Geographic Variation of *Elaphe guttata* (Reptilia: Serpentes) in the Atlantic Coastal Plain

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Variation in 11 characters of *Elaphe guttata* is analyzed in 264 specimens (149 males, 116 females) from 18 localities along the Atlantic Coastal Plain. Six characters exhibit clinal variation: ventrals, subcaudals, body blotches, tail length/total length ratios, amount of ventral pigment and amount of blotch border pigment. Meristic and morphometric clines generally run from low counts in the north to high counts in the south. Pigmentation decreases clinally from southern Florida through the lower Keys. Discordant variation is present in the remaining five characters. The results support a recent inclusion of *E. g. rosacea* in the synonymy of *E. g. guttata.*

ELAPHE guttata is a wide ranging species occurring throughout much of North America east of the Rocky Mountains and south of the 40° N latitude. A disjunct population occurs along the border of central Colorado-Utah (Conant, 1975). In the Atlantic Coastal Plain it is found from the New Jersey Pine Barrens south to Key West, Florida, a distance of some 2000 kilometers. Within this area two species are sometimes recognized; *E. g. guttata*,which occurs on the mainland and *E. g. rosacea*, of the Florida Keys.

Until recently variation in *E. guttata* has been little studied. Woodbury and Woodbury (1942) examined variation relative to the western disjunct population. Dowling (1951a) was the first to publish, pro parte, any broad account and then only to demonstrate differences in widely scattered parts of its range. Duellman and Schwartz (1958) compared three characters of four samples in Florida. Most recently Thomas (1974) analyzed the variation of *E. guttata emoryi* and selected samples in the southeast. His conclusions on the status of *rosacea* are based on samples from areas in northern and southern Florida. My study analyzes the variation of *E. guttata* in the Atlantic Coastal Plain in 18 samples to determine geographic trends of meristic, pattern and color variation and the validity of a distinct subspecific population in the Florida Keys.

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Materials and Methods

A total of 264 specimens of *Elaphe guttata* were examined. Ventrals were counted as proposed by Dowling (1951b); subcaudals from the vent to and including the terminal spine; dorsal body blotches from the one immediately posterior to the spear point pattern on the head to and including the one over the anus. Blotches connected by a bridge of pigment were counted as separate blotches. Dorsal scale rows were counted at one head length posterior to the parietal scales, at midbody and at one head length anterior to the anal plate. The following head scale counts were taken as defined by Peters (1964): frontal, loreals, parietals, preoculars, postoculars, temporals, supralabials, infralabials, anterior chin shields and posterior chin shields. Amount of ventral pigmentation was compared by constructing an arbitrary code of 0 to 5 (Fig. 1). This was matched to a 12 scale segment at midbody. The amount of black pigment surrounding the dorsal body blotches was also compared with a code of 0 to 5; 0 = no pigment, 1 = pigment width ¼ scale length, 1 = ½ scale length, 3 =

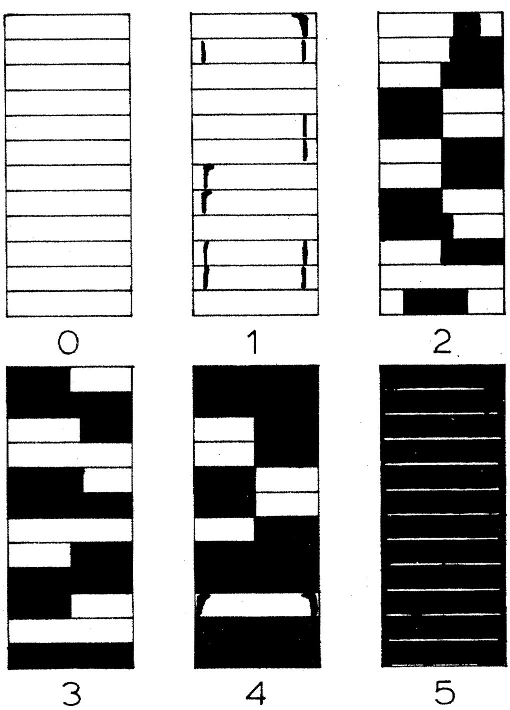

Fig. 1. Ventral pigmentation code for Atlantic Coastal Plain *Elaphe guttata*.

