

**BULLETINS**  
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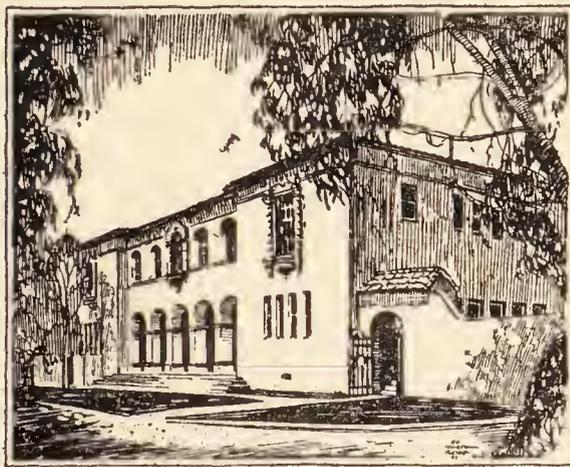
**No. 17**

**Four Papers on the Applications of Statistical  
Methods to Herpetological Problems**

- I. THE FREQUENCY DISTRIBUTIONS OF CERTAIN  
HERPETOLOGICAL VARIABLES
- II. ILLUSTRATIONS OF THE RELATIONSHIP BETWEEN  
POPULATIONS AND SAMPLES
- III. THE CORRELATION BETWEEN SCALATION AND LIFE  
ZONES IN SAN DIEGO COUNTY SNAKES
- IV. THE RATTLESNAKES LISTED BY LINNAEUS IN 1758

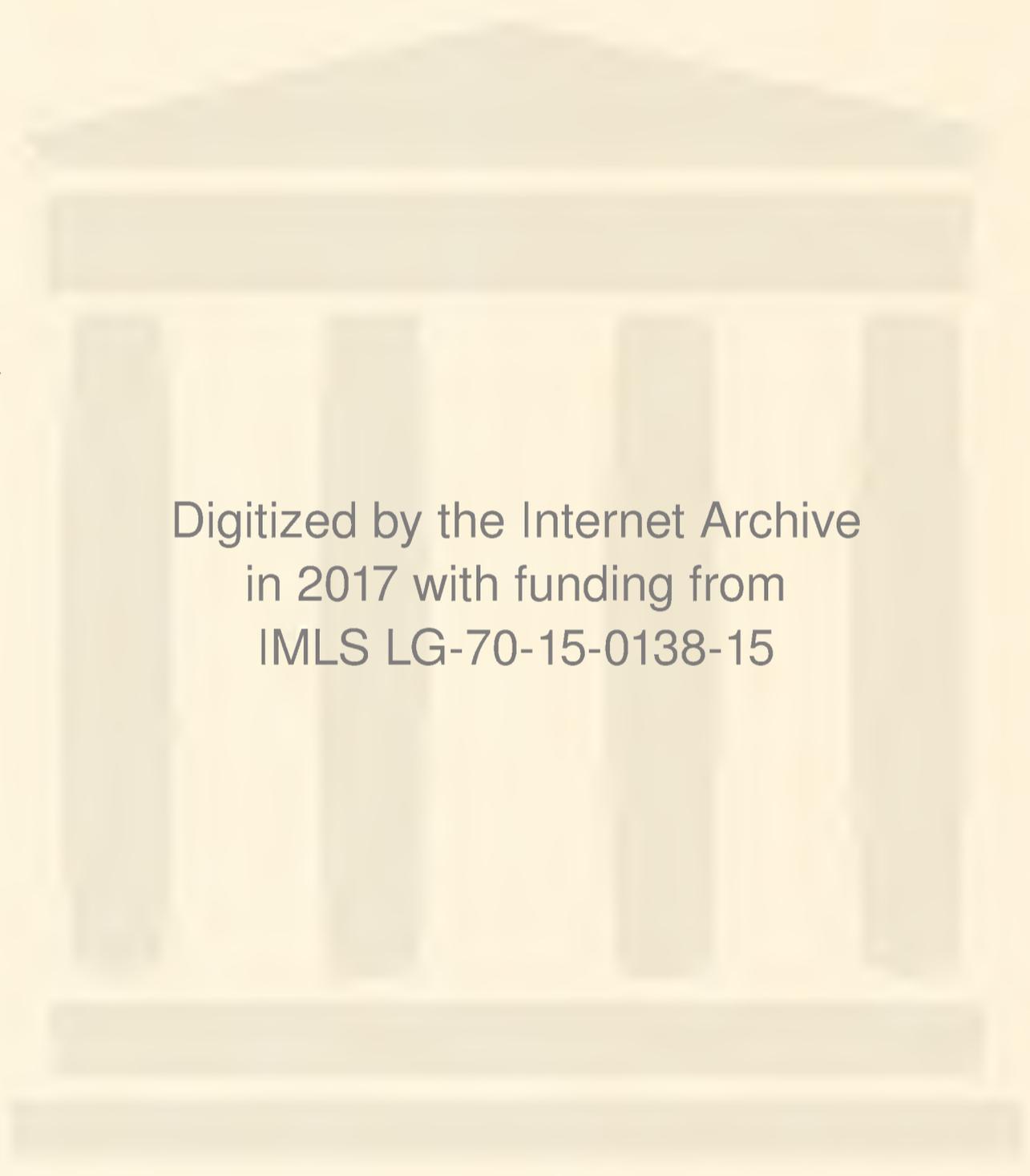
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**SAN DIEGO, CALIFORNIA**

**October 15, 1941**



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APPLICATIONS OF STATISTICAL METHODS TO  
HERPETOLOGICAL PROBLEMSI. THE FREQUENCY DISTRIBUTIONS OF CERTAIN  
HERPETOLOGICAL VARIABLES

## INTRODUCTION

The methods of mathematical statistics may be used to advantage in the investigation of a number of herpetological problems; they will often validate conclusions as to species relationships, morphology, ontogeny, and genetics. They are particularly valuable in assessing the significance of differences, relative degrees of variation, and the reality of correlations. But the accuracy of several of the formulas most commonly used depends to some extent on the closeness of adherence of the distribution of the variates to the normal probability curve.<sup>1</sup> For example, in taxonomic problems, one of the most frequently used formulas is that for determining the significance of the difference between two means, or the related problem of the probability that two samples were drawn from the same population and therefore represent the same species. This formula assumes a normal distribution of the population variates, although giving satisfactory results with moderate departures from normality.<sup>2</sup> Similarly, normality is assumed in applying the correlation coefficient.<sup>3</sup> Certain descriptive indicators, such as the interquartile range, do not give a satisfactory picture of a distribution unless that distribution is substantially normal.

Since, in taxonomy, we are interested primarily in the population which a sample represents, rather than the sample itself, it is usually desirable to have some indication of the probability that the sample was drawn from a normally distributed population. For the fortuities of sampling cause deviations from a normal distribution in the sample, even though the population from which the sample has been drawn is normally distributed. In herpetological work of the kind here under consideration, the sample may comprise from one to several hundred specimens of preserved laboratory material available for study; the population is the much larger, but unknown, group of live animals which were in the wild at the time the sample specimens were collected.

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<sup>1</sup> For references covering the statistical terms and methods used see the appendix and bibliography. In this discussion it is to be understood that a "normal" distribution is one in which the frequency distribution of the variates follows the normal probability curve.

<sup>2</sup> Kenney, vol. 2, p. 141.

<sup>3</sup> Treloar, p. 104.

It is the purpose of this paper to set forth the results of an investigation of some typical herpetological distributions of scale counts, morphological features, and pattern to see whether normal distributions are frequent; and particularly to determine the nature of the deviations from normal in certain especially important characters. For if substantially normal distributions are the rule, as demonstrated in large samples representing these characters (ventral scale counts, for example), we may with some assurance presume normality in taxonomic problems involving closely related species, even though the available samples are too small to warrant final conclusions with respect to normality. (Larger samples permit greater assurance than smaller as to the probability of non-normality in the basic population.) If it be indicated that the variates in a certain character are distributed normally in several species, we need not investigate completely the distribution in some related form; if a visual inspection shows the dispersion to be substantially normal we may safely use any formulas which give accurate results with approximate normality, as, for example, that for determining the significance of the difference between averages.

#### IMPORTANCE OF HOMOGENEITY

In an investigation of the shape of a dispersion curve we should be sure of the homogeneity of the sample, otherwise an inaccurate conclusion may be drawn. Care must be exercised not to complicate the situation by the introduction of extraneous variables or stratification. Thus, if sexual dimorphism be present, the sexes should be tested separately; for if the ventral scutes in each sex of a certain snake be distributed normally, but there is a sex difference, then combining the sexes will produce a platykurtic (flat-topped) distribution, or even one which is bimodal. Hence, in such a combination a non-normal result may merely be an inefficient proof of sexual dimorphism. Similarly, geographically widespread samples are usually to be avoided in testing dispersion curves, for kurtosis or skewness may be only a cumbersome proof of geographic variation or incipient speciation.

If there be doubt as to the existence of sexual or territorial dimorphism, one of the usual tests for the significance of differences should be made before treating the entire collection as a homogeneous unit. This may seem like arguing in a circle, since one of the purposes of determining normality is to validate the significance test. However, the latter is substantially accurate even with some departure from normality, provided the distribution is unimodal and not strongly skewed. Sometimes a platykurtic distribution may in itself suggest an unrecognized heterogeneity, if the same character is known to be normally distributed in other populations. For example, if the ventral scale counts of male rattlesnakes ordinarily have a normal distribution and they are found to be markedly platykurtic in a certain territory, one might suspect the presence of an unrecognized species confused with the one being investigated. Such a test would have indicated the composite character of *Crotalus*

*cinereous* in Arizona, before the recognition and acceptance of *C. scutulatus* as a valid species. However, the same result can usually be achieved somewhat more simply by comparing the coefficients of variation in suspected populations with samples from other areas wherein the populations are assuredly homogeneous.

Sometimes it may be desired to study distributions within a species or subspecies as a whole, even though territorial variations are known to exist intraspecifically. In such cases an attempt should be made to draw equal samples from each territorial or other element of the population, lest the result be distorted by the over-emphasis of the more numerous sections of the general sample.

Accuracy, in making counts and in sexing, is essential if the results are to have value. For example, if there be sexual dimorphism in a certain character, inaccurate sexing will cause the distribution in each sex to be skewed toward the other. Also, there must be a uniform method of making counts. Herpetological methods are not highly standardized; if data are accumulated from more than one source there must be assurance that uniform rules were employed in deciding questionable counts.

#### TESTS OF NORMALITY

Two types of tests of normality are in current use: (1) the chi-square test for goodness of fit; and (2) the comparison of certain moments of the sample distribution with the corresponding moments of the normal curve. Although involving somewhat less computation than a test of moments, the chi-square method has been criticized because of the necessity of grouping the small edge-frequencies, and because it ignores the signs and distribution of the differences of the class frequencies from normal; that is, it does not distinguish between kurtosis and skewness, or their directions—lepto- from platykursis, or positive from negative skewness.<sup>4</sup> Both of these methods will be found discussed at length in statistical texts (see the appendix and bibliography) together with the nomenclature of aberrations from the normal curve (Figs. 1-5). Graphic methods, such as plotting the points of a distribution against the normal curve of best fit, either on rectangular co-ordinates or using a probability scale, will also give a picture of the fit, although they will not indicate the probability that the parent population is non-normal.<sup>5</sup> In fact, it will often be found worthwhile to plot the theoretical against the actual frequencies, after a chi-square calculation has been made, in order to visualize the departure

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<sup>4</sup> Geary and Pearson, p. 1. Although the chi-square test is criticized because of the subjective factor involved in grouping edge-classes, there are cases where one or two freak specimens too greatly affect moment determinations. These, often juveniles which probably would not survive, should usually be eliminated.

<sup>5</sup> Codex Book Co. Arithmetic Probability Paper No. 3127 will be found useful; also the Otis Normal Percentile Chart of the World Book Co. Pearl (1940) p. 382 suggests another method of making a visual comparison between an empirical distribution and the normal curve.

from normality. This is of particular value if one desires to find whether a certain attribute maintains a similar quality of deviation from the normal curve through several species; that is, whether this kind of deviation is characteristic of the attribute. Occasionally it will be desired to investigate such characteristics deviations further by fitting to other curves than the normal probability curve. See Croxton and Cowden, pp. 293-304, Elderton, pp. 58-127.

#### SCALE ROWS

The tapering bodies of most species of snakes are usually correlated with changes in the number of dorsal scale rows. In order to discuss the shape of the dispersion curve of this character it is necessary to define the particular count which is to be used as a basis of investigation.

In most taxonomic work either the number of rows at mid-body is cited, or the number at the neck, at mid-body, and just before the vent.

There are four types of suppression (or lack of suppression) of scale rows between the neck and the vent: (1) a constant number; (2) a constant number from neck to mid-body, followed by a decrease to the vent; (3) a continuously decreasing number from neck to vent; (4) an increase from neck (at its point of least diameter) to mid-body, followed by a decrease toward the vent. While many species, and even genera, adhere to only one of these methods, others may follow two or more, since, after all, there is no very sharp line between them. In fact, there is not entire agreement as to the definitions of the three points at which the rows are to be counted; usually they are (1) on the neck one head-length posterior to the hinge of the jaw; (2) at mid-body half-way between the head and vent; and (3) a short distance anterior to the vent, to avoid the irregularities involved in the considerable diminution in body diameter at that point.

Complete studies of scale rows involve, not a determination of the number of rows at these arbitrary and somewhat ill-defined points, but rather a two-dimensional picture presenting the sequence number of each row suppressed (considering the row bordering the ventrals as No. 1), and the point of suppression, the latter being located by the number of the ventral scute (counting from the head toward the tail) opposite which the suppression occurs. This introduces a more complicated set of variables than can be the subject of the present investigation which, therefore, will be restricted to the number of rows at mid-body. But the term will be used in the rather broad sense of the maximum rows evident in a transverse band at approximately the central part of the body, rather than at a single carefully determined mid-point. This will avoid variations produced by a rigid definition rather than a true condition of the scale rows; it will not differentiate between suppression just anterior or posterior to the exact mid-body.

Another difficulty in dealing with the distribution of scale rows lies in the strong tendency toward uneven rows in nearly all genera. This results from the fact that most counts are made up of a mid-dorsal row and two equal sets of lateral rows on either side, thus producing an odd-numbered total. Thus only in genera wherein the mid-dorsal row is occasionally suppressed, as for example in *Trimorphodon*, or in individuals having unequal numbers of lateral rows, is there an even-numbered total. Even where the mid-body count is considered to be the maximum found in a band extending both anterior and posterior to the true mid-point there are cases of unbalance, that is, bilateral asymmetry, wherein a row is suppressed much sooner on one side than the other, or fails entirely to appear on one side. Sometimes a row may be represented by only a few scattered scales.

