable area in the Mississippi Valley and in the Gulf coastal region, and intermediates between them in this region are apparently few and of sporadic occurrence.

2. Both *sipedon* and *fasciata* also occur sympatrically in fresh-water

habitats in northeastern North Carolina. Whereas *fasciata* is virtually confined to fresh water in this region, *sipedon* also occupies a brackish- or salt-water habitat on the Outer Banks of North Carolina and along the shores of Pamlico Sound. Hybrids between the two occur, apparently sporadically, where fresh and salt water meet.

3. The two forms are allopatric along the Fall Line in Georgia and the Carolinas, but hybrids characterized by wide variations in pattern occur in a few localities where the ecological balance obviously has been seriously disturbed by the activities of mankind.

4. There is evidence of genic introgression in southern Illinois, and introgression may also occur in other localities (quite probably in the Fairwold Pond near Columbia, South Carolina) where the two forms have apparently been brought into recent contact by serious disruption of habitats.

5. No data are at hand from anywhere within the ranges of the two species that would conform with criterion "a" above, and the assumption is possible that there is nowhere a clear transition from *sipedon* to *fasciata* that could be considered as intergradation.

SUMMARY

A new interpretation of the *sipedon-fasciata* complex of the water snake genus *Natrix* is proposed. *Natrix fasciata* is elevated to specific status with the inclusion of three fresh-water races, *fasciata*, *confluens*, *pictiventris;* pending studies on the salt-marsh snakes, the forms *clarki*, *compressicauda*, and *taeniata* are retained as additional races of *fasciata*. The remaining members of the complex, namely, *sipedon*, *pleuralis*, and *insularum*, are left in the species *Natrix sipedon*.

Sympatry between the species *sipedon* and the species *fasciata* is demonstrated over a wide area, with specific instances listed from Arkansas, Florida, Georgia, Illinois, Louisiana, Mississippi, North Carolina, Oklahoma, and Tennessee.

The two species are allopatric in many other areas; for example, from east central North Carolina to Georgia their respective ranges meet on opposite sides of the Fall Line. Intermediate specimens that combine characters of both *sipedon* and *fasciata* are described from several localities near the Fall Line in South Carolina and Georgia where there is evidence of recent disturbance of the habitat by mankind. Such intermediate specimens are believed to be the products of hybridization.

Many specimens of *sipedon* from near the common boundary of the two species in the Carolinas and extreme southeastern Virginia exhibit head

patterns that include a dark postocular element grossly similar to the dark postocular stripe that is characteristic of *fasciata.* This phenomenon is interpreted as convergence.

Natrix sipedon occurs on the Outer Banks of North Carolina and in brackish waters along the inner (mainland) edge of Pamlico Sound. *Natrix fasciata* in the same general region is confined to fresh-water habitats on the mainland, except that it apparently has fortuitously reached the Shackleford Banks, which lie close inshore. On this island, on the adjacent mainland, and at the head of the Pungo River estuary, in all of which fresh- and brackish-water habitats are in close proximity, there is evidence of hybridization between *sipedon* and *fasciata.*

ACKNOWLEDGMENTS

Many persons have assisted in the preparation of this paper; a number of them have already been mentioned in the text. I am especially indebted to Mr. Albert E. Sanders, of Columbia, South Carolina, for his enthusiastic interest, his painstaking checking of obscure localities in the Southeast, his drafting of the base map from which figure 10 was prepared, for the gift of many specimens, and for numerous other favors. Mrs. Norma Rothman has done most of the scale counting, contributing scores of woman-hours on this important but time-consuming chore. Mr. William M. Palmer collected and presented many snakes, including numerous gravid females, from several parts of North Carolina. Mr. Carl Gerhardt, Mr. James S. Hartin, Mr. James W. Hinnant, Mr. Perry Rogers, Mr. Barry Rothman, Mr. Richard Thomas, and Mr. David E. Whitehead all provided specimens from critical localities. Dr. J. William Cliburn, Dr. Bruce B. Collette, Dr. Coleman J. Goin, Dr. Richard B. Loomis, Mr. Wilfred T. Neill, Dr. Donald W. Tinkle, Mr. Frederick A. Ulmer, Jr., and Dr. Robert G. Webb all supplied helpful data.