¾ scale length, 4 = scale length and 5 = greater than 1 scale length. An average of the anterior, midbody and anal blotches was used as the actual value. When hemipenes were not in evidence, sex was determined by dissection.

Data were analyzed with the Means Procedure of the SAS package (Barr and Goodnight, 1972) on the Virginia Commonwealth University computer. Sample means were compared with Kruskal-Wallis, Student-Newman-Kuels and t-tests where deemed necessary. The term "significant", where used, refers to samples which differ from each other at the .05 level. Because of sexual dimorphism in three characters samples were separated by sex. In some cases this so reduced the sample size that conclusions are tentative.

Specimen localities were plotted on a map and grouped into geographical units. Usually, these units involve one or two counties. This breakdown resulted in 18 samples defined in Appendix A and Fig. 2. Samples of less than 5 are included for the purpose of geographic completeness.

Character Analysis

Ventral scales.—The number of ventral scales varies from 205–238 in males and from 210–244 in females. Males average six fewer ventrals in the various samples.

This character exhibits a weak north–south cline with northern counts being fewer than southern counts (Fig. 3). Except for the Upper Keys (Q) and Manatee Co. (O) samples, the male mean in the Lower Keys (R) differs significantly from samples north of it. The female mean in (R) is not significantly different from the Canaveral (M) or Manatee Co. (O) sample mean but does differ significantly from the other samples.

Subcaudal scales.—Male subcaudals range from 55–84 and those of females from 47–81. Females average 3.5 fewer scales than males.

Like ventrals, subcaudal scale counts for both sexes increase north to south (Fig. 4). Lower Keys (R) males do not differ significantly from either those in the Upper Keys (Q) or Dade Co. (P) samples. Lower Keys (R) females differ significantly from Dade Co. (P) females but not those in the Upper Keys (Q).

Temporal scales.—Thirty-six primary and secondary temporal scale combinations were recorded. R-L and L-R are combined. Most of the variation from the normal count of 2 + 3/2 + 3 (42.1%) involves divided primary and/or added secondary temporal scales. Samples of ⩾10 have 4 to 10 combinations with the Lower Keys (R) sample having a mode of 14. No geographical or sexual variation is present.

Labial scales.—The majority of the specimens have 8-8 supralabials (97.7%). Only six have other counts: 6-8, 7-7, 8-7 (2) and 8-9 (2). This consequently changed the supralabials entering the eye, normally the 4th and 5th. Infralabials are more variable. Of the eight counts recorded the symmetrical 11-11 combination occurs with the highest frequency (76.0%). R-L and L-R counts are combined. No geographically or sexually correlated variation is present.

Other head scales.—Few of the other head scales examined deviated from a constant. Parietals are paired in all but NCSM 912 which has a single parietal. Preocular scales are 1-1 except for FSC 1273 with a 1-2 count. The following counts are constant for all specimens examined: divided anal, frontal 1, loreals 1-1, postoculars 2-2, anterior chin shields 2 and posterior chin shields 2.