But these even-numbered specimens are the exception rather than the rule; they will rarely reach eight per cent of the total, and in most species will be fewer. In checking the distribution of these variates against normality these even-numbered specimens may be allocated to the uneven classifications next above and below; that is, if there are 10 specimens with 24 rows, add 5 to the number with 23 and 5 to the number with 25. The series of uneven numbers can then be tested for normality of distribution. However, it is best, in those genera where there is true bilateral asymmetry (not the suppression of the mid-dorsal itself, as in *Trimorphodon*), to consider the laterals, rather than the total dorsals, as the variable. This is done by deducting the mid-dorsal row and determining the distribution of the laterals. In this method a snake with, say, 24 scale rows is presumed to have a mid-dorsal, 12 laterals on one side and 11 on the other; while, of course, one with 25 rows has a mid-dorsal and two sets of 12 laterals each. Thus we can make the type of transformation shown in Table 1. This distribution of laterals can then be checked for normality in the usual way.

TABLE 1

SAN DIEGO COUNTY *Crotalus viridis oregonus*  
CONVERSION OF DORSALS TO LATERALS

Number of dorsal rows	Number of specimens	Number of lateral rows			
		11	12	13	14
23	7	14	....	....	....
24	5	5	5	....	....
25	440	....	880	....	....
26	37	....	37	37	....
27	121	....	....	242	....
28	1	....	....	1	1
29	2	....	....	....	4
Total	613	19	922	280	5

The scale rows of most snakes at mid-body are too nearly invariant to require or justify an investigation of normality. The smaller and slimmer colubrids are often almost or quite without variation. For example, 213 specimens of *Sonora occipitalis* from eastern San Diego County all have 15 scale rows. The distribution in 274 specimens of *Diadophis amabilis similis* from western San Diego County is 13(12), 14(7), 15(255).<sup>6</sup> Of 334 specimens of *Phyllorhynchus decurtatus perkinsi* from desert San Diego County all have 19 scale rows except four, which are distributed as follows: 17(1), 18(2), and 21(1). Of 202 specimens of *Rhinocheilus lecontei* from southern California all but four have 23 scale rows; of the four aberrants, three have 25, and the other 24 scale rows. Some of the larger species have a greater diversity. For example, 431 specimens of *Lampropeltis getulus californiae* (both pattern phases) from cismontane San Diego County have the following distribution: 22(2), 23(354), 24(27), 25(48); or, expressed as laterals, 10(2), 11(737), 12(123).

This distribution does not exhibit enough variation to warrant a test for normality, but some of the larger colubrids may have a sufficient spread to justify such a test. For example, 178 specimens of *Pituophis catenifer annectens* from coastal San Diego County have the following dispersion of laterals: 13(2), 14(22), 15(111), 16(169), 17(48), 18(4). A chi-square test indicates that the dispersion probably approximates a normal distribution ( $P = 0.25$ ).<sup>7</sup>

It is to be presumed that some of the larger species of the Boidae, with their high numbers of scale rows, would have some interesting variations, but securing sufficient data presents obvious difficulties. Among the smaller boids we have the following distribution of the laterals of 103 specimens of *Lichanura roseofusca roseofusca* from western San Diego County: 17(2), 18(5), 19(35), 20(93), 21(67), 22(4). By the chi-square test  $P = 0.13$ . In *Charina bottae* 142 specimens are distributed as follows: 19(17), 20(88), 21(89), 22(41), 23(36), 24(13). Here  $P$  is less than 0.001, for the distribution is skewed; however, these data represent a territorially non-homogeneous population from a large area, which has affected the result.

The rattlesnakes exhibit a moderate degree of variation in scale rows, no doubt because of their thick bodies; for it can be shown that among snakes there is often a positive intrageneric, and even intrafamily correlation of the number of scale rows with adult body diameter; and, assuming

<sup>6</sup> Throughout this paper, in expressing distributions in this way, the values of the variate will be stated first, followed in parentheses by the frequency of occurrence of that value.

<sup>7</sup> The chi-square test for normality does not state the probability that a certain distribution is normal; it answers the question in this way: "If the population from which this sample was drawn were indeed normal, what percentage or proportion of similarly sized samples, drawn at random, would exhibit as great, or a greater, departure from normality than this one?" So in a way it gives a negative rather than a positive answer to the question. If we take the often-used probability limit of 0.05 we merely determine (when  $P$  is above 0.05) that there is not a strong indication that the parent distribution is *not* normal.

a constant coefficient of variation, the thicker species will have a higher number of scale-row classes.

Table 2 sets forth the data on the five largest homogeneous series of rattlers available to me.

TABLE 2  
DISTRIBUTION OF LATERAL SCALE ROWS IN  
HOMOGENEOUS SERIES OF RATTLESNAKES

Number of Lateral Rows	Platteville series <i>C.v. viridis</i>	Pierre series <i>C.v. viridis</i>	Pateros series <i>C.v. oreganus</i>	S. D. County series <i>C.v. oreganus</i>	San Lucan series <i>C. lucasensis</i>
11	4	....	12	19	....
12	493	387	894	922	15
13	1113	895	322	280	523
14	56	64	2	5	148
15	....	....	....	....	5
16	....	....	....	....	3
Totals	1666	1346	1230	1226	694

These distributions are unimodal, but the dispersions are not great enough—that is, there are not enough classes—to determine whether there is a tendency away from normality.

Summarizing the scale-row study, it may be said that in most species of snakes the scale rows are too constant to permit useful determinations of whether such variation as there is follows a normal dispersion. Probably only the largest boids would produce results of interest. The significance of differences in scale rows may best be ascertained by means of a chi-square test of an Rx2 table,<sup>8</sup> rather than by determining the difference between means. No doubt the location of the termination of dropped rows will warrant statistical examination in some cases. Sexual dimorphism is sometimes present, either in the number of rows, or the point of termination of suppressed rows.

#### VENTRALS

The most important character employed in intrageneric classification is the ventral scale count, for it may be determined with accuracy and usually has a high degree of constancy in any territorially homogeneous series, the coefficient of variation approximating 2 per cent. Yet it is sub-

<sup>8</sup> For the use of this method see such texts as Mills, p. 633; Snedecor, p. 164; Simpson and Roe, p. 295; Pearl, p. 329.

ject to sufficient plasticity to show the effects of ecological and other changes.

Chi-square tests of a number of species of colubrids indicate that normality of distribution is probably the rule, the results being shown in Table 3 for several homogeneous series.

TABLE 3  
EVIDENCE OF NORMALITY  
IN THE DISTRIBUTION OF VENTRAL SCALE COUNTS  
OF EXAMPLE COLUBRIDS

Species	Area	Sex	Number of Specimens	Chi-square Probability P
<i>Diadophis a. similis</i> .....	Coastal S. D. Co.	M	128	0.22
		F	131	0.82
<i>Phyllorhynchus d. perkinsi</i> .....	Desert S. D. Co.	M	126	0.73
		F	99	0.29
<i>Pituophis c. annectens</i> .....	Coastal S. D. Co.	M	96	0.76
		F	80	0.05
<i>Thamnophis hammondi</i> .....	San Diego Co.	M	170	0.61
		F	159	0.93
<i>Thamnophis o. ordinoides</i> .....	Nw. Oregon	M	149	0.81
		F	151	0.41
<i>Lampropeltis g. californiae</i> .....	San Diego Co.	M	202	0.46
		F	171	0.60
<i>Geophis nasalis</i> .....	Volcan Zunil	M	124	0.26
		F	89	0.45

P in the table indicates the proportion of similarly sized samples that would show a departure from normality at least as great as that shown by the available sample, if the population sampled were truly normal. Thus the evidence for normality of distribution is quite strong in this group of colubrids.

The five homogeneous series of rattlesnakes have been investigated by the alternative method of moments. The results are shown in Table 4.

TABLE 4  
EVIDENCE OF  
SKEWNESS AND KURTOSIS IN VENTRAL SCALE COUNTS  
IN HOMOGENEOUS SERIES OF RATTLESNAKES  
BY THE METHOD OF MOMENTS

Species	Series	Sex	Number of Specimens	Probability <sup>9</sup>	
				Skewness	Kurtosis
<i>C.v. viridis</i> .....	Platteville	M	441	0.44	0.73
		F	392	0.64	0.08
<i>C.v. viridis</i> .....	Pierre	M	342	0.79	0.007
		F	331	0.45	0.44
<i>C.v. oregonus</i> .....	Pateros	M	326	0.80	0.05
		F	289	0.00001-	0.81
<i>C.v. oregonus</i> .....	San Diego Co.	M	292	0.57	0.16
		F	278	0.74	0.72
<i>C. lucasensis</i> .....	San Lucan	M	168	0.0009	0.0004
		F	125	0.00001-	0.00001-

These dispersions were also checked by the chi-square method and all were found to be well above the 5 per cent limit toward normality, except in the case of the Pateros females, but including *lucasensis*, which Table 4 shows to be non-normal. Thus we find substantial agreement between the two methods except in the case of the *lucasensis* series. Here it is determined that the low probability disclosed by the moment method results from two specimens (defective young) in each sex. These, of course, are grouped with others in the edge-classes when employing the chi-square method, and hence have small effect on the result. If we drop them out and recalculate the results by the moment method we have the following:

	Male	Female
P (skewness) .....	0.43	0.62
P (kurtosis) .....	0.46	0.63

Thus there is little evidence of abnormality in *lucasensis* when these aberrant individuals are omitted.

As to the directions of the deviations, we find that the skewnesses are all positive, indicating a long tail toward the right, that is, a surplus of the higher ventral counts. With respect to kurtosis, six cases are positive

<sup>9</sup> As in the case of the chi-square test, the method of moments tests the evidence of non-normality, rather than normality, by determining the ratios of certain departures from normality to their standard errors. From these ratios the significance of the departures may be determined. In the above table, if the probability is above 0.05, there is assumed to be no strong evidence for non-normality in the parent population. Any result smaller than 0.01 is taken to indicate a high probability of non-normality.

(leptokurtic), the other four negative; obviously there is no weight of evidence for a trend toward either a peaked or a flat-topped curve being the mode.

In the worm snakes, genus *Leptotyphlops*, the dorsals, rather than the ventrals, are used in taxonomy. The chi-square test applied to 56 specimens of *L. b. humilis* from western San Diego County, and to 40 specimens of *L. b. cabuila* or *cabuila-humilis* intergrades from the desert slope of the county, indicate normal distributions, although the number of specimens is too small to permit a fully adequate determination. 108 specimens of *L. dulcis dulcis* from Texas have a definitely flat-topped distribution ( $P = .001-$ ). However, this population may not be homogeneous, as discussed elsewhere.<sup>10</sup>

#### SUBCAUDALS

The distributions of the subcaudals in some typical series of colubrids are shown in Table 5. The evidence is in favor of normality in most cases.

TABLE 5  
EVIDENCE OF NORMALITY IN THE  
DISTRIBUTION OF SUBCAUDAL SCALE COUNTS IN COLUBRIDS

Species	Area	Sex	Number of Specimens	Chi-square Probability P
<i>Diadophis a. similis</i> .....	Coastal S. D. Co.	M	119	0.02
		F	118	0.28
<i>Phyllorhynchus d. perkinsi</i> .....	Desert S. D. Co.	M	126	0.05
		F	94	0.53
<i>Pituophis c. aunelectens</i> .....	Coastal S. D. Co.	M	88	0.64
		F	80	0.48
<i>Thamnophis hammondi</i> .....	San Diego Co.	M	149	0.74
		F	133	0.92
<i>Thamnophis o. ordinoides</i> .....	Nw. Oregon	M	110	0.44
		F	122	0.35
<i>Lampropeltis g. californiae</i> ...	San Diego Co.	M	184	0.90
		F	154	0.27
<i>Geophis nasalis</i> .....	Volcan Zunil	M	115	0.06
		F	84	0.001-

<sup>10</sup> Trans. S. D. Soc. Nat. Hist., Vol. 9, No. 18, p. 103, 1940.

The same result is apparent in the subcaudals of the rattlesnakes (Table 6), analyzed by the method of moments, although the foreshortened tails of the rattlesnakes render this character less important than in the sharp-tailed snakes.

TABLE 6  
EVIDENCE OF  
SKEWNESS AND KURTOSIS IN SUBCAUDAL SCALE COUNTS IN  
HOMOGENEOUS SERIES OF RATTLESNAKES  
BY THE METHOD OF MOMENTS

Species	Series	Sex	Number of		Probability	
			Specimens	Skewness	Kurtosis	Kurtosis
<i>C.v. viridis</i> .....	Platteville	M	441	0.76	0.21	
		F	390	0.09	0.001-	
<i>C.v. viridis</i> .....	Pierre	M	342	0.41	0.51	
		F	331	0.46	0.85	
<i>C.v. oreganus</i> .....	Pateros	M	324	0.57	0.93	
		F	289	0.002	0.07	
<i>C.v. oreganus</i> .....	S. D. County	M	294	0.38	0.29	
		F	279	0.72	0.24	
<i>C. lucasensis</i> .....	San Lucan	M	168	0.22	0.50	
		F	123	0.85	0.04	

Thus, while not every test results in a probability above 0.05 the general indication is toward normality. I have rechecked the Platteville and Pateros females, the two cases which show the greatest probability of non-normality. I find that in both there are several high counts, possibly the result of inaccurately sexing juveniles, always a possibility in handling some hundreds of these little specimens. If we employ the chi-square test, which groups these end-classes, we find for the Platteville series  $P = 0.82$ , and for the Pateros series  $P = 0.55$ . Thus the appearance of non-normality results from these few aberrant specimens, totaling only about one per cent of the available material.

These distributions afford good examples of the extent of the departures from the normal curve of sets of variates in which there is strong evidence that the parent populations are truly normal. For instance, these are the detailed figures for the female Pierre *viridis*:

Number of Subcaudals	Actual Distribution	Theoretical Distribution (A)	Theoretical Distribution (B)
16	1	1.84*	2.18*
17	10	9.36	10.00
18	34	32.19	32.80
19	65	68.53	67.86
20	95	90.88	89.17
21	74	74.92	74.04
22	36	38.37	38.86
23	13	12.24	12.98
24	2	2.42	2.71
25	1	0.32*	0.39*
Total	331	331.07	330.99

Column A gives the theoretical distribution by ordinates, Column B, by areas. I have stated that in cases such as this, where the variates can take only integral values, I have usually determined the theoretical distribution by the first method. It will be observed that the area method gives a slightly more platykurtic curve than the other. The actual distribution is exceedingly close to either, closer in fact than would be obtained in nine out of ten random samples if the parent population is indeed normally distributed; for  $P = 0.95$  when the value of chi-square is obtained by comparing with the ordinate curve, or  $P = 0.93$  if the area curve is taken.