Specimens were borrowed through the courtesy of the following persons: Dr. James E. Böhlke and Mr. Edmond V. Malnate, of the Academy of Natural Sciences of Philadelphia (A.N.S.P.); Mr. Charles M. Bogert and Dr. Richard G. Zweifel, of the American Museum of Natural History (A.M.N.H.); Mr. Neil D. Richmond, of the Carnegie Museum (C.M.); Dr. Albert Schwartz (formerly) and Dr. E. Milby Burton, of the Charleston Museum (Ch.M.); Dr. William J. Hamilton, Jr., of Cornell University; Dr. Robert F. Inger, of the Chicago Natural History Museum; Dr. Joseph R. Bailey, of Duke University; Dr. William L. Engels and Dr. Douglas A. Rossman, of the University of North Carolina (Engels' private collection—W.L.E.); Dr. John B. Funderburg, of Florida Southern

College; Dr. Philip W. Smith, of the Illinois State Natural History Survey (I.N.H.S.); Dr. George H. Lowery, Jr., of the Louisiana State University Museum of Zoology (L.S.U.M.Z.); Dr. J. William Cliburn, of the Mississippi Southern College (M.S.C.); Dr. Ernest E. Williams, of the Museum of Comparative Zoölogy (M.C.Z.); Mr. Roger Rageot, of the Norfolk Museum; Messrs. Harry T. Davis and William M. Palmer, of the North Carolina State Museum (N.C.S.M.); Dr. Hobart M. Smith, of the University of Illinois Natural History Museum; Dr. Harold A. Dundee, of Tulane University (T.U.); Dr. Norman E. Hartweg and Mr. Frederick R. Gehlbach, of the University of Michigan Museum of Zoology (U.M.M.Z.); Dr. Doris M. Cochran, of the United States National Museum (U.S.N.M.); and Dr. Harry W. Freeman, of the University of South Carolina Research Collections (U.S.C.R.C.).[1] Several of the persons associated with these many collections rendered valued and appreciated assistance in other ways. Mrs. Ruth G. Endy and Miss Judith E. Cohen typed the manuscript.

Mr. Charles M. Bogert, Dr. William M. Clay, Mr. Edmond V. Malnate, and Dr. Philip W. Smith all read the manuscript and offered constructive criticisms. I am particularly grateful to Dr. Clay for his deep interest in the subject, for many helpful suggestions, and for the loan of a copy of his manuscript thesis. The photograph reproduced as figure 11 was contributed by Mr. James S. Hartin; that for figure 12 by Mr. Richard Thomas. All other illustrations, including photographs, drawings, and maps, are by my wife, Mrs. Isabelle Hunt Conant, who not only helped thus tangibly but who, because my herpetological research is conducted at home, endured many months when virtually every evening and weekend were devoted to this investigation.

LITERATURE CITED

ANDERSON, EDGAR

1949. Introgressive hybridization. New York, John Wiley and Sons, Inc., pp. i–x, 1–109, figs. 1–23, pls. 1–5.

BARBOUR, THOMAS

1943. A new water snake from North Carolina. Proc. New England Zool. Club, vol. 22, pp. 1–2, pl. 1.

BATTS, BILLY S.

1960. Distribution of *Pseudacris nigrita nigrita* and *Pseudacris nigrita feriarum*

[1] While this paper was in press, word was received that Freeman is, at the present time, associated with the College of Charleston, and all specimens herein designated by the initials U.S.C.R.C. have been transferred to the Charleston Museum collection.

in the piedmont and coastal plain regions of North Carolina. Herpetologica, vol. 16, pp. 45–47, fig. 1.