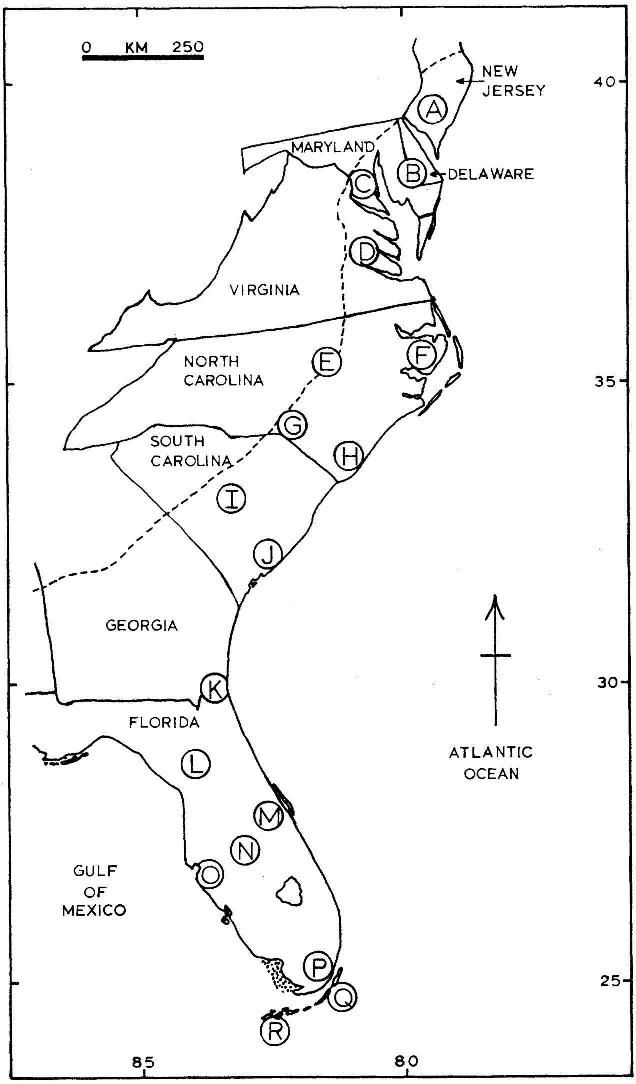

Fig. 2. Sample localities for the Atlantic Coastal Plain *Elaphe guttata*. Dashed line represents Fall Line. Appendix A gives detailed locality data.

Dorsal scale row formulae.—Fifty-five abbreviated dorsal scale row formulae were recorded for 248 specimens. The most common is 25-27-19 (24.2%). Forty-three % of the variation involves an addition or reduction of 1–2 scales anteriorly and posteriorly. There is no geographic or sexual variation in this character.

Thomas (1974) indicated that *E. guttata* males generally have 19 or fewer scale rows near the tail, whereas females usually have 20 or more. In my samples 86.9% of the males and 71.1% of the females have 19 or fewer posterior-dorsal scale rows compared to 13.1% of the males and 28.9% of the females with 20 or more such rows. Thus, Thomas' conclusions are not strongly supported by Atlantic Coastal Plain *E. guttata.*

Position of the umbilicus.—A sufficient number of hatchling specimens were available for comparison of this character in five samples. A cline is evident for both sexes (Table 1). Males average 3.6 fewer ventral scales to the anterior edge of the umbilicus than females. It appears this is a sexually dimorphic character and, indeed, has been used as such by Edgren (1951), Palmer (1971) and Richmond (1954). This is

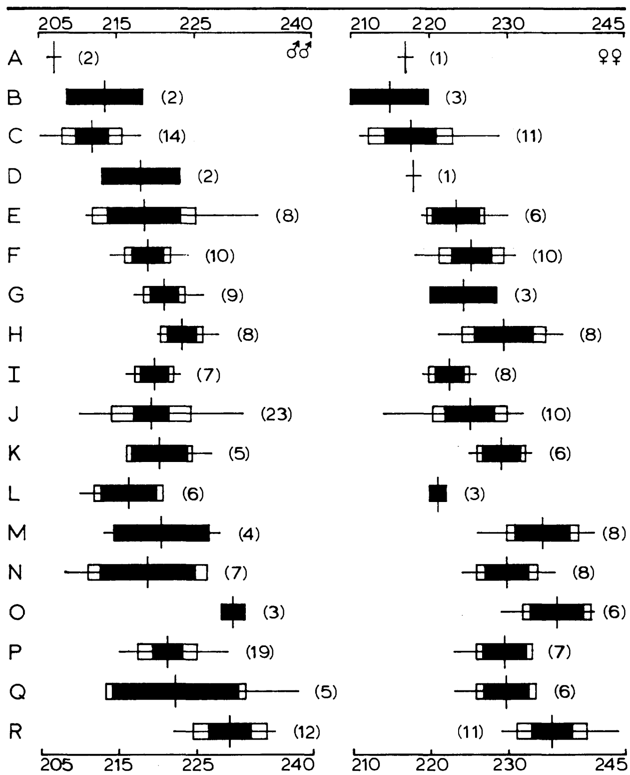

Fig. 3. Variation in number of ventral scales of Atlantic Coastal Plain *Elaphe guttata*. Letters identify the sample localities illustrated in Fig. 1. Mean is represented by a vertical line, horizontal line represents the range, white rectangle one standard deviation and black rectangle two standard errors of the mean. Sample size is in parentheses.

not the case, however, as pointed out by Martof (1954) and Thomas (1974). The value in this analysis is that it substantiates the clinal variation and sexual dimorphism of the ventral scale counts.