#### LABIALS AND OTHER HEAD SCALES

The labials, in homogeneous series of colubrids, seldom have a sufficient variation to indicate more than a strong unimodal tendency. In the rattlers there is more variation, usually five or more classes being present, and from these the trend toward normality can be ascertained. The distributions in the five series which have been used before are shown in Table 7.

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\* 16 or less; 25 or more.

TABLE 7  
DISTRIBUTION OF LABIAL SCALE COUNTS IN  
HOMOGENEOUS SERIES OF RATTLESNAKES

## SUPRALABIALS

	Platteville	Pierre	Pateros	S. D. Co.	San Lucan
12 .....	11	6	....	1	2
13 .....	89	65	18	28	4
14 .....	542	362	190	225	13
15 .....	728	625	600	569	103
16 .....	256	233	351	320	308
17 .....	35	54	67	69	203
18 .....	4	1	3	11	56
19 .....	....	....	....	....	4
Total .....	1665	1346	1229	1223	693
P (by chi-square)	0.01	0.001-	0.07	0.025	0.08

## INFRALABIALS

12 .....	1	....	....	....	....
13 .....	12	9	....	1	1
14 .....	106	90	30	51	1
15 .....	487	428	232	301	11
16 .....	641	503	532	502	61
17 .....	382	254	363	295	198
18 .....	79	56	71	48	275
19 .....	6	5	2	12	124
20 .....	....	....	....	2	20
21 .....	....	....	....	....	4
Total .....	1664	1345	1230	1212	695
P (by chi-square)	0.24	0.02	0.89	0.31	0.20

It will be noted that there is a greater indication of non-normality in the supralabials than the infralabials. A study of the former by the method of moments indicates that the trend away from normality is brought about by a leptokursis, the peak being sharper than that of a normal curve.

Sometimes it is desirable to investigate entire species to determine curve shapes, especially if, in a character, there is reason to believe that little territorial variation is involved; for the greater number of specimens will give greater assurance of the curve shape. However, if there be territorial variation it is obvious that there will be a tendency toward greater dis-

persion in the larger samples; so that if homogeneous segments of the population have normal distributions, the combinations will tend toward platykursis.

There is not much variation in the labials of *C.v. viridis*, especially in the northern part of its range. I have therefore investigated the curve shapes of the labials in all the specimens available to me, to see whether these larger samples tend to verify the non-normality of the supralabials and the normality of the infralabials, as indicated by the Platteville and Pierre series. The data are as follows:

	10	11	12	13	14	15	16	17	18	19	Total
Supra- labials ...	2	8	33	279	1460	2125	817	153	10	....	4887
Infra- labials....	....	1	2	47	284	1434	1834	897	214	14	4827

The results are as follows:

	P (chi-square)	P (moments)	
		Skewness	Kurtosis
Supralabials .....	0.0001-	0.037	0.000001-
Infralabials .....	0.05	0.415	0.222

It will be seen that there is strong evidence that the supralabial frequency is not normal; in fact, the value of *P* for kurtosis is very much smaller than the figure given, for the distribution is strongly peaked. On the other hand, these tests, especially that based on moments, indicate that the infralabial distribution is probably normal.

Occasionally other head scales vary sufficiently to warrant investigation. For example, consider this distribution of the minimum scales between the supraoculars in the Pierre series of *C. v. viridis*: 1(7), 2(145), 3(370), 4(138), 5(12). By the method of moments we find *P* (skewness) to be 0.20, and *P* (kurtosis) 0.69. In the Platteville series of 831 specimens the distribution is 1(4), 2(71), 3(381), 4(311), 5(51), 6(12), 7(1). This distribution is definitely skewed, and *P* (chi-square) is 0.01. A species with a high number of scales in the supraocular bridge is *C. ruber*, in which the distribution among 243 specimens from all areas is 4(6), 5(35), 6(96), 7(75), 8(29), 9(2). This is markedly skewed distribution. The distribution in *C. lucasensis* is more symmetrical: 3(3), 4(34), 5(70), 6(135), 7(70), 8(24), 9(1); total 337. *C. m. molossus* and *C. scutulatus* are two forms in which these minimum scales across the frontal area are strongly skewed. For example, in 148 *C. m. molossus* the variation is 2(86), 3(29), 4(21), 5(10), 6(1), 7(1), giving what is known as a J-shaped curve. *C. scutulatus* is even more strongly skewed: 1(3), 2(324), 3(37), 4(5), 5(1); total 370. This is quite a different distribution from that of *C. cinereous (atrox)* which in all specimens avail-

able to me is as follows: 3(76), 4(276), 5(230), 6(90), 7(11), 8(1); total 684. In determining the significance of the difference between two such non-normal distributions as these, it is best to use an Rx2 table, rather than a comparison of means. Such a test would show the probability of a common origin to be far below 0.0001, clearly demonstrating the validity of *scutulatus*.

The scales in the prefrontal area on the snout of a rattlesnake may be distributed normally, although usually either skewed, platykurtic, or both. In *C. scutulatus* there is slight skewness (P by chi-square = 0.07 in 274 specimens). But in the Pierre series of *viridis* the distribution in 672 specimens is decidedly flat-topped and P (chi-square) is less than 0.001.

A few species of snakes have considerable diversity in loreals, although most are rather constant. A form exhibiting variation is *Lichanura r. roseofusca*, wherein we find the following distribution: 2(1), 3(22), 4(56), 5(69), 6(11), 7(5). This indicates the possibility of a normal distribution in the parent population, for P (chi-square) is found to be 0.09. Also in this species we have an ocular ring, with no definite distinction to be drawn between supra-, pre-, sub-, or post-oculars. The distribution in 163 counts is as follows: 7(5), 8(16), 9(70), 10(61), 11(9), and 12(2). P is 0.17 and a normal distribution is therefore possible.

In *Pituophis* the prefrontals are subject to considerable variation. For example, in 120 specimens of *P. c. annectens* from San Diego County the distribution is 2(4), 3(7), 4(91), 5(6), 6(9), 7(2), 8(1). This clearly is not a normal distribution, being sharply peaked at 4, and P is much less than 0.001.

#### LIZARD SCALES

Lizard scale distributions are also useful in taxonomic problems and may be checked for normality by the same methods. Thus in 56 specimens of *Sceloporus j. jarrovi* the scales around the body indicate a normal distribution (P = 0.59). In 760 specimens of *Cnemidophorus t. tessellatus* from all areas, the distribution of ventrals is surprisingly close to normal (P = 0.88). In the same species 1424 counts of the scales on the fourth toe show a leptokurtic distribution as follows: 17(12), 18(92), 19(337), 20(673), 21(205), 22(86), 23(15), 24(4). In this distribution, by the chi-square test, P is found to be much below 0.001. Similarly the number of dorsal scale rows in a large series of *Anniella p. pulchra* is peaked in distribution. In 1506 counts in *C. t. tessellatus* (sexes combined), the femoral pores indicate that the distribution may be normal (P = 0.27). I think there will be a growing tendency to apply statistical methods in future taxonomic studies of the lizards, particularly in verifying the significance of differences, for they have a greater number of countable characters than snakes.

#### TURTLE SCUTES

Southern California is a territory notably poor in chelonians and I have no original data on turtles. I have tested the distributions of the scutes of

*Lepidochelys olivacea*, cited in the "Tetrapod Reptiles of Ceylon" by P. Deraniyagala. The total scutes in 378 specimens (p. 133) are not distributed normally (P less than 0.001), for the distribution is decidedly platykurtic. The costals (p. 137) in 756 counts are both platykurtic and skewed (P less than 0.001). The vertebrales may possibly be normally distributed (P = 0.08), although this particular sample is platykurtic.

#### PATTERN

Where the pattern of a snake or lizard includes bands, saddles, blotches, or spots, the numbers on the body, tail, or both are frequently used in taxonomy. They often approach normality in distribution. Thus in 180 specimens of *Pituophis c. annectens* we find for the body blotches P = 0.06; in the tail spots of 89 males P = 0.32 and in 80 females P = 0.90.

In the five large series of rattlesnakes a normal distribution is indicated, as shown in Table 8. In one case—the Pateros *oreganus* female tail rings—the distribution is strongly skewed; in three others the variation is limited to only three classes and the tendency is indeterminate.

TABLE 8  
CHI-SQUARE TEST OF NORMALITY OF  
BODY BLOTCHES AND TAIL RINGS IN  
HOMOGENEOUS SERIES OF RATTLESNAKES

Series	Body Blotches		Tail Rings			
	Number	P	Males		Females	
			Number	P	Number	P
Platteville <i>viridis</i> .....	832	0.09	440	0.20	392	0.41
Pierre <i>viridis</i> .....	672	0.28	342	0.32	330	0.81
Pateros <i>oreganus</i> .....	616	0.22	326	0.33	290	0.001—
San Diego Co. <i>oreganus</i> .....	579	0.90	285	0.15	283	....
San Lucan <i>lucasensis</i> .....	339	0.13	198	....	146	....

#### BROODS

The sizes of broods of young snakes have been shown to be correlated with the size of the mothers, larger females having more young.<sup>11</sup> Thus the frequency distribution of brood sizes may depend on the dispersion of fertile females, as well as on the variation for any given size of mother. The only series which I have available, large enough to afford a determination, comprises data on broods and developing eggs of *Crotalus v. viridis*. Of these there are a total of 303 sets. The distribution is found to be both platykurtic and positively skewed; P (chi-square) is 0.006. It may well be

<sup>11</sup> Occ. Papers S. D. Soc. Nat. Hist., No. 1, p. 16, 1936.

that a more nearly normal distribution would be in evidence in a series from mothers within a narrow length-range. The data available are not sufficient to permit checking this possibility.

#### RATTLES

One rattle-variable is the number of rattles in adult strings. Data on this subject have been given in a discussion of the rattle.<sup>12</sup> The distributions in two series, the Platteville and San Lucan, including both complete and broken strings, are found to be leptokurtic in the first case (chi-square  $P$  less than 0.001) and possibly normal in the second ( $P = 0.13$ ). True normality could not be expected in these cases since, with very large series, a considerable number of snakes should have less than no rattles—an obvious impossibility.

#### HEMIPENES

In some species the spines and fringes of the hemipenes are quite variable, although the spines, if non-uniform, are often difficult to count with accuracy. In a series of *C. scutulatus* the spines seem normally distributed ( $P = 0.29$ ) and the fringes likewise ( $P = 0.72$ ).

#### MEASUREMENTS

Thus far I have dealt with scales, blotches, and other countable quantities, characters which can only take integral values. Because of their scalation most reptiles are well supplied with such countable characters (only fish equal them), a fortunate provision from the standpoint of ascertaining the significance of differences. However, even in herpetology, dispersion curves of measurements and weights are of interest. They are of importance in determining factors affecting variation and correlation, and in calculating the frequency of expectation of unusual specimens. But in using measurements in most difference problems we are confronted by the complication that proportionalities are subject to ontogenetic variation. We are seldom concerned with the total variation within a species from birth to death; more often we wish to know the extent of variation at a single age or life period, since it is only within such limitations that a three-dimensional variation can be reduced to two dimensions, permitting an analysis of the frequency distribution. For usually the measurements to be used are of a relative or proportional nature involving two variables—for example the ratio between some part of the body and the whole; and although such ratios eliminate the unit of measurement, they do not obviate the effects of ontogeny. It is seldom that a body part remains in constant ratio with another part (or with the body as a whole) throughout life. Where such ontogenetic changes in proportionality are in evidence, to determine dispersion we must either have a very large assemblage of specimens at a single value of the independent variable—that is to say, at

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<sup>12</sup> Occ. Papers S. D. Soc. Nat. Hist., No. 6, pp. 18-19, 1940.

a given age or size—or we must make some assumptions and convert the available specimens to a standard value of the independent variable. This usually involves the determination of the probable size of a body part at a standard value of the body size. This may then be followed by a study of the frequency distribution of the dependent variable at what is equivalent to a cross-section of the dispersion surface. For example, if it be desired to determine the dispersion of the head size of a snake as a proportion of body size, we first set a standard body size (usually somewhere in the adult range) and then translate the head lengths of all the available specimens to what they would probably be at this standard body size. The translation is effected by determining the regression line for all specimens and then assuming that any specimen, in growing to (or returning to) the standard size, would do so by maintaining a constant percentage deviation from the regression line. This assumption is validated by the fact that the coefficients of dispersion of characters of this type seem to remain substantially constant through life. The results of several studies of this nature, with example computations, have already been published.<sup>13</sup> It is only by the use of such calculations that sufficient data can be secured to permit the study of frequency distributions.

In a population of snakes—rattlesnakes for example—the lengths do not approach a normal distribution. On the contrary it is bimodal, for the young of the year are rather sharply differentiated from the adolescents and adults.<sup>14</sup> The young of the year taken by themselves are probably normally distributed with respect to body length as shown by the following tests on homogeneous series:

Series	Number of Individuals	P (chi-square)
Zacatecas <i>nigrescens</i> .....	82	0.51
San Patricio <i>cinereous</i> .....	139	0.64
Pierre <i>viridis</i> .....	152	0.77
Platteville <i>viridis</i> .....	229	0.01

Only the Platteville series is distributed non-normally; it is negatively skewed.

A set of miscellaneous broods totaling 320 young snakes, when the individual lengths were expressed as percentages of the mean of each brood, had a dispersion giving a chi-square value of  $P=0.25$ .

Starting with young of the year having substantially normal distributions, it would be interesting if we could trace the progress of each age-class as it passes through maturity until it finally disappears, losing indi-

<sup>13</sup> Ratio of weight to length, Occ. Papers, S. D. Soc. Nat. Hist., No. 3, p. 47, 1937; ratio of head length to body length overall, idem, No. 4, p. 22, 1938; ratio of fang length to head and body length, idem, No. 5, p. 36, 1939.

<sup>14</sup> Occ. Papers S. D. Soc. Nat. Hist., No. 3, p. 20, 1937.

viduals continuously along the way, to see whether the distribution continues normal. But studies have shown that it is impossible to segregate successive classes by size after the first year; for even in their second year the most rapidly growing adolescents will have overtaken the smallest adults of the preceding year, thus preventing an accurate segregation. Subsequently the adults grow so slowly (probably never stopping growth entirely as do mammals and birds), compared to individual variations, that the separation of the age-classes becomes continually smaller and the overlap between successive years greater. While we may assume that the distribution of each age-class remains normal, since they start with such a distribution as young of the year, and second year individuals having complete strings of 5 rattles have been found to approach normality, we cannot prove this continuity. A complete population of adolescents and adults is both positively skewed and platykurtic, as might be expected from the nature of a curve comprising the sum of several normal curves of successively decreasing areas.