BLANCHARD, FRANK NELSON

1923. A new North American snake of the genus *Natrix*. Occas. Papers, Mus. Zool., Univ. Michigan, no. 140, pp. 1–6, 1 map.

BOULENGER, GEORGE ALBERT

1893. Catalogue of snakes in the British Museum (Natural History). London, vol. 1, pp. i–xiii, 1–448, figs. 1–26, pls. 1–28.

CARR, ARCHIE FAIRLY, JR., AND COLEMAN JETT GOIN

1942. Rehabilitation of *Natrix sipedon taeniata* Cope. Proc. New England Zool. Club, vol. 21, pp. 47–54, pls. 6–7.

CLAY, WILLIAM MARION

1938. A synopsis of the North American water snakes of the genus *Natrix*. Copeia, pp. 173–182.

[MS.] The taxonomy and phylogenetic relationships of the water snakes, *Natrix erythrogaster* and *N. sipedon*. Ann Arbor, University of Michigan, thesis completed in 1936.

CLIBURN, J. WILLIAM

1957. Some southern races of the common water snake, *Natrix sipedon*. Herpetologica, vol. 13, pp. 193–202, figs. 1–3.

COLLETTE, BRUCE BADEN

1962. The swamp darters of the subgenus *Hololepis* (Pisces, Percidae). Tulane Stud. Zool., vol. 9, pp. 115–211, figs. 1–18.

CONANT, ROGER

1943a. The milk snakes of the Atlantic coastal plain. Proc. New England Zool. Club, vol. 22, pp. 3–24, pls. 2–4, 1 map.

1943b. *Natrix erythrogaster erythrogaster* in the northeastern part of its range. Herpetologica, vol. 2, pp. 83–86.

1958. A field guide to reptiles and amphibians. Boston, Houghton Mifflin Co., pp. i–xviii, 1–366, figs. 1–62, pls. 1–40, maps 1–248.

1961. A new water snake from Mexico, with notes on anal plates and apical pits in *Natrix* and *Thamnophis*. Amer. Mus. Novitates, no. 2060, pp. 1–22, figs. 1–2.

COOKE, CHARLES WYTHE

1936. Geology of the coastal plain of South Carolina. Bull. U. S. Geol. Surv., no. 867, pp. i–vi, 1–196, figs. 1–2, pls. 1–18.

COPE, EDWARD DRINKER

1900. The crocodilians, lizards and snakes of North America. Rept. U. S. Natl. Mus., for 1898, pp. 153–1294, figs. 1–347, pls. 1–36.

CRENSHAW, JOHN WALDEN, JR., AND WILLIAM FRANKLIN BLAIR

1959. Relationships in the *Pseudacris nigrita* complex in southwestern Georgia. Copeia, pp. 215–222, figs. 1–4.

ENGELS, WILLIAM LOUIS

1942. Vertebrate fauna of North Carolina coastal islands: A study in the dynamics of animal distribution: I. Ocracoke Island. Amer. Midland Nat., vol. 28, pp. 273–304, figs. 1–11.

1952. Vertebrate fauna of North Carolina coastal islands: Shackleford Banks. *Ibid.*, vol. 47, pp. 702–742, figs. 1–13.

FENNEMAN, NEVIN M.

1938. Physiography of eastern United States. New York, McGraw-Hill Book

Co., pp. i–xiv, 1–714, figs. 1–197, pls. 1–7.

GORDON, ROBERT EDWARD

1952. A range extension for the watersnake, *Natrix sipedon pleuralis* Cope. Copeia, pp. 116–117.

GOSSE, PHILIP HENRY

1851. A naturalist's sojourn in Jamaica. London, pp. i–xxiv, 1–508, pls. 1–8.

LOENNBERG, EINAR

1894. Notes on reptiles and batrachians collected in Florida in 1892 and 1893. Proc. U. S. Natl. Mus., vol. 17, no. 1003, pp. 317–339, figs. 1–3.

MCCONKEY, EDWIN H.