Dorsal body blotches.—There is no significant difference between male and female sample means for this character.

The overall trend appears to be a slight increase in counts north to south (Fig. 5). Except for the Manatee Co. sample (O) there is no significant difference between the Lower Keys sample (R) mean and other Fla. and Ga. sample means (K-N, P-Q).

Ventral pigment.—Results of this character analysis are presented in Fig. 6. The variation in amount of ventral pigmentation is relatively the same throughout the Atlantic Coastal Plain except for the Upper and Lower Keys (Q-R). In samples P–R the decrease appears to be clinal. The Lower Keys sample (R) is significantly different from samples north of it. The Upper Keys sample (Q) is significantly different from northern samples except for Polk-Highlands (N).

This lack of ventral pigment is the major criterion used in distinguishing *rosacea* from its nominate form. However, juveniles from the Lower Keys usually have amounts of pigment similar to those found on the mainland (Duellman and Schwartz, 1958; Thomas, 1974). The three Lower Keys juveniles in this study (SV $\geqslant$ 384 mm) have an average pigmentation code of 2.3. Both Duellman and Schwartz (1958) and Thomas (1974) suggest the difference between juveniles and adults is ontogenic.

Dorsal blotch border pigment.—The amount of black pigment surrounding the dorsal blotches varies from none to greater than scale deep. The results (Fig. 6) show that, with the exception of the Dade Co. (P) sample, specimens

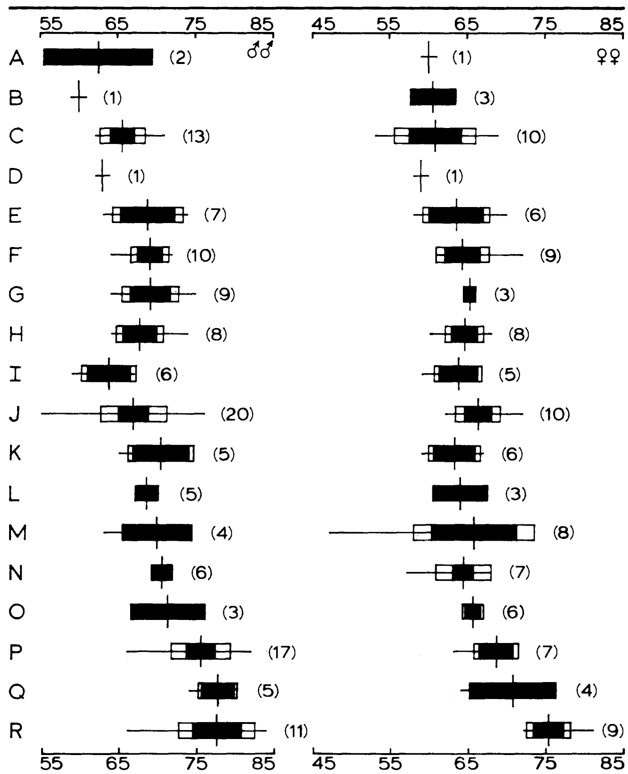

Fig. 4. Variation in number of subcaudal scales in Atlantic Coastal Plain *Elaphe guttata*. See Fig. 3 for explanation of symbols.

from Florida have less border pigment than those farther north. There appears to be a slight north–south clinal decrease in the Keys (P-R). The samples north of Florida have border pigment averaging greater than 0.5 scale length in width and those in Florida, except Dade Co., average less than or equal to 0.5 scale length in width. The Lower Keys sample (R) is significantly different from the Upper Keys (Q) and Dade Co. (P) samples but not from the Polk-Highlands (N) and Manatee Co. (O) samples.