It would be useful if the sizes of an adult population of snakes could be shown to have a normal distribution, and the mean and standard deviation could be determined; for from such parameters we could determine the probable frequency of occurrence of unusually large specimens, certainly a matter of interest.

But this is a difficult assignment. First, very large samples would be required, some hundreds of specimens of each sex, at least; for as there is sexual dimorphism in size in most species, the sexes must be treated separately. There must be no conscious selection with respect to size; the sample must be truly representative of the population as a whole. This will at once eliminate the larger species from consideration owing to the practical difficulty of collecting, preserving, and measuring great numbers of large individuals. There is the further complication that incomplete tails are numerous among the larger specimens of many species, particularly of those with slender tails such as the racers. This tends to distort the true frequency distribution. But most important of all, there is the difficulty of segregating the adolescents, as already mentioned. To avoid this complication there is some possibility of investigating only the right hand half of the curve of distribution; that is, the half above the mean which contains the largest specimens. Probably the garter snakes, because of their occurrence in large numbers, and their ease of capture around certain ponds and lakes will offer the best material for an investigation of this kind. To determine with any degree of certainty whether the distribution is normal, and particularly whether the largest specimens occur with greater or less frequency than would be expected with a normal distribution, would probably require the measurements of at least 500 specimens of each sex.

I have no such series available, but I have checked the two best homogeneous series at hand, although admittedly they are quite inadequate in

numbers to afford conclusive evidence respecting the shape of the dispersion curve. These are series of the little snakes *Diadophis amabilis similis* and *Phyllorhynchus decurtatus perkinsi*. In the interest of homogeneity I have restricted the investigation to specimens from San Diego County, since territorial variations in size are evident in many species. By rather arbitrary methods I have attempted to eliminate adolescents. The statistics of the adult populations are as follows, all lengths being given in millimeters:

	<i>Diadophis a. similis</i>		<i>Phyllorhynchus d. perkinsi</i>	
	Males	Females	Males	Females
Number .....	101	86	119	70
Mean length .....	294.1	340.9	392.1	406.6
Standard deviation .....	38.64	50.11	53.10	32.85
Length of an individual 2 standard deviations above the mean .....	371.4	441.1	498.3	474.3
Theoretical number greater than this length (2.28%)..	2.30	1.96	2.71	1.60
Actual number greater than this length .....	2	4	0	2

It will be noted that in two cases (*Diadophis* males and *Phyllorhynchus* females) the actual number of specimens at least two standard deviations larger than the mean is as near the theoretical number as possible. The number of large *Diadophis* females is four instead of two as calculated; while in the case of the *Phyllorhynchus* males there should be about three specimens above 498.3 mm. long, whereas actually there are none so large. But it is interesting to note that the largest specimens come close to expectation, for the three largest are 490, 491, and 495 mm., respectively. At least we can say, for these admittedly inadequate tests, that they offer no particular evidence that the size distributions of these adult populations are not normal with respect to the presence of unusually large individuals.

One of the important correlative studies that may be made is that of weight on length. I have determined<sup>15</sup> that the dispersion around the regression line of 818 individuals of the Platteville *viridis* (standardized as discussed above) are probably not normally distributed for P (chi-square) is 0.003. The distribution is skewed.

Head length dispersions are found to be normally distributed about the regression lines of head on body length over-all, in two series investigated.<sup>16</sup>

833 Platteville <i>viridis</i>	P (chi-square)	0.893
715 Pierre <i>viridis</i>	P (chi-square)	0.226

<sup>15</sup> Occ. Papers S. D. Soc. Nat. Hist., No. 3, p. 47, 1937.

<sup>16</sup> Idem. p. 18. A graphic illustration of one of the distributions is given.

Similarly the distribution of fang lengths about either the fang-head or the fang-body regression lines are probably normally distributed. The results in the Platteville series were as follows:

Fang on head length, 519 specimens,  $P$  (chi-square) = 0.351

Fang on body length overall, 526 specimens,  $P$  (chi-square) = 0.165.

One measurement which remains unchanged in each individual during life is that of rattle width; that is, the width of any specific rattle of the sequence. Using only specimens with complete strings, so that the sequence number of each ring is known, the frequency distribution of measurements of any particular ring can be determined. An investigation of a number of series, upon which I hope to publish some notes later, would indicate that the distribution approximates normality. For example, the chi-square  $P$  for 448 buttons (No. 1 rings) of the Platteville series is 0.155. This particular series is somewhat platykurtic, but not excessively so.

#### ILLUSTRATIVE SAMPLING

To illustrate the variations in a series of random samples from a truly normal population, I have assumed a hypothetical homogeneous population comprising 100,000 snakes (all of one sex) with a mean ventral scale count of 100 and a coefficient of variation of 2 per cent, which is a degree of variation closely approached by many species. Thus, the standard deviation is two scales. Then, by the use of random sampling numbers (Tippett, 1927; Fisher and Yates, 1938, pp. 18 and 82) I have selected ten random samples, each comprising 100 specimens. The distributions of the entire normal population and each of the samples is shown in Table 9. The fit for all samples taken together is, by the chi-square test,  $P = 0.77$ , which is quite high; that is, the fit is very close. If we take only the first five sets of samples, the fit is not so good, for  $P = 0.20$ , the greatest deviation from normal being the low number of specimens with 101 ventrals (drawn 73; expected 88.0). Some of the individual samples will be observed to have still poorer fits.

TABLE 9

DISTRIBUTION OF VENTRALS IN A HYPOTHETICAL POPULATION OF 100,000 SNAKES  
 NORMALLY DISTRIBUTED, TOGETHER WITH 10 RANDOM SAMPLES  
 EACH COMPOSED OF 100 SPECIMENS

Number of Ventrals	Composition of Population*	Samples										Total of Samples	
		1	2	3	4	5	6	7	8	9	10		
91	1	....	....	....	....	....	....	....	....	....	....	....	...
92	7	....	....	....	....	....	....	....	....	....	....	....	...
93	44	....	....	....	....	....	....	....	....	....	....	....	...
94	222	....	....	....	....	....	....	....	....	....	1	2	3
95	876	1	1	....	1	....	2	3	....	1	1	1	10
96	2,700	5	4	4	4	4	3	....	3	4	1	1	32
97	6,476	7	7	8	6	5	5	9	8	3	6	6	64
98	12,098	15	12	15	9	15	12	10	11	5	10	10	114
99	17,603	20	18	20	18	22	24	21	14	18	17	17	192
100	19,946	16	17	17	20	16	21	17	23	20	19	19	186
101	17,603	16	14	13	16	14	16	15	18	20	23	23	165
102	12,098	9	17	16	14	8	8	15	12	13	9	9	121
103	6,476	6	8	3	8	8	7	8	9	9	6	6	72
104	2,700	4	1	4	3	4	2	1	1	4	2	2	26
105	876	1	1	....	1	3	....	1	1	2	3	3	13
106	222	....	....	....	....	1	....	....	....	....	1	1	2
107	44	....	....	....	....	....	....	....	....	....	....	....	....
108	7	....	....	....	....	....	....	....	....	....	....	....	....
109	1	....	....	....	....	....	....	....	....	....	....	....	....
Total	100,000	100	100	100	100	100	100	100	100	100	100	100	1000

\* Calculated by ordinates, not areas.

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## SUMMARY

A considerable number of tests, both by the chi-square method and the method of moments, indicate that many of the countable variable characters studied in herpetology, particularly in problems of taxonomy, follow a normal distribution, or one closely approximating such a distribution. Amongst others this is found to be the case with ventral scale counts, probably the most important single character used in herpetological classification.

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APPENDIX

I have tried, as far as possible, to eliminate descriptions of routine statistical methods from the herpetological discussion, mentioning only unusual points. Statistical texts of such number and variety have lately appeared that extensive references are no longer necessary. However, some references are given below for the use of those not familiar with these methods; they are limited to a few on each separate element.

The characteristics of the normal curve: Walker (199-211), Treloar (76-83), Simpson and Roe (70-75), Croxton and Cowden (265-271).

Skewness and kurtosis: Croxton and Cowden (234-245), Treloar (32-35), Goulden (28-31).

Tables of the normal curve: Abridged tables will be found in nearly every statistical text, a particularly convenient set being those of Camp (380-385). The following are more detailed and extensive: Davenport and Ekas (164-172), Kelley (14-114), Glover (392-411), Pearson, part 2 (2-10).

Biological approximations to the normal curve: Simpson and Roe (129-132), Treloar (34-35). See also the interesting comment in the Preface to Kelley's Tables.

Fitting the normal curve to data: (a) by areas, Arkin and Colton (106-108), Chaddock and Croxton (123-126), Croxton and Cowden (275-280); (b) by ordinates, Arkin and Colton (108-109), Croxton and Cowden (271-275).

The chi-square test for normality: Arkin and Colton (109-112), Mills (626-630), Treloar (219-226).

Chi-square tables: Fisher (118-119), Fisher and Yates (27), Pearson, Part I (26-28), Davis and Nelson (399-405).

The moment tests for skewness and kurtosis: Arkin and Colton (145-149), Geary and Pearson (1-15), Yule and Kendall (154-166), Tippett (33-42), Goulden (27-32), Fisher (54-56; 74-79), Madow (515-517).

In applying the chi-square test I have used the standard deviation of the sample, rather than the estimated standard deviation of the population (Fisher, 53). Edge classes have been combined until the theoretical frequency was at least 5 in each group. The classes, as suppressed, in all cases numbered less than 20 (Kenney, Vol. 2, p. 170). The degrees of freedom were taken at 3 less than the number of classes as suppressed (Rider, pp. 109-110), since the theoretical distribution is made to conform to the actual in total number of variates, mean, and standard deviation. In fitting a normal curve to the data, except in a few cases where grouping has been necessary, I have used the ordinate, rather than the area method, as seems to be preferable for discrete variates (Baten, p. 94). For this reason Shepard's correction was not made in calculating the standard deviation of the sample. The differences involved in employing the two methods will usually be unimportant, unless near some assumed critical level of significance.

I have used Fisher's methods in determining the significance of skewness and kurtosis.

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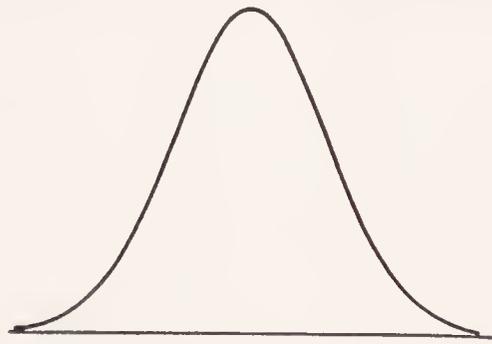


FIG. 1

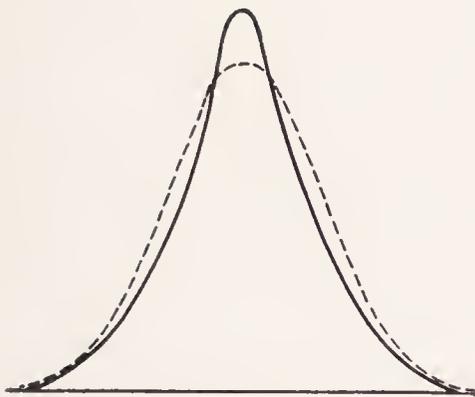


FIG. 2

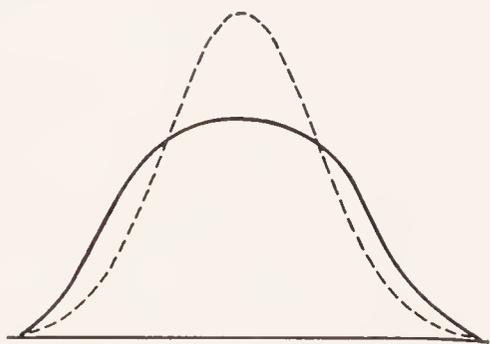


FIG. 3

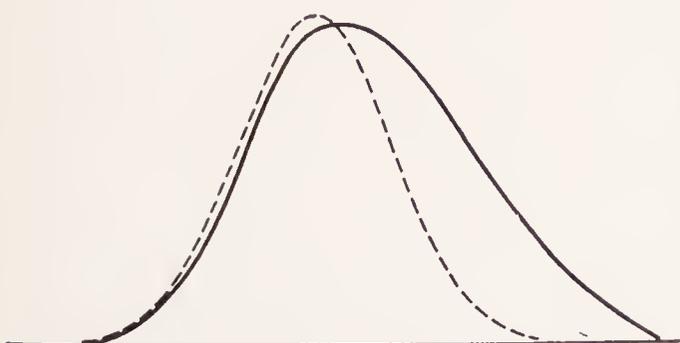


FIG. 4

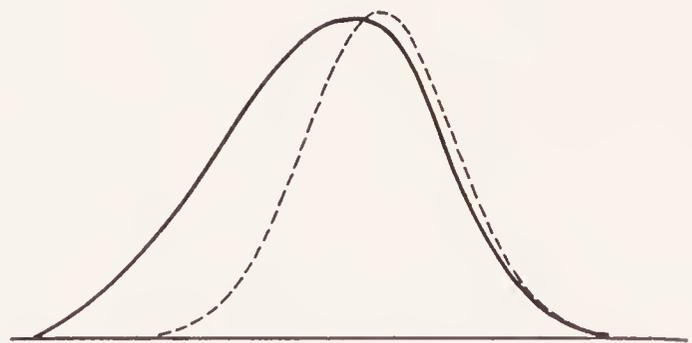


FIG. 5

Figure 1. Normal Curve.

Figure 2. Leptokurtic Distribution.

Figure 3. Platykurtic Distribution.

Figure 4. Positive Skewness.

Figure 5. Negative Skewness.



## II. ILLUSTRATIONS OF THE RELATIONSHIP BETWEEN POPULATIONS AND SAMPLES

### INTRODUCTION

The relationship between a sample, whether an individual specimen or a series of specimens, and the total population out of which it was collected, is always somewhat uncertain. We have the sample before us; it is tangible; we know as much about it as our senses and our methods of investigation permit us to learn. Behind it lies the population which the sample represents, indefinite and nebulous, and in many ways unknown. It is true that the methods of mathematical statistics permit the approximate definition of a population from a sample; yet even with these formulas the population is presented only as a sort of shadow, outlined by statements to the effect that it probably has such and such characteristics, and there is a certain percentage of chance that it falls within such and such limits. But its exact form, character, and limitations we can never know.