1954. A systematic study of the North American lizards of the genus *Ophisaurus*. Amer. Midland Nat., vol. 51, pp. 133–171, figs. 1–5, pls. 1–2.

MAYR, ERNST, EARLE GORTON LINSLEY, AND ROBERT LESLIE USINGER

1953. Methods and principles of systematic zoology. New York, McGraw-Hill Book Co., pp. i–x, 1–328, a–h, figs. 1–45, al–a2.

NEILL, WILFRED T.

1946. Notes on banded water snakes from Georgia. Copeia, pp. 255–256.

1954. Ranges and taxonomic allocations of amphibians and reptiles in the southeastern United States. Publ. Res. Div., Ross Allen's Reptile Institute, vol. 1, pp. 75–96.

1957. Distributional notes on Georgia amphibians, and some corrections. Copeia, pp. 43–47.

PARKER, MALCOLM V.

1939. The amphibians and reptiles of Reelfoot Lake and vicinity, with a key for the separation of species and subspecies. Jour. Tennessee Acad. Sci., vol. 14, pp. 72–101, figs. 1–14.

1948. A contribution to the herpetology of western Tennessee. *Ibid.*, vol. 22, pp. 20–30.

RHOADS, SAMUEL N.

1895. Contributions to the zoology of Tennessee: No. 1, Reptiles and amphibians. Proc. Acad. Nat. Sci. Philadelphia, vol. 47, pp. 376–407.

ROBERTSON, WILLIAM BECKWITH, AND EDWIN L. TYSON

1950. Herpetological notes from eastern North Carolina. Jour. Elisha Mitchell Sci. Soc., vol. 66, pp. 130–147.

SCHWARTZ, ALBERT

1957. Chorus frogs (*Pseudacris nigrita* LeConte) in South Carolina. Amer. Mus. Novitates, no. 1838, pp. 1–12, fig. 1.

SMITH, PHILIP WAYNE

1957. An analysis of post-Wisconsin biogeography of the prairie peninsula region based on distributional phenomena among terrestrial vertebrate populations. Ecology, vol. 38, pp. 205–218, figs. 1–46.

1961. The amphibians and reptiles of Illinois. Illinois Nat. Hist. Surv. Bull., vol. 28, pp. i–vi, 1–298, figs. 1–252, 1 pl.

STEJNEGER, LEONHARD, AND THOMAS BARBOUR

1917. A check list of North American amphibians and reptiles. Cambridge, Harvard University Press, pp. i–iv, 5–125.

1923. [Same title.] Second edition. Cambridge, Harvard University Press, pp. i–x, 1–171.

1933. [Same title.] Third edition. Cambridge, Harvard University Press, pp. i–xiv, 1–185.

1939. [Same title.] Fourth edition. Cambridge, Harvard University Press, pp. i–xvi, 1–207.

1943. [Same title.] Fifth edition. Bull. Mus. Comp. Zoöl., vol. 93, pp. i–xix, 1–260.

STUCKEY, JASPER LEONIDAS, AND WARREN G. STEEL

1953. Geology and mineral resources of North Carolina. North Carolina Dept. Conserv. and Development, Educ. Ser., no. 3, pp. i–vi, 1–34, figs. 1–2, pl. 1.

TAYLOR, EDWARD HARRISON

1929. A revised checklist of the snakes of Kansas. Univ. Kansas Sci. Bull., vol. 19, pp. 53–62.

1935. A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces* with an account of the distribution and relationships of its species. Kansas Univ. Sci. Bull., vol. 23, pp. 1–643, figs. 1–84, pls. 1–43.

WERLER, JOHN E., AND JAMES MCCALLION

1951. Notes on a collection of reptiles and amphibians from Princess Anne County, Virginia. Amer. Midland Nat., vol. 45, pp. 245–252, figs. 1–5.

WOODMAN, NANCY CARPENTER

[MS.] The systematic status of *Natrix sipedon* in the interior highlands. Fayetteville, University of Arkansas, thesis completed in 1959.