Tail length/total length ratio.—Male ratios average about 1% higher than females. Ratios do not appear to be clinal except for a weak increase from Dade Co. (P) through the Lower Keys (R) for both sexes (Table 2). Females from the Lower Keys (R) differ significantly from Dade Co. (P) females but not those in the Upper Keys (Q). There is no significant difference between males in these three samples.

The percentage of incomplete tails was determined when it appeared that sample sizes in some cases were greatly reduced. The result showed that 17.2% of all specimens have parts of the tail missing; 18.3% of the males and 15.7% of the females. No geographic or sexual variation is present.

Discussion and Summary

Most variation found in snake species is thought to have a genetic basis; but, as Fox (1948) and Fox et al. (1961) demonstrate, the environment may influence morphological expression. It may be best, until such problems can be clarified, to classify snake variation without regard to causes. The classifications used here are sexual, geographical and discordant. The term "discordant" herein refers to that variation not differentiated by either sex or geography. Ontogenic variation is not considered in this paper. This scheme is adapted from those used by Grobman (1941) and Myers (1967).

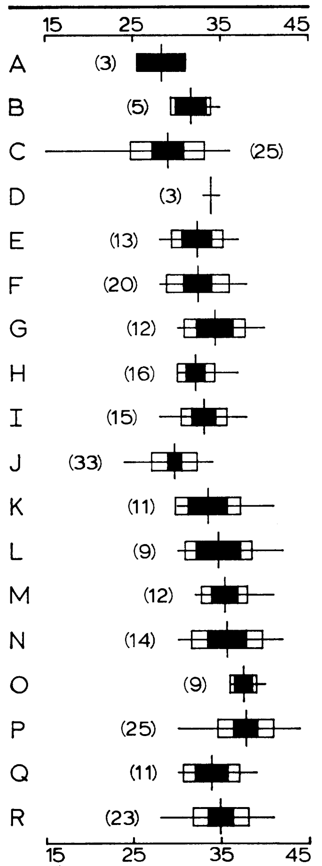

Fig. 5. Variation in number of dorsal body blotches of Atlantic Coastal Plain *Elaphe guttata*. See Fig. 3 for explanation of symbols.

TABLE 1. GEOGRAPHIC VARIATION IN NUMBER OF VENTRAL SCALES TO UMBILICUS OF ATLANTIC COASTAL PLAIN *Elaphe guttata*. (N = sample size, S.D. = one standard deviation, 2 S.E. = two standard errors of the mean.)

Sample	N	Mean	Range	S.D.	2 S.E.
		MALES			
C	5	180.8	174–187	5.26	4.70
E	4	189.3	181–195	6.02	6.02
F	5	190.0	185–194	3.54	3.17
H	7	191.9	188–199	3.67	2.77
O	3	199.7	199–201	1.15	1.33
		FEMALES			
C	6	181.2	175–186	4.26	3.48
E	2	194.5	190–199	6.36	8.99
F	7	192.4	185–198	4.79	3.48
H	5	197.0	184–204	8.00	7.16
O	5	204.6	200–208	3.21	2.87

Sexual variation in Atlantic Coastal Plain *Elaphe guttata* is present in three characters: ventrals, subcaudals and tail length/total length ratios. Males have fewer ventrals, more subcaudals and a greater tail length/total length ratio than females. Since males have slightly shorter bodies and longer tails to accommodate the hemipenial muscles these differences would be expected.

Geographic variation is present to some degree in six of the characters examined: ventrals, subcaudals, dorsal blotches, ventral pigment, blotch border pigment and tail length/total length ratios. Both ventral and subcaudal counts show a weak clinal increase from Maryland to the Florida Keys. Dorsal blotch counts appear to increase slightly north to south and decrease through the Keys. Amounts of ventral pigment show no clinal variation through southern Florida but do decrease clinally through the Keys. Florida *E. guttata* have less black pigment surrounding the dorsal blotches than those farther north. This character decreases clinally from Dade Co. to Key West, Florida. Tail length/total length ratios are nonclinal but for a weak increase from southern Florida to the lower Keys.