In herpetology, as in other branches of biology, we deal with samples. They are the particular specimens which we have been able to acquire for study. Some of these samples, often the first collected, are assigned special importance by being selected as taxonomic or nomenclatorial reference guides or anchors. These are the types. But all the while we are studying and classifying these samples, and attempting to differentiate them from others, we are not really thinking of the samples themselves, but of the populations, still in the wild, which the samples represent. For if taxonomy is to have any real purpose, it is not primarily the determination of the similarities and differences between two or more individuals which we have at hand, but is a judgment respecting these similarities and differences as they are manifested in the original populations from which the samples were drawn. Whether we use the mathematical formulas for estimating the characteristics of populations from samples, or draw inferences as to these characteristics somewhat unconsciously, we are nonetheless really aiming at a definition of the population rather than the sample.

Of course it is individual variation that leads to the uncertainty. Were the animals of a single kind invariant we would know at once all about a population (except its number) from a single sample. But all animals, however closely related, differ in some degree from each other; the problem is to estimate, from the known spread in a sample, how wide the range of these differences becomes in an entire population. Even if two samples are different we cannot be sure, without investigation, that both may not be included within the spread or range of the entire population. For example, one snake may have 150 ventral scutes and another specimen 160. How are we to know whether the entire population—a single homogeneous group of these snakes—does not contain individuals running from as low

as 145 to as high as 170 scutes, thus including both? Parenthetically, I may say that this discussion has nothing to do with the interpretation of the extent of these differences into classification—that is, whether a given difference is great enough to warrant subspecific or specific recognition, or whether it should be considered merely an intrasubspecific territorial or ecological variation. The problem has to do with the determination of differences rather than their interpretation in taxonomy and nomenclature.

The reasons why the relationships between samples and parent populations are sometimes ignored, even today when the statisticians have made available the formulas governing such relationships, are, first, their expression in mathematical terms, which may seem too abstract to permit visualizing the result; and secondly, the absence of the population itself for comparison. For the latter remains always hazy and ill-defined, and we never know how well our description, based on the samples, really fits it. We may presume that the larger the sample the more representative it becomes of the population—that is, the more closely its characteristics are likely to approach those of the population, but we must accept this largely on faith or inherent common sense. This leads to a tendency to treat the sample as if it were the population, and to draw unwarranted conclusions with respect to identities, similarities, and differences from other populations.

While in actual practice we can never secure an entire population for study (except of an animal approaching extinction) we may experiment with theoretical or artificial populations, in any size and form desired, by setting up large groups of individuals segregated into classes premised on the variation in some particular character. An example of such a population, using subcaudal scales as the basic character, would be the following, comprising, for the sake of simplicity, only four classes:

Number of Subcaudals:	Number of Specimens
13	185
14	2,149
15	131,650
16	477
	<hr/>
Total population	134,461

From such a population we may then select samples quite at random and thus see in operation, without recourse to mathematical formulas, the principles which cause samples to resemble their parent populations; and how they fluctuate and differ from other samples drawn from the same or different populations. Thus, we will have before us, for continuous examination and comparison, both the entire parent population, simplified and perfected in character as compared to a real population, and the

sample. We can watch the sample grow (in numbers, not in the size of its individuals) and witness the favorable effects of larger samples or the adverse effects of heterogeneity in samples. All the while the formulas of the mathematicians will be at work, but we will not be using them; we will see only their results. To carry out such a program the tests on artificial populations which follow have been made; they will serve to illustrate some of the principles of the relationship between populations and samples.

An artificial population has certain fundamental advantages over any real one. First, as previously mentioned, it may be visualized in its entirety, and thus be made available for comparison with samples; secondly, it may be very large, so large in fact, that it may be assumed to remain unchanged in composition when a few individuals have been withdrawn as a sample; and lastly, it may be designed to follow any scheme of variation, and to fit that scheme perfectly, avoiding the complicating peculiarities found in every real population. For in considering a real population it is often difficult to divorce the relationship to be demonstrated from the particular characteristics of that species, its variations and morphology.

When these tests on theoretical populations are made there is no guarantee that the result will follow a particular course, for each sample will be a truly random or chance sample. Thus, one may start out to prove a given point (for instance that the means of two separate samples tend to approach each other as the samples are increased in size) and by some freak of chance the first trial might prove exactly the opposite. But repeated trials will surely demonstrate the truth of this proposition; in the long run the results will follow the mathematical formulas, but without their seeming complications. For this reason several tests will usually be made to illustrate each type of relationship.

It should be stated for the benefit of those unfamiliar with statistical methods that there is nothing having the slightest originality or novelty developed herein with respect to the mathematical relationships between populations and samples. And of course I am not presenting these illustrative examples for the purpose of proving the validity of mathematical formulas; such proofs are available in any statistical text. The purpose of the tests is to give a direct picture of the relationship, without recourse to the formulas. However, from time to time, after demonstrating a relationship by example, I have pointed out, in the interest of clarity, what formula is involved, and how well the illustrative test follows it. But certainly this is with no idea of furnishing a proof where none is needed.

#### ARTIFICIAL POPULATIONS

Populations may vary in several ways, such as the number of individuals included, the arithmetical mean or average value of a character, and the extent and nature of its variability, that is, how closely and in what way it is dispersed about the mean. In the present discussion, in the interest of simplicity, I shall prepare my populations according to rather rigid specifi-

cations. First, only one character at a time will be considered; for example, a population will be made up of a group of individuals having different numbers of ventral scutes and all other features of real reptiles will for the time be ignored. Secondly, with a few exceptions, each population will contain exactly 100,000 individuals, this number being sufficiently large to demonstrate the results of sampling without being cumbersome. However, the removal of a few individual specimens will not change the relative class-compositions of the remaining population, which is treated, in this regard, as if it were infinite. Next, the characters discussed will be of the type always expressible in integral terms, as far as any single specimen is concerned; that is, they will be countable (rather than measurable) characters, such as ventrals, subcaudals, body blotches, etc. Further, in the interest of simplicification, the population will always be so arranged that its arithmetical mean or average will be expressible as an integer; for example, the mean in these hypothetical populations will always be exactly 166 ventrals, or 48 blotches, instead of 166.352 ventrals, or 48.713 blotches, as would be the case in a real population. This simplification can be made without in any way interfering with the demonstration of the trends of samples, but has the important practical advantage that the number of individuals in each class above the mean equals the number in the corresponding class below, if the distribution be symmetrical. Finally, the populations will be normally distributed, that is, the variations will follow the normal curve of error. This distribution has several advantages: it has been extensively investigated and tabled, and thus the populations can be set up with only the most elementary calculations; its distribution may be fully described and fixed by three simple statistics (the mean, the number of individuals, and the standard deviation); and finally, this type of distribution is closely approximated by many characters in natural history, and herpetology is no exception, as shown by investigations previously made.<sup>1</sup>

I have stated that these normal populations may be completely defined by three statistics—the number of individuals, the mean, and the standard deviation. It will be desirable to show how populations change when one of these statistics or parameters varies while the other two remain constant.<sup>2</sup>

In Tables 1, 2, and 3, such variations are set forth. I have chosen to consider the populations as representing the distribution of the ventral scutes in a hypothetical species of snake; of course, they might equally well have signified any other character. Table 1 shows three normal populations, each about 100 times as large as the next. To avoid confusion these have not been given the slight adjustment necessary to cause them to total exactly to the nearest even thousand.

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<sup>1</sup> See Part I of this series.

<sup>2</sup> The word "statistic" is usually taken to refer to a numerical characteristic of a sample, while "parameter" refers to the corresponding characteristic of a population.

TABLE 1

Effect of Variation in the Number of Individuals in a Population.

Number of Ventrols	Population No. 1	Population No. 2	Population No. 3
95.....	....	....	15
96.....	....	13	1,338
97.....	4	443	44,318
98.....	54	5,399	539,910
99.....	242	24,197	2,419,707
100.....	399	39,894	3,989,423
101.....	242	24,197	2,419,707
102.....	54	5,399	539,910
103.....	4	443	44,318
104.....	....	13	1,338
105.....	....	....	15
Total .....	999	99,998	9,999,999

An interesting feature of Table 1 is the increase in the over-all range—minimum to maximum—that follows an increased population.

In Table 2 the mean of one population has been shifted from 100 to 98. It will be observed that the sizes of the groups or classes of variates remain otherwise unaffected.

TABLE 2

Effect of Variation in the Mean of a Population.

Number of Ventrols	Population No. 1 Mean = 100	Population No. 2 Mean = 98
94.....	....	13
95.....	....	443
96.....	13	5,399
97.....	443	24,197
98.....	5,399	39,894
99.....	24,197	24,197
100.....	39,894	5,399
101.....	24,197	443
102.....	5,399	13
103.....	443	....
104.....	13	....
Total.....	99,998	99,998

In Table 3 the effect of changing the standard deviation ( $\sigma$ ) of a population is shown, the number of specimens remaining constant at 100,000, and the mean at 100. It will be noted that the spread or scatter increases, for the standard deviation is a measure of dispersion. In this and subsequent populations I have in some instances made slight adjustments in the last figure of one or two of the most populous classes to cause the total to equal 100,000 exactly. This facilitates comparisons without changing to an appreciable degree the chances involved in drawing random samples from that population.

TABLE 3  
Effect of Variation  
In the Standard Deviation of a Population

Ventrals	Population No. 1 $\sigma = 0.8$	Population No. 2 $\sigma = 1.0$	Population No. 3 $\sigma = 1.333$
94.....	.....	.....	1
95.....	.....	.....	26
96.....	.....	13	332
97.....	44	443	2,380
98.....	2,191	5,399	9,714
99.....	22,831	24,197	22,586
100.....	49,868	39,896	29,922
101.....	22,831	24,197	22,586
102.....	2,191	5,399	9,714
103.....	44	443	2,380
104.....	.....	13	332
105.....	.....	.....	26
106.....	.....	.....	1
Total.....	100,000	100,000	100,000

A few notes on the method of forming these populations should be recorded. Since we are dealing with characters that can take only discrete values, the ordinates rather than the areas of the normal curve have been used in segregating a population into classes. If one sets up a population by areas, the square of the standard deviation will always come out too high by  $1/12$ , this being the amount of Sheppard's correction for grouping. But in the present instance, since the variates are integral, they always take a central position in each class and no correction should be made. A comparison of distributions by ordinates and areas is given in Table 4 for one value of the standard deviation ( $\sigma = 1$ ). It will be noted that the area basis gives a slightly wider dispersion.

TABLE 4  
Effect of Calculating Distributions  
by Ordinates and by Areas

Number of Ventrols	Population No. 1 by Ordinates	Population No. 2 by Areas
96.....	13	23
97.....	443	598
98.....	5,399	6,060
99.....	24,197	24,173
100.....	39,896	38,292
101.....	24,197	24,173
102.....	5,399	6,060
103.....	443	598
104.....	13	23
Total.....	100,000	100,000

The standard deviation of the population as finally set up is never exactly equal to that sought, even when the ordinate method is employed. However, no population that I have used differs in its standard deviation from the figure desired by more than 0.001. For example, in the third population given in Table 3, the standard deviation calculated, after the population was set up, was found to be 1.33312 instead of 1.33333. Obviously, this slight difference will not affect the results in the sampling tests that I have made. The particular table employed in setting up the populations is that of W. F. Sheppard in Karl Pearson: *Tables for Statisticians and Biometricians*, Part 1, Ed. 3, 1930, pp. 2-8.

It will be observed that changing the mean or the number of individuals in a population utilizes the same or proportionate numbers in each class; only a change in the standard deviation requires a completely new set of figures. For the purposes of this investigation, populations of 100,000 with the following 9 values of the standard deviation were set up: 0.667, 0.8, 1, 1.333, 2, 2.857, 4, 6.667, 10. It was found that these would fit almost any variable character used in herpetological classification closely enough to test an illustrative sampling problem.

Before leaving these populations for the experiments in sampling, I wish to show the effect of heterogeneity on a composite population, each component of which is normally distributed. Let us assume a population composed of 100,000 males and an equal number of females, and observe the effect on the distribution of the combined ventral scale counts, as sexual dimorphism increases. The standard deviation will be taken as 1.333 in both sexes, but the means will be caused to diverge. In the first composite population both sexes average 100 ventrals; in the second, the females average 101 and the males 99; in the third the females 102 and

males 98, etc. In each successive distribution the difference between the means increases by 2, but the composite mean remains at 100. The results are shown in Table 5. It will be observed in a case such as this, that, if the means are different, the composite distribution ceases to be normal;

TABLE 5  
Effect of Heterogeneity on Composite Populations  
when Each Component is Normally Distributed.  
 $\sigma = 1.333$

Number of Ventrols	Difference Between the Means of Males and Females			
	0	2	4	6
91.....	....	....	....	1
92.....	....	....	1	26
93.....	....	1	26	332
94.....	2	26	332	2,380
95.....	52	333	2,380	9,714
96.....	664	2,406	9,715	22,586
97.....	4,760	10,046	22,612	29,923
98.....	19,428	24,966	30,254	22,612
99.....	45,172	39,636	24,966	10,046
100.....	59,844	45,172	19,428	4,760
101.....	45,172	39,636	24,966	10,046
102.....	19,428	24,966	30,254	22,612
103.....	4,760	10,046	22,612	29,923
104.....	664	2,406	9,715	22,586
105.....	52	333	2,380	9,714
106.....	2	26	332	2,380
107.....	....	1	26	332
108.....	....	....	1	26
109.....	....	....	....	1
Total .....	200,000	200,000	200,000	200,000

it becomes flat-topped, and, as the difference between the means increases, it even becomes bimodal, as is evident in the last two columns. It can be shown that bimodality begins when the differences between the means exceeds twice the standard deviation. Estimating population characteristics from samples, using rules and formulas premised on the substantial normality of the population, will not produce accurate results when the normal components differ enough to produce marked abnormality in the composite group. Thus, combining sexes should usually be avoided in making comparisons, if there be an important degree of sexual dimorphism.

#### THE METHODS OF RANDOM SAMPLING

Random sampling tables are available and their use described in the following publications: (a) Tracts for Computers, No. 15, Random

Sampling Numbers arranged by L. H. Tippett, pp. VIII + 24, Cambridge University Press, 1927; (b) Statistical Tables for Biological, Agricultural, and Medical Research, by Fisher and Yates, pp. 18-20, 82-87, London and Edinburgh, 1938. The first table comprises 208 columns, each column containing 50 4-figure numbers; the second 30 columns, each column containing 50 10-figure numbers. The individual single-figure columns can be grouped in a great variety of ways; any five contiguous single-figure columns may be employed as random selections of 5-figure numbers, which may in turn be used directly in drawing individuals from a population of 100,000. For example, we set up our population with equivalent limiting numbers as given in Table 6. Then we have only to decide on a method of selecting five figure numbers from one of the columns (or combinations of parts of columns) in either table and we have a series of ventral counts by chance. We may use dice, cards, a roulette wheel, or bingo numbers to select both the page and the group of columns which are to be used.

TABLE 6

An Example Application of Random Sampling Numbers.

Number of Ventrols	Population Distribution	Inclusive Numbers
96.....	13	00001*-00013
97.....	443	00014-00456
98.....	5,399	00457-05855
99.....	24,197	05856-30052
100.....	39,896	30053-69948
101.....	24,197	69949-94145
102.....	5,399	94146-99544
103.....	443	99545-99987
104.....	13	99988-100000*
Total.....		100,000

\* The number 00000 is recorded as 100,000.

Suppose our method of selection leads to the numbers in columns 25-29 on p. XII of Tippett. Then the first five samples are represented by the numbers 00433, 48901, 27228, 72094, and 13224. Referring to Table 6, we find that we have drawn, in order, snakes with counts of 97, 100, 99, 101, and 99 ventrols.

Random selections from heterogeneous populations may be made by using dice, the odd numbers representing males, for example, and the even females. Or, if the population components are not evenly divided, we may use cards or a roulette wheel, allocating the numbers in any desired ratios; or a two or three figure column, selected by lot from either of the

tables of random numbers. It is only necessary that we play the game fairly and use a system without bias. Many ways of solving such problems of selection will readily suggest themselves to any one accustomed to games of chance. Even the tables of random sampling numbers may be supplanted by the use of numbered discs or balls, although this will slow selection and introduce the possibility of bias through mechanical imperfection. The totalizer wheels of an old speedometer may be used as a selector by freeing them from each other, but they must be well balanced to avoid concentration on particular numbers.

#### VARIATIONS OF THE MEAN

So much for discussions of the methods of setting up populations and drawing random samples from them. We shall now put these schemes to work to illustrate various relationships between populations and samples, and how samples tend to vary. We shall, as far as possible, select illustrations approximating situations found in the herpetological field.

It is first desired to follow the trend in the mean of the ventral scale counts in samples representing a homogeneous population of rattlesnakes. The investigation is limited to one sex so that sexual dimorphism will not complicate the result. There are, as usual, 100,000 individuals in the population. The mean is 200 ventrals, and the coefficient of variation is 2 per cent, a figure representative of homogeneous series of rattlers. The standard deviation is then 4, since  $\sigma = VM/100$ . Next, we make four entirely separate selections from this population, each comprising 20 specimens, entering each specimen in the order of its selection, and recalculating the mean (to one figure after the decimal point) as each snake is added to the collection. The results are set forth in Table 7.

TABLE 7

Changes in the Mean with Increasing Sizes of Samples.  
Ventral Scutes : Population Mean 200.

Speci- men Number	Sample No. 1		Sample No. 2		Sample No. 3		Sample No. 4	
	Specimen Count	Mean	Specimen Count	Mean	Specimen Count	Mean	Specimen Count	Mean
1	199	199.0	206	206.0	199	199.0	198	198.0
2	200	199.5	200	203.0	200	199.5	204	201.0
3	199	199.3	202	202.7	197	198.7	197	199.7
4	199	199.2	200	202.0	201	199.3	201	200.0
5	204	200.2	201	201.8	201	199.6	197	199.4
6	199	200.2	195	200.7	203	200.2	202	199.8
7	204	200.6	203	201.0	203	200.6	201	200.0
8	201	200.6	199	200.7	199	200.4	199	199.9
9	201	200.7	192	199.6	197	200.0	201	200.0
10	208	201.4	200	199.8	201	200.1	189	198.9
11	200	201.3	203	200.1	203	200.4	203	199.3
12	200	201.2	206	200.6	205	200.8	211	200.3
13	192	200.5	198	200.4	194	200.2	199	200.2
14	195	200.1	202	200.5	204	200.5	201	200.2
15	196	199.8	201	200.5	199	200.4	201	200.3
16	203	200.0	198	200.4	202	200.5	211	200.9
17	198	199.8	202	200.5	204	200.7	196	200.6
18	206	200.2	200	200.4	202	200.8	206	200.9
19	200	200.2	206	200.7	200	200.7	198	200.8
20	201	200.3	197	200.6	198	200.6	200	200.8

NOTE:—To visualize the population from which these samples were drawn see the second column in Table 18.

The outstanding conclusion that may be drawn from these samples is the close adherence of all the means throughout to the true population mean of 200. Sample 2 starts out high but soon settles down and adheres closely to the true mean. An unusual feature of this particular set of results is the fact that all four have produced means above the true mean; ordinarily we would expect some above and some below.

One would naturally conclude from this table that the true mean of a population may be very closely gauged by relatively small samples. However, it is to be remembered that ventrals are the most constant characters of scutellation and that this population is homogeneous. Were we dealing with a widespread population with a greater variation the results would have fluctuated considerably more.

Let us take a more variable character, that of body blotches. Here the coefficient of variation is usually about 10 per cent. We shall assume a species having an average blotch count of 40 blotches with a standard

deviation of 4. Again we follow the separate developments of four samples as set forth in Table 8. A considerable fluctuation will be observed while the samples are small; but all soon approach 40 and the maximum deviation, when 20 specimens have been included in each sample, is only 0.9, this being in Sample 2. However, in drawing conclusions from both Tables 7 and 8, one should not give too much weight to the final line, but should scan the fluctuations in the individual specimens and the effect on the moving average as each sample grows.

TABLE 8  
Changes in the Mean with Increasing Sizes of Samples.  
Body Blotches. Population Mean 40.

Specimen Number	Sample No. 1		Sample No. 2		Sample No. 3		Sample No. 4	
	Specimen Count	Mean	Specimen Count	Mean	Specimen Count	Mean	Specimen Count	Mean
1	37	37.0	36	36.0	44	44.0	42	42.0
2	39	38.0	40	38.0	44	44.0	42	42.0
3	39	38.3	44	40.0	36	41.3	37	40.3
4	49	41.0	42	40.5	45	42.3	27	37.0
5	44	42.0	46	42.0	42	42.2	45	38.6
6	39	41.2	37	40.8	41	42.0	41	39.0
7	39	40.9	43	41.1	39	41.6	44	39.7
8	34	40.0	40	41.0	41	41.5	40	39.8
9	35	39.4	35	40.3	42	41.6	34	39.1
10	42	39.7	42	40.5	43	41.7	42	39.4
11	42	39.9	45	40.9	37	41.3	45	39.9
12	41	40.0	43	41.1	40	41.2	37	39.7
13	47	40.5	47	41.5	38	40.9	41	39.8
14	33	40.0	38	41.3	43	41.1	36	39.5
15	37	39.8	41	41.3	39	40.9	41	39.6
16	41	39.9	43	41.4	45	41.2	42	39.7
17	41	39.9	38	41.2	32	40.6	47	40.2
18	36	39.7	41	41.1	39	40.6	32	39.7
19	40	39.7	36	40.9	32	40.1	46	40.1
20	44	39.9	42	40.9	42	40.2	34	39.8

NOTE:—To visualize the population from which these samples were drawn see Table 13.

The mathematical formula which describes these fluctuations in the mean of samples selected from a normal population states that the standard error of the sample means equals the standard deviation of the population divided by the square root of the number in the sample, that is  $\sigma_m = \sigma/N^{1/2}$ . Another way of describing the scatter of such sample means is to say that about 68 per cent will fall within a range  $\sigma/N^{1/2}$

above and below the true population mean. Taking the populations from which the samples in Tables 7 and 8 were selected, we find (since  $\sigma$  was 4 in both cases) that  $\sigma/N^{1/2} = 4/4.472$  or about 0.9. Hence, in the case of the ventrals, with a population mean of 200, 68 per cent of the means (of samples comprising 20 individuals) should fall between 199.1 and 200.9. All four of our samples do fall within this range, which is somewhat closer than expectation, as one in 3 might well have been presumed to fall outside. Similarly, with respect to Table 8, all four samples (at the 20 specimen level) fall well within the range of 39.1 to 40.9, which again is somewhat closer than expectation. If we take this table at the 9 specimen level, where the 68 per cent range is  $4/9^{1/2}$ , or 1.333 above and below the mean, we find that Sample 3 falls outside this range.

Another way of indicating how the range of the means of samples tends to narrow with an increased number of specimens, is to show the 50 per cent range limits of means of samples of the same population from which the samples in Table 8 were drawn, that is, a population with a mean of 40 blotches and a standard deviation of 4. The following figures show the limits which, in the long run, will include 50 per cent of the sample means, about 25 per cent being above the stated range, and 25 per cent below.

Number of Specimens in the Sample	50 Per Cent Range of Means
1	37.3 - 42.7
2	38.1 - 41.9
3	38.4 - 41.6
4	38.6 - 41.4
5	38.8 - 41.2
10	39.1 - 40.9
15	39.3 - 40.7
20	39.4 - 40.6
25	39.5 - 40.5
50	39.6 - 40.4
100	39.7 - 40.3

Before leaving this matter of the trends in means, I wish to show the effects of heterogeneity in samples. Suppose that collections are made over a widespread territory in which there are racial differences. Also sexual dimorphism is evident, yet the taxonomist ignores these variations and combines all the specimens at hand to calculate a mean ventral scale count. How then will the means vary as between samples, as specimens are added? Let us assume population characteristics closely approaching the condition in the rattlesnake *Crotalus cinereous*. The population is comprised of two-thirds males and one-third females,<sup>3</sup> and the territorial

<sup>3</sup> Meaning the population as it affects collections. While the true populations of the sexes are approximately equal, there are reasons why twice as many males reach collections as females. Occ. Papers S. D. Soc. Nat. Hist., No. 1, p. 8, 1936.

ratios are in the following percentages: Texas 50, New Mexico 20, Arizona 30. The average ventral scale counts in the separate populations are as follows:

	Males	Females
Texas .....	179	182
New Mexico .....	182	185
Arizona .....	185	188

The standard deviation is 4 in all populations.

Table 9 shows the variations in the means of four samples under these decidedly mixed conditions. It will be noted that the fluctuations are considerably greater than in Table 7.

TABLE 9

Changes in the Mean with Increasing Sizes of Samples.  
Showing the Effect of Heterogeneity.  
Ventral Scale Counts

Speci- men Number	Sample No. 1		Sample No. 2		Sample No. 3		Sample No. 4	
	Specimen Count	Mean	Specimen Count	Mean	Specimen Count	Mean	Specimen Count	Mean
1	183	183.0	182	182.0	177	177.0	181	181.0
2	177	180.0	183	182.5	184	180.5	184	182.5
3	171	177.0	173	179.3	169	176.7	182	182.3
4	177	177.0	178	179.0	181	177.7	180	181.8
5	175	176.6	191	181.4	183	178.8	179	181.2
6	179	177.0	181	181.3	182	179.3	177	180.5
7	184	178.0	189	182.4	181	179.6	180	180.4
8	177	177.9	183	182.5	182	179.9	192	181.9
9	182	178.3	177	181.9	175	179.3	182	181.9
10	184	178.9	185	182.2	182	179.6	191	182.8
11	192	180.1	186	182.5	170	178.7	174	182.0
12	179	180.0	175	181.8	185	179.3	190	182.7
13	178	179.8	192	182.7	181	179.4	180	182.4
14	183	180.1	185	182.8	189	180.1	190	183.0
15	184	180.3	181	182.7	182	180.2	179	182.7
16	186	180.7	181	182.6	186	180.6	188	183.0
17	181	180.7	174	182.1	188	181.0	172	182.4
18	177	180.6	174	181.6	175	180.7	188	182.7
19	192	181.1	181	181.6	187	181.0	182	182.7
20	180	181.1	186	181.9	185	181.2	185	182.8

It should be understood that although the basic populations have the proportionate distributions which I have indicated, the composition of the samples, through the operation of the laws of chance, may deviate considerably therefrom. The selections were made through the use of a roulette wheel and Tippett's table. The samples, drawn at random, have the following compositions:

Sample Number	Texas		New Mexico		Arizona	
	Males	Females	Males	Females	Males	Females
1	13	2	2	2	....	1
2	3	9	3	1	3	1
3	5	1	4	1	7	2
4	10	1	2	2	5	....
	—	—	—	—	—	—
Total	31	13	11	6	15	4

This is the kind of effect that one often meets in species that are poorly represented in collections. One must view each of the samples in Table 9 as a separate entity, the others being presumed unavailable, to see whether the variations might actually give one the impression of different forms.

#### RANGES OF VARIATION

The over-all ranges of various numerical characters are often used in keys or in the definition of species. But it should be recognized that, just as sample means tend to draw closer to population means and narrow in their fluctuations as the number of specimens in a sample increases, so the range tends to widen, approaching, but rarely reaching, the population range. The range in small samples often gives an unwarranted impression of narrow dispersion.

To illustrate these tendencies I shall use the same populations as formed the bases of Tables 7-9, but shall draw from each population 4 new samples, each comprising 25 specimens. In this case, to make the trends more readily evident, I shall not list the scale count or number of blotches of each specimen as it is added to the collection, but will enter only those which set new maximum or minimum records. The results are presented in Tables 10-12.

With regard to Table 10 it will be observed that no sample closely approaches the population range of 183 to 217, the lowest of the 100 individuals drawn being 191 and the highest 211. Sample 1 is peculiar in that the first specimen drawn proved to be the highest of the entire 25, while in Sample 3 the complete range for this sample was reached with the fourth specimen. Quite a difference is to be observed between samples, in the over-all range attained up to the 25th specimen.

TABLE 10

Changes in the Range with Increasing Sizes of Samples.  
 Ventral Scutes. Population Mean 200;  
 Absolute Range 183 to 217.

Specimen Number	Sample No. 1		Sample No. 2		Sample No. 3		Sample No. 4	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
1	208	208	197	197	198	198	199	199
2	203	....	195	....	....	....	....	200
3	200	....	....	200	....	207	197	....
4	198	....	....	....	192	....	....	201
5	197	....	....	....	....	....	....	....
6	....	....	....	....	....	....	....	203
7	....	....	....	202	....	....	....	....
8	....	....	....	....	....	....	....	....
9	....	....	....	....	....	....	....	....
10	....	....	....	204	....	....	....	....
11	....	....	....	....	....	....	....	....
12	....	....	....	....	....	....	....	205
13	....	....	....	....	....	....	194	....
14	....	....	....	211	....	....	....	....
15	195	....	....	....	....	....	....	....
16	....	....	....	....	....	....	....	....
17	....	....	....	....	....	....	....	....
18	....	....	....	....	....	....	....	....
19	....	....	....	....	....	....	....	....
20	....	....	....	....	....	....	191	....
21	....	....	....	....	....	....	....	....
22	....	....	....	....	....	....	....	....
23	....	....	194	....	....	....	....	....
24	....	....	....	....	....	....	....	....
25	....	....	....	....	....	....	....	....
Final Score	195	208	194	211	192	207	191	205

NOTE:—To visualize the population from which these samples were drawn see the second column in Table 18.