The trend of low northern counts to southern highs has been established for other serpents in parts of the Atlantic Coastal Plain. Myers (1967) demonstrated that number of ventrals in *Rhadinaea flavilata* increase clinally from the Carolinas to Florida. Palmer (1971) produced evidence that the erythristic population of *Sistrurus miliarius* in North Carolina has fewer ventrals than populations south of it. Rossman (1963) showed that *Thamnophis sauritus* ventrals and subcaudals generally increase in number from Maryland to southern Florida. The reverse trend has been shown for ventrals in *Natrix rigida* (Huheey, 1959) and for three characters in *Heterodon paltyrhinos* (Edgren, 1961). The trend of increasing counts in southern Florida and then decreasing through the Keys has been shown for ventrals and subcaudals in *Coluber constrictor paludicola* and *Storeria dekayi* (Duellman and Schwartz, 1958).

Discordant variation of Atlantic Coastal Plain *E. guttata* exists in number of temporals, infralabials, supralabials, dorsal scale row formulae and percent incomplete tails.

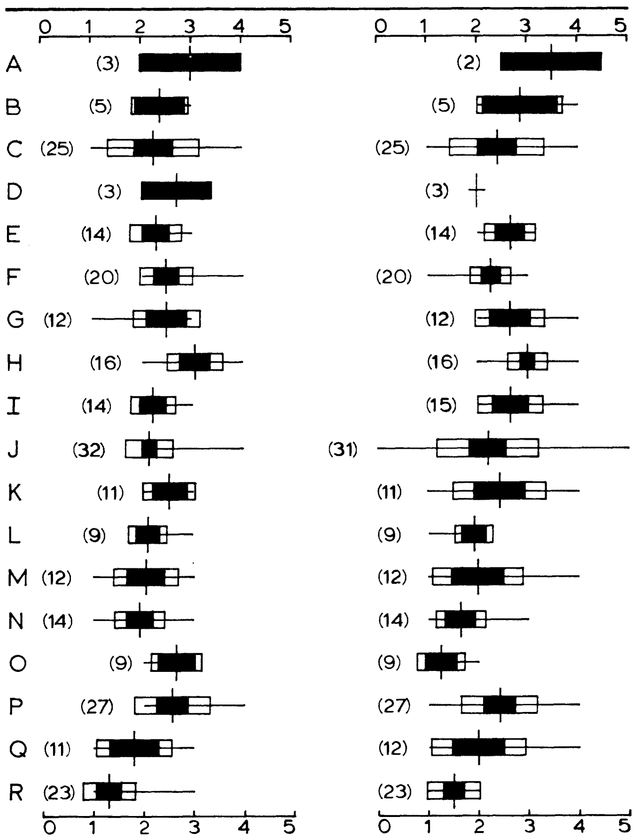

Fig. 6. Left. Variation in amount of pigment on the ventral scales of Atlantic Coastal Plain *Elaphe guttata*. Right. Variation in amount of black pigment surrounding dorsal body blotches of Atlantic Coastal Plain *Elaphe guttata*. See Fig. 3 for explanation of symbols.

The *rosacea* Problem

Elaphe guttata rosacea was first described by Cope (1888) from a single specimen. Barbour (1920), in adding it to the American Check List, changed the name from *Coluber rosaceus* to *Elaphe rosacea*. Neill (1949) reduced it to subspecific status as did Dowling (1951a). In his dissertation, Dowling (1951a) examined specimens from New Jersey, South Carolina, Manatee Co. and Key West, Florida and indicated that clinal variation may be present. He concluded that "should future study prove variation to be a straight cline, then *E. guttata rosacea* (Cope) would become a synonym of *E. g. guttata*". Duellman and Schwartz (1958) examined samples from Alachua Co., Dade Co., Upper Keys and Lower Keys, Florida and, on the basis of smooth clines, did, indeed, place *rosacea* in synonymy of its nominate race. Paulson (1968) subjectively reexamined these samples and decided that *rosacea* should be maintained. Finally, Thomas (1974) presented data on ventrals and subcaudals and body blotches and concluded, along with the fact that samples from other areas studied exhibit smooth clines, that the name *rosacea* is a synonym of *E. g. guttata*. He suggests the eastern morph be termed "red-phase" and the Florida Keys morph the "rosy-phase".