Table 11 is interesting in showing a considerable variation in the final scores; particularly Sample 2 reaches a range rather close to the true population range for so few specimens.

TABLE 11

Changes in the Range with Increasing Sizes of Samples.  
 Body Blotches. Population Mean 40;  
 Absolute Range 23 to 57.

Specimen Number	Sample No. 1		Sample No. 2		Sample No. 3		Sample No. 4	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
1	39	39	43	43	44	44	43	43
2	36	....	41	....	41	....	39	....
3	....	....	....	....	....	46	....	....
4	35	....	36	....	40	....	....	....
5	....	....	....	44	....	....	38	....
6	....	40	....	....	....	....	....	....
7	....	....	....	....	....	....	....	....
8	....	....	....	45	....	49	37	....
9	....	46	....	....	36	....	....	....
10	....	....	....	....	....	....	36	....
11	....	....	....	....	35	....	....	....
12	....	....	....	....	....	....	....	....
13	....	....	....	....	....	....	....	....
14	....	....	....	....	....	....	....	....
15	....	....	....	....	....	....	....	....
16	....	....	29	....	....	....	....	45
17	....	....	....	46	....	....	....	....
18	....	....	....	50	....	....	....	....
19	....	....	....	....	....	....	....	....
20	....	....	....	....	32	....	....	....
21	....	....	....	....	....	....	....	....
22	....	....	....	....	....	....	....	....
23	....	....	....	....	....	....	....	47
24	....	....	....	....	....	....	....	....
25	....	....	....	....	....	....	....	....
Final Score	35	46	29	50	32	49	36	47

NOTE:—For the population distribution see Table 13.

Before proceeding to the effects of heterogeneity I wish to carry further the range experiments on the population used in Table 11, by bringing the samples up to 200 each; but to conserve space I shall combine each series in groups of ten. Thus it will only be possible to tell within a range of 10 specimens when a new record was made. The results are set forth in Table 12. It will be seen how much greater are the ranges attained in this table with 200 specimens in each sample, as compared to those in Table 11 having 25 specimens per sample. This relationship between the number of specimens available and the extreme range of a character should

always be given consideration in taxonomic work, not too much dependence being placed on over-all ranges derived from small samples.

TABLE 12

Changes in the Range  
with Increasing Sizes of Samples by Groups of 10.  
Body Blotches. Population Mean 40;  
Absolute Range 23 to 57

Specimen Number	Sample No. 1		Sample No. 2		Sample No. 3		Sample No. 4	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
1 to 10	33	44	34	50	36	50	34	45
11 to 20	....	46	....	....	31	....	....	49
21 to 30	....	....	29	....	....	51	....	....
31 to 40	....	48	....	....	....	....	32	....
41 to 50	30	....	....	....	....	....	....	....
51 to 60	....	....	....	....	....	....	....	....
61 to 70	....	....	....	51	....	....	27	....
71 to 80	....	....	....	....	....	....	....	....
81 to 90	....	49	27	....	30	....	....	....
91 to 100	....	....	....	....	....	....	....	....
101 to 110	....	....	....	....	....	....	....	....
111 to 120	....	....	....	....	....	....	....	....
121 to 130	....	....	....	....	....	....	....	....
131 to 140	....	....	....	....	....	....	....	....
141 to 150	....	....	....	....	....	....	....	51
151 to 160	....	....	....	....	....	....	....	....
161 to 170	....	....	....	....	....	....	....	....
171 to 180	....	....	....	....	28	....	....	....
181 to 190	....	....	....	....	....	....	....	....
191 to 200	....	....	....	....	....	....	....	....
Final Score	30	49	27	51	28	51	27	51

NOTE:—For the population distribution see Table 13.

A table giving the relationship between the standard deviation of a normal distribution and the mean range, as it varies with the number of specimens in the sample, is available in Pearson's Tables for Statisticians and Biometricians, Part II, Table XXII, pp. 165-166, 1931. We find from this table that the mean range attained in my Table 11 should be about 15.7; the actual ranges are 11, 21, 17, and 11 blotches, which gives a mean of 15. In Table 12 the final ranges were 19, 24, 23, and 24; mean 22.5. From Pearson's table we learn that the range should average 5.49 times the standard deviation (4), or 22.0; this is good agreement for only 4 samples. Theoretically a sample comprising 5 specimens will have

about twice the range shown by the first two specimens, while 60 specimens will again double the range of the first five. But even 1000 specimens will not again double the range; they will add only 40 per cent.

This matter of range is thought to be of sufficient interest and importance to warrant the presentation of Table 13, which shows the actual population from which the samples in Tables 11 and 12 were drawn.

TABLE 13

Normal Distribution of Body Blotches in a  
Population of 100,000 Specimens.  
Mean 40; Standard Deviation 4.

Number of Blotches	Number of Specimens
23	1
24	3
25	9
26	22
27	51
28	111
29	227
30	438
31	793
32	1,350
33	2,157
34	3,238
35	4,566
36	6,049
37	7,529
38	8,802
39	9,667
40	9,974

The other half of the distribution is not given since it duplicates the first half in reverse; that is, there are 9,667 specimens with 41 blotches, 8,802 with 42, etc.

A random sample of 4000 specimens drawn from this population had a range of 23 to 54 blotches; in other words, the lowest individual in the population was drawn, but the highest drawn was 3 below the absolute maximum contained in the population.

Table 14 represents the results of sampling the same composite population discussed under Table 9. The spread is increased and the results are more erratic than those disclosed in sampling homogeneous populations. The results are somewhat similar to sampling a normal population with a higher standard deviation, but this is not exactly true, as the com-

TABLE 14

Changes in the Range  
with Increasing Sizes of Samples,  
Showing the Effect of Heterogeneity.  
Ventral Scale Counts;  
Absolute Range 162 to 205.

Specimen Number	Sample No. 1		Sample No. 2		Sample No. 3		Sample No. 4	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
1	187	187	188	188	185	185	183	183
2	....	191	185	....	....	189	182	....
3	....	....	184	....	....	193	....	193
4	184	....	178	....	178	....	178	....
5	182	....	....	....	....	....	....	....
6	....	....	....	....	....	....	....	....
7	....	....	....	....	....	....	176	....
8	....	....	....	....	177	....	....	....
9	....	....	....	....	....	....	....	....
10	181	....	....	....	....	....	....	....
11	171	....	....	....	....	....	....	....
12	....	....	....	....	....	....	....	....
13	....	....	175	....	....	....	....	....
14	....	....	....	....	....	....	....	....
15	....	....	....	....	....	....	....	....
16	....	....	....	....	....	....	....	....
17	....	....	....	....	....	....	....	....
18	....	....	....	....	....	....	....	....
19	....	....	....	....	....	....	....	....
20	....	....	....	....	....	....	....	....
21	....	....	....	....	....	....	....	....
22	....	....	....	193	....	....	....	....
23	....	....	....	....	....	....	....	....
24	....	....	....	....	....	....	....	....
25	....	....	....	....	....	....	....	....
Final Score	171	191	175	193	177	193	176	193

posite population is not normally distributed. It should be understood that while Tables 9 and 14 are drawn from the same composite population, they are based on separately selected samples. A comparison of the trends in the means, as indicated by Tables 7, 8, and 9, with trends and variations in the over-all ranges as shown in Tables 10, 11, 12, and 14, will demonstrate how much more accurately the mean represents the population mean than the range in the sample represents the population range. For example, compare the results of Tables 8 and 11, Table 11 being used only up to and including Specimen 20:

	Mean	Minimum	Maximum
Population Parameter.....	40.0	23	57
Sample 1 .....	39.9	35	46
2 .....	40.9	29	50
3 .....	40.2	32	49
4 .....	39.8	36	45

It is not only that the sample range fails to reach the population range, for this is to be expected, but there is a considerable discrepancy between the several sample ranges as compared with the slight variation between the sample means.

In subsequent studies of dispersion, comparisons are drawn between population parameters and sample statistics, with respect to the mean and range, where each sample comprises 100 specimens, instead of only 20 as above. The results are set forth in Table 22. The consistency of sample means, and the lack of dependability in the maxima and minima are there evident. Further, it is to be remembered that these results are derived from populations that are truly normal. In real populations it is quite likely that there may be fringe specimens in greater number than are expected in a normal distribution, especially if juveniles are included. For juvenile specimens are occasionally so distorted and aberrant that they probably would not survive. Although the range of a character is often used in taxonomic work, especially to show whether there is an overlap between two forms, it is really a rather poor indicator because of its lack of close adherence to the range of the population. It should never be used without a statement giving the number of specimens in the sample; otherwise it is almost without value.

Later, in discussing dispersion in samples, the use of the interquartile range, as a dispersion indicator, will be examined, and additional examples of the relationship between population and sample ranges will be adduced.

#### DISPERSIONS OF SAMPLES COMPARED TO THOSE OF POPULATIONS

Thus far I have discussed the relationships of samples and parent populations in respect of the two simplest and most frequently used herpetological statistics—the mean and the range of variation. Illustrations have

been given showing how these sample statistics change, and in general tend to approach the population parameters as the samples increase in size. There remains the important attribute of dispersion, that is the scatter of the variates about the mean—how closely they adhere to the mean and what the nature of the dispersion may be. This is an extremely important statistic in taxonomic problems, especially those having to do with the significance of differences between subspecies or species. For, given a certain difference between means, the extent of the overlap between two forms will obviously depend upon the extent to which the variates spread on each side of the mean.

Returning to the relationship between samples and the populations from which they were drawn, I again resort to the method of illustration by drawing a number of samples from each of several different populations, setting them beside each other in tabular form to facilitate a visual comparison. Since samples of appreciable size are rarely identical (each sample having its own individuality), no single sample can outline this relationship completely, which is the reason for drawing a number of illustrative samples from each population.

TABLE 15

Changes in the Dispersion of a Sample with Enlargement of the Sample.  
Infralabials: Mean = 16,  $\sigma = 1$

Number of Infralabials	Distribution of Population	Successive Sample Steps										
		1	2	3	4	5	6	7	8	9	10	11
12	13	..	..	..	..	..	..	..	..	..	..	..
13	443	..	..	..	..	..	..	1	1	1	1	1
14	5,399	..	..	..	..	..	..	..	..	2	5	19
15	24,197	..	1	2	3	3	5	10	15	24	48	129
16	39,896	1	1	1	1	1	1	7	15	38	74	199
17	24,197	..	..	..	..	1	3	4	16	32	61	125
18	5,399	..	..	..	..	..	1	3	3	3	9	25
19	443	..	..	..	..	..	..	..	..	..	2	2
20	13	..	..	..	..	..	..	..	..	..	..	..
Total	100,000	1	2	3	4	5	10	25	50	100	200	500

In presenting tables showing the trends of means and over-all ranges with the growth of samples, each specimen increment was shown separately. This is usually too cumbersome a method when illustrating the relationship between the dispersion in samples and populations; however, in Table 15 I have set forth such a growth of one sample by successive steps, using, as the population, an assumed distribution of infralabials in a species of rattlesnake, this particular distribution being closely approxi-

mated in several species. Table 15 shows how, as a sample grows, it tends more closely to approximate the parent population in the character of its dispersion. But even at 200 specimens the discrepancies are quite conspicuous; in this particular sample there are too few specimens with 14 infralabials and too many with 17. By the time the sample has been built up to 500 specimens these imperfections have mostly disappeared, and the sample shows a closer resemblance to the parent population. In making such a comparison, however, it is important to recall how seldom we have a herpetological sample as large as 500 specimens.

TABLE 16

Dispersions of 10 Samples, Each Comprising 100 Individuals.  
Infralabials: Mean = 16,  $\sigma = 1$

Number of Infralabials	Distribution of Population	Sample Number										Total	
		1	2	3	4	5	6	7	8	9	10		
12	13	....	....	....	....	....	....	....	....	....	....	....	....
13	443	....	2	....	....	2	....	1	....	1	....	....	6
14	5,399	1	9	7	4	9	3	3	1	7	7	....	51
15	24,197	29	24	15	15	29	30	22	34	21	16	....	235
16	39,896	40	37	39	47	37	36	38	39	43	42	....	398
17	24,197	24	25	37	30	20	28	33	21	23	27	....	268
18	5,399	6	3	2	4	2	3	3	4	4	8	....	39
19	443	....	....	....	....	1	....	....	1	1	....	....	3
20	13	....	....	....	....	....	....	....	....	....	....	....	....
Total	100,000	100	100	100	100	100	100	100	100	100	100	100	1000

Table 16 uses the same population, drawing therefrom 10 new samples, each containing 100 specimens. A considerable variation amongst the samples will be noted; each seems to have an individuality of its own. In the summation of the ten samples, bringing the total to 1000 specimens, there is a rather marked deficiency in specimens having 18 infralabials, and correspondingly an overabundance of those with 17. Some of the samples are badly distorted, while others more closely follow the distribution of the population. Sample No. 9 is probably the closest fit to 1/1000 of the population, while No. 3 is particularly unbalanced. A chi-square test of the total of the 1000 specimens gives  $P = 0.21$ .<sup>4</sup> This is not a particularly good fit, for it shows that 79 similarly drawn samples out of 100 would more closely approximate the distribution of the population.

<sup>4</sup> In making these chi-square tests I have taken the degrees of freedom as one less than the number of classes as suppressed, since a fit has been forced only with respect to the totals of the theoretical and actual distributions.

But the principal point to be observed with respect to these samples, comparing each with the others, and with the parent population from which they were drawn, is the varying impression that a taxonomist might gain from them, having in mind the fact that the taxonomist would have only one sample before him, neither the population nor the other samples being available.

Tables 15 and 16 gave the results of random sampling from a population having a rather closely concentrated character; after all there is not much variation in the infralabials of any homogeneous series of rattlesnakes. Table 17 sets forth the results of sampling a population which is divided into a greater number of classes. The character considered is the subcaudal scale count; the mean is 30 and the standard deviation 2. Thus the coefficient of variation is 6.67 per cent. Such a distribution is not unusual; it is closely approximated, for example, by female *Phyllorhynchus decurtatus perkinsi*. It will be observed that, from the separate samples, one gains a less accurate suggestion of the parent population than was the case with the more concentrated character of Table 16. Sample 2 is particularly distorted; Sample 9 is good as far as the central classes are concerned, but poorly distributed in the edge-classes. The grand total of 1000 specimens rather closely approximates the parent curve (P by chi-square = 0.61), although there is an overabundance of specimens with 32 subcaudals, and a shortage of those with 28.





a mean of 200, a standard deviation of 4, and therefore, a coefficient of variation of 2 per cent. The fluctuations in the samples are definitely greater than in Tables 16 and 17, and it is still more difficult to picture the population dispersion from that of any single sample. Even when the sample totals 1000 specimens (an almost unprecedented collection in herpetological work, when it is recalled that such a sample would represent only one sex and from a single district) the distribution does not closely resemble that of the population, although the fit is not much worse than the average to be expected (chi-square  $P = 0.31$ ).