Of the five characters in the Lower Keys that differ significantly from either the Upper Keys or Dade Co. samples none have a coefficient of difference (Mayr, 1969) greater than 0.9. This is well under the 1.28–1.5 minimum recognized as justification for subspecific status (Mayr, 1969).

Although the gap between the Keys and the mainland may presently be a barrier to gene flow it cannot be considered an intrinsic isolating mechanism (Mayr, 1963). Results of my analysis suggest that gene flow has occurred in

TABLE 2. VARIATION IN TAIL LENGTH/TOTAL LENGTH RATIOS OF ATLANTIC COASTAL PLAIN *Elaphe guttata*. (See Table 1 for explanation of symbols; ratios expressed in percent.)

Sample	N	Mean	Range	S.D.	2 S.E.
		MALES			
A	1	14.9	–	–	–
B	1	13.4	–	–	–
C	13	15.9	14.2–17.6	1.05	0.58
D	1	16.4	–	–	–
E	7	16.5	14.0–18.0	1.30	0.98
F	9	16.3	14.3–17.6	1.08	0.72
G	9	15.9	14.4–17.7	1.07	0.71
H	8	16.5	14.7–17.7	0.89	0.63
I	6	15.1	14.1–16.6	0.89	0.73
J	20	15.7	13.2–20.2	1.74	0.78
K	5	16.8	15.3–18.7	1.24	1.11
L	5	16.3	14.5–17.9	1.30	1.16
M	5	16.0	13.9–17.2	1.29	1.15
N	7	16.3	14.5–19.2	1.58	1.19
O	2	17.0	16.6–17.4	0.56	0.80
P	18	17.0	15.5–19.0	1.04	0.49
Q	4	17.2	16.7–18.6	0.92	0.92
R	11	17.9	15.6–19.6	1.33	0.80
		FEMALES			
A	1	12.5	–	–	–
B	3	15.3	14.4–15.8	0.78	0.90
C	10	15.6	12.3–17.2	1.52	0.96
D	1	15.2	–	–	–
E	6	15.1	12.8–17.0	1.49	1.22
F	9	15.6	13.8–17.4	0.99	0.66
G	3	15.0	14.2–15.8	0.80	0.92
H	8	15.9	14.3–20.1	1.85	1.31
I	5	15.3	14.1–16.8	1.01	0.90
J	10	14.5	13.1–16.8	1.39	0.88
K	6	15.5	14.2–17.1	1.10	0.90
L	3	16.4	15.8–16.8	0.51	0.59
M	6	14.9	13.6–16.4	1.13	0.92
N	6	15.7	15.3–16.3	0.41	0.33
O	7	15.5	14.6–16.6	0.65	0.49
P	6	15.2	14.2–15.9	0.62	0.51
Q	4	16.0	13.6–18.0	1.81	1.81
R	9	17.0	15.3–18.6	1.23	0.82

the relatively recent past and that these insular populations have not differentiated substantially from the mainland populations; thus, Thomas' (1974) inclusion of *E. g. rosacea* in the synonymy of *Elaphe guttata guttata* is supported.

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SPECIMENS EXAMINED

AMNH 3496-7, 8751, 8786, 22995, 28947, 64695, 65641-43, 73643, 97523. ABS, identified by collecting date. 10-16-47, 7-18-49, 6-30-68, 2-2-72, 6-10-72. BZ 8-9, 15-18, 20-23, 85, 190, 332, 343, 446. Ch.M 28.193, 30.216.2, 30.254, 33.202, 33.213a-d, 34.250.1, 34.361, 35.408, 36.175, 46.74, 46.76, 49.104.22, 53.33, 53.95.1, 53.106.10, 53.188, 54.89.2, 54.89.3, 54.91.2-.4, 55.84.2, 55.137.5, 56.42.1, 56.62, 56.82, 56.118, 60.61.169-170, 60.61.174, 71.74. FSC 700, 1273-74, 1501, 1586, 1653. RS/HSH 127, 242, 551. MCZ 268, 4382, 6841, 7465, 8313, 14456, 34072, 44753, 45228-33, 46151, 127748-50, 129320, 129322, 129328, 129366. NCSM 1833, 1835-42, 1845, 1848-49, 1851-53, 2042, 2133, 2196, 2335, 2812, 3170, 3189, 3793, 4066-72, 4467, 4698-4706, 5168, 5177, 5727, 7505, 7865, 9895, 10348, 11413, 12387, 12910. NHSM 363, 806, 892, 912, 1276, 1407, 1802. UMMZ 68435, 75817a-h, 84133-41, 92324, 98648, 98691, 100837, 101045-49, 103839-43, 103845-52, 103857-68, 106224, 108219, 109334, 111374. USNM 1615, 1621, 4732, 8366, 9601, 9692-93, 13688, 14141, 14418, 14830, 16230, 19485, 26301-02, 30942, 32086, 32527, 32705, 33926, 38157-59, 48288-89, 64200, 67455, 69649, 79953, 83483-86, 84305, 84478, 91393, 92477, 92748, 95796, 95854, 108751-52, 120703, 124143a-b, 130139, 132395, 145371, 156795-96, 160454, 166104, 195856. VCU 40. WMP 4164.

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Appendix A

The 18 sample localities for Atlantic Coastal Plain *Elaphe guttata* are as follows:

A. *New Jersey.*—from Burlington and Atlantic cos, New Jersey. This is the northernmost known population of *E. guttata* in the Atlantic Coastal Plain (3).

B. *Delmar.*—from Sussex County, Delaware and Caroline and Wicomico cos, Maryland. Separated from A by the Delaware River (5).

C. *Maryland.*—from Anne Arundel, Baltimore, Calvert, Charles, Prince Georges and St. Mary's cos, Maryland and Washington, D.C. These localities combined represent an area approximately 1.5 that covered in sample A. Separated from B by the Chesapeake Bay (26).

D. *Virginia.*—from Caroline, Gloucester and Hanover cos, Virginia. These are the only specimens available of the four known from the Va. Coastal Plain. Separated from C by the Potomac and Rappahannock rivers (3).

E. *Wake Co.*—from Wake Co, North Carolina. This locality is bordered to the east by the Fall Line and is 250 km south of D (14).

F. *Hyde-Tyrrell.*—from Dare, Hyde and Tyrrell cos, North Carolina. This sample lies 145 km east of E and is bordered to the north by the Albemarle Sound and to the south by the Pamlico Sound (20).

G. *Robeson-Scotland.*—from Robeson and Scotland cos, North Carolina, 100 km southwest of E (12).

H. *New Hanover Co.*—from New Hanover Co, North Carolina. Located 110 km southeast of G and separated by the Cape Fear R. (16).

I. *Lexington-Richland.*—from Lexington and Richland cos, South Carolina, 130 km southwest of G (15).

J. *Charleston Co.*—from Charleston Co, South Carolina, 125 km southeast of I and 170 km southwest of H (33).

K. *Southeast Georgia.*—from Duval Co, Florida and Camden, Glenn and Ware cos, Georgia. Located 195 km south of J and separated by the Savannah R. (11).

L. *Alachua-Marion.*—from Alachua and Marion cos, Florida, 100 km south of K (9).

M. *Canaveral.*—from Canaveral and Orange cos, Florida, 120 km southeast of L (12).

N. *Polk-Highlands.*—from Highlands and Polk cos, Florida. This locality lies 90 km southwest of M and 105 km south of L. All specimens are from the Lake Wales Ridge area, an island during the Pleistocene interglacials (see Zug, 1968) (14).

O. *Manatee Co.*—from Manatee Co, Florida, 100 km southwest of N (9).

P. *Dade Co.*—from Dade Co, Florida. All specimens are from the Miami—Homestead area (27).

Q. *Upper Keys.*—from Key Largo, Upper Matecumbe Key and Lower Matecumbe Key, Monroe Co, Florida. Separated from P by Barnes Sound (12).

R. *Lower Keys.*—from Big Pine Key, Little Pine Key, Sugarloaf Key and Key West, Monroe Co, Florida. These islands lie 65 km southwest of Q (23).