TABLE 19

Dispersion of 3 Small Samples.  
Ventrals: Mean = 200,  $\sigma = 4$

Number of Ventrals	Sample Number		
	1	2	3
191 .....	1	...	....
192 .....	...	1	....
193 .....	...	....	....
194 .....	...	....	....
195 .....	...	1	....
196 .....	...	1	1
197 .....	2	....	2
198 .....	...	3	2
199 .....	1	2	2
200 .....	...	....	1
201 .....	...	....	1
202 .....	...	....	....
203 .....	...	....	....
204 .....	1	....	....
205 .....	...	....	1
206 .....	...	....	1
207 .....	...	....	....
208 .....	...	....	....
209 .....	1	....	....
Total .....	6	8	11

NOTE:—For the population distribution see Table 18.

With smaller samples the results are still more haphazard. Table 19 illustrates three collections of sizes that often are representative of some of the rarer forms in museums. In this table the population from which the samples were drawn has been omitted; it is the same as that given in Table 18. The three samples happen to be so oddly dispersed that they hardly appear to have been drawn from the same population, and separately they give no indication whatever of the true distribution of the parent population.

TABLE 20  
Dispersion of 10 Samples, Each Comprising 100 Individuals.  
Total Dorsal Blotches: Mean = 100,  $\sigma = 6.67$ .

Number of Blotches	Distribution of Population	Sample Number										Total	
		1	2	3	4	5	6	7	8	9	10		
72 to 80*	170	1	....	....	....	....	....	....	1	....	....	....	2
81	103	....	....	....	....	....	....	....	....	....	....	....	....
82	156	1	1	....	1	....	....	....	....	....	....	....	3
83	232	....	....	....	....	....	1	1	....	....	....	....	2
84	336	1	....	1	1	....	....	....	1	....	1	....	5
85	476	1	....	....	....	....	....	1	2	1	2	....	7
86	660	....	....	....	....	....	2	1	1	1	2	....	7
87	894	1	....	3	1	....	1	2	1	3	1	....	13
88	1,184	1	1	....	....	2	2	....	1	....	....	....	7
89	1,534	1	....	1	2	3	1	2	....	2	....	....	12
90	1,943	....	3	1	....	4	1	3	4	3	4	....	23
91	2,406	3	3	7	3	1	3	....	1	1	2	....	24
92	2,913	4	5	5	....	2	2	3	....	2	1	....	24
93	3,448	4	2	3	4	4	1	....	2	4	....	....	24
94	3,991	4	4	7	4	7	1	9	5	1	3	....	45
95	4,517	7	3	5	1	3	8	4	5	3	3	....	42
96	4,999	7	4	8	4	5	8	3	6	6	7	....	58
97	5,408	4	3	4	4	5	3	8	7	4	5	....	47
98	5,721	4	7	3	8	6	2	7	7	6	8	....	58
99	5,917	5	8	9	8	6	4	4	7	3	8	....	62
100	5,984	3	8	6	4	5	2	2	8	6	7	....	51
101	5,917	5	13	5	10	1	8	6	4	7	1	....	60
102	5,721	7	2	3	3	3	7	8	8	7	8	....	56
103	5,408	10	2	11	8	6	6	6	7	6	7	....	69
104	4,999	6	7	2	5	5	4	10	8	3	7	....	57
105	4,517	2	4	2	8	5	8	3	4	4	9	....	49
106	3,991	2	3	3	3	2	4	4	4	7	5	....	37
107	3,448	6	4	3	5	5	9	2	1	4	2	....	41
108	2,913	3	6	3	2	7	3	3	1	2	4	....	34
109	2,406	1	2	....	4	4	2	2	....	2	1	....	18
110	1,943	2	1	3	3	4	....	1	3	2	2	....	21
111	1,534	1	....	....	1	1	4	1	....	3	....	....	11
112	1,184	1	1	....	....	1	1	....	....	3	....	....	7
113	894	1	....	....	....	1	....	1	....	1	....	....	4
114	660	....	....	1	2	....	1	1	....	....	....	....	5
115	476	....	....	....	1	1	....	....	1	....	....	....	3
116	336	....	1	....	....	....	1	....	1	2	....	....	5
117	232	....	1	....	....	....	....	....	....	....	....	....	1
118	156	1	....	....	....	1	....	....	....	....	....	....	2
119	103	....	1	....	....	....	....	....	....	....	....	....	1
120 to 128*	170	....	....	1	....	....	....	....	1	....	1	....	3
Total	100,000	100	100	100	100	100	100	100	100	100	100	100	1000

\* The extreme upper and lower classes are combined to save space. The two low counts (Samples 1 and 7) were both 79 blotches; the three high counts were 121 in Sample 3; 122 in Sample 7; and 125 in Sample 9. The populations in the group 72 to 80 inclusive are 1, 2, 3, 5, 9, 16, 26, 42, 66; total 170. The same figures reversed give the totals of groups 120 to 128.



TABLE 22

Means and Ranges Calculated from the Populations and Samples Comprising  
Tables 16, 17, 18, and 20.

Population Sample No. 1	Table 16			Table 17			Table 18			Table 20		
	Mean	Min.	Max.									
Parameter	16.00	12	20	30.00	21	39	200.00	183	217	100.00	72	128
1	16.05	14	18	30.03	24	36	200.15	190	208	99.39	79	118
2	15.83	13	18	30.22	25	35	200.44	191	209	100.30	82	119
3	16.12	14	18	30.02	25	37	200.22	190	208	98.64	84	121
4	16.15	14	18	29.65	24	34	199.32	190	211	100.84	82	115
5	15.74	13	19	30.09	25	34	200.09	191	208	100.58	88	118
6	15.98	14	18	30.10	23	35	200.19	189	212	100.63	83	116
7	16.08	13	18	30.35	25	35	199.51	188	208	99.48	79	122
8	15.96	14	19	30.13	25	35	199.23	192	209	99.24	84	116
9	15.96	13	19	30.05	26	34	199.90	190	209	100.89	85	125
10	16.13	14	18	30.20	25	35	198.71	189	209	99.63	84	110
Total (Sample of 1000)	16.00	13	19	30.08	23	37	199.78	188	212	99.96	79	125

Having taken the trouble to draw at random the 40 separate samples of 100 individuals each, which comprise Tables 16, 17, 18, and 20, we may as well use the data thus accumulated to demonstrate once more the high degree of consistency in sample means as indicators of the corresponding parameters of the parent population, and the wide fluctuations in the over-all range. The results for all four tables are set forth in Table 22.

By examples I have shown that the mean of a sample, except in the case of very small samples, is usually closely representative of the mean of the population. Also, it has been shown that the range of a sample is a rather undependable indicator of the scatter of the population, for too much depends not only on the size of the sample, but also on chance, to say nothing of the occasional presence of a true monster or freak. But it is often impossible or undesirable to present the complete distributions, as has been done in Tables 16, 17, 18, and 20. How, then, are dispersions to be more briefly indicated or summarized?

The most useful statistic for this purpose is undoubtedly the standard deviation, or some multiple thereof; and the taxonomist should become sufficiently familiar with it to be able to visualize the extent of dispersion from a knowledge of the standard deviation, provided the distribution is normal or substantially so. Some relationships of interest with respect to such a normal distribution, are the following:

The range of the mean  $\pm 0.6745 \sigma$  will include 50% of the population.  
 The range of the mean  $\pm \sigma$  will include 68.27% of the population.  
 The range of the mean  $\pm 2 \sigma$  will include 95.45% of the population.  
 The range of the mean  $\pm 3 \sigma$  will include 99.73% of the population.

Since the standard deviation of a population may be rather closely estimated from that of a sample, it is evident that the population dispersion may also be assessed. It is from the relationship between the standard deviations of samples and populations that the most accurate guesses can be made respecting the chances that two populations overlap, and the extent of the overlap if it be present.

In mathematical terms the standard deviation of a sample has the following relationship with the standard deviation of the population:  $s = \sigma[(N - 1)/N]^{1/2}$ , where  $s$  is the standard deviation of the sample,  $\sigma$  the optimum estimate of the standard deviation of the population, and  $N$  the number of specimens in the sample. Thus, standard deviations of samples tend to be somewhat smaller than those of their parent populations, but they closely approximate the population deviations when  $N$  is large. For example, the ratio is .89 when  $N$  is 5, .95 when  $N$  is 10, and .995 when  $N$  is 100. Furthermore, the standard error of the standard deviation is  $\sigma/(2N)^{1/2}$ , which in turn indicates that about 68 per cent of the standard deviations of samples should fall within the range  $\sigma[1 \pm 1/(2N)^{1/2}]$ . For example, if  $\sigma$  be 4 and the samples comprise 100 individuals each, about 68 per cent of the samples will have standard deviations between 3.72 and 4.28.

Reverting again to our illustrative populations and the samples drawn therefrom, as set forth in Tables 16, 17, 18, and 20, we have available the known standard deviations of the populations and may calculate by simple formulas the standard deviation of each sample. From these the optimum estimates of the standard deviation of each population can be calculated and thus compared to the known population parameters. The results of such comparisons are set forth in Table 23.

TABLE 23

Standard Deviations Calculated from the Populations and Samples  
Comprising Tables 16, 17, 18, and 20.

	Table 16	Table 17	Table 18	Table 20
Population Parameter	1.00	2.00	4.00	6.67
Sample No. 1	.90	2.23	3.65	6.88
2	1.06	1.88	3.83	6.37
3	.94	2.05	3.84	6.34
4	.90	2.05	4.13	6.26
5	1.07	2.14	3.80	6.85
6	.91	2.24	3.95	6.75
7	.94	1.91	3.68	6.94
8	.92	1.89	3.60	6.05
9	1.03	2.00	3.88	7.35
10	1.01	2.11	3.99	5.95
Total (Sample of 1000)	.97	2.05	3.86	6.60

NOTE: The standard deviations listed under the samples are the optimum estimates of the standard deviations of the populations derived from the samples

While I reiterate that these tests are only illustrative and are not for the purpose of proving well known mathematical formulas, it may not be amiss to compare the dispersions of the standard deviations in each group of ten samples in Table 23 with the calculated standard errors. The results are as follows:

Group	Population Standard Error of Standard Deviation	Population Standard Error of Standard Deviation Calculated from Samples
Table 16	0.071	0.073
Table 17	0.141	0.129
Table 18	0.283	0.164
Table 20	0.472	0.445

We see that these results check fairly well, having in mind the fact that the calculated dispersions are premised on so few as 10 samples. The standard error derived from Table 18 is quite low, and this random distribution is further unusual in that all but one of ten samples have dispersions below the expected value.

We return now to our fundamental problem, namely, the degree of consistency of statistics based on the standard deviation as indicators of the dispersion in parent populations. Obviously, if we have the choice of several statistics, each of which is a multiple of the standard deviation, the relative discrepancies from the corresponding population parameters will remain proportionally constant, regardless of which is chosen. I have therefore selected as the first illustrative examples the interquartile range ( $M \pm .6745 \sigma$ ), rather than the mean plus and minus twice or three times the standard deviation, although the latter are often useful as quick indicators of the probable overlap (or lack of overlap) between two forms. The term interquartile range, as I employ it, is premised on the assumption of a normal (and hence symmetrical) distribution in the population; thus, the mean and the median coincide, and the deviations are expressed as if they were deviations from the mean. The interquartile range normally contains one-half of the population.

In Table 24 I have set forth the estimated population interquartile ranges as calculated from the samples which comprise Tables 16, 17, 18, and 20, and the true population parameters. It will be seen that this descriptive term is, relatively speaking, both consistent and well representative of the true population parameter. In other words, from this statistic of a sample we may gain a good insight concerning an important character of an unknown population.

TABLE 24  
Interquartile Ranges Calculated from the  
Populations and Samples Comprising Tables 16, 17, 18, and 20.

	Table 16	Table 17	Table 18	Table 20
Population Parameter.....	15.33-16.67	28.65-31.35	197.30-202.70	95.50-104.50
Sample No. 1.....	15.44-16.66	28.52-31.54	197.69-202.61	94.75-104.03
2.....	15.11-16.55	28.95-31.49	197.86-203.02	96.00-104.60
3.....	15.49-16.75	28.64-31.40	197.63-202.81	94.36-102.92
4.....	15.56-16.74	28.37-31.03	196.53-202.11	96.61-105.07
5.....	15.02-16.46	28.65-31.53	197.52-202.66	95.96-105.20
6.....	15.37-16.59	28.59-31.61	197.53-202.85	96.05-105.21
7.....	15.45-16.71	29.06-31.64	197.03-201.99	94.80-104.16
8.....	15.34-16.56	28.85-31.41	196.80-201.66	95.16-103.32
9.....	15.26-16.66	28.70-31.40	197.28-202.52	95.93-105.85
10.....	15.45-16.81	28.84-31.56	196.02-201.40	95.61-103.65
Total (Sample of 1000)	15.35-16.65	28.70-31.47	197.18-202.38	95.51-104.41

As a final indication of the consistency of a statistic related to the standard deviation, I shall compare the range represented by the mean, plus and minus 3 times the standard deviation, with the maximum or over-all range.

The former, in a normal distribution, includes 99.73 per cent of the population, the latter, 100 per cent in any distribution. For this test I take only the population and samples of Table 20, this being the most variable population I have used. The results are presented in Table 25.

TABLE 25

Comparison of Maximum Range with  $M \pm 3\sigma$  in the  
Population and Samples of Table 20.  
Total Dorsal Blotches. Mean = 100,  $\sigma = 6.67$ .

	Overall Range		Range from $M \pm 3\sigma$
	Min.	Max.	
Population Parameter.....	72	128	80.0-120.0
Sample No. 1.....	79	118	78.7-120.0
2.....	82	119	81.2-119.4
3.....	84	121	79.6-117.7
4.....	82	115	82.0-119.6
5.....	88	118	80.0-121.1
6.....	83	116	80.4-120.9
7.....	79	122	78.7-120.3
8.....	84	116	81.1-117.4
9.....	85	125	78.9-122.9
10.....	84	110	81.8-117.5
Total (Sample of 1000)	79	125	80.2-119.8

We see that the population minimum is 72, while the sample minimums vary from 79 to 88; the population maximum is 128 and the sample maximums vary from 110 to 125. On the other hand the sample statistics represented by  $M \pm 3\sigma$  are much more consistent indicators of the corresponding population parameter; for the population low figure is 80.0 while the samples vary between 78.7 and 82.0, and the population high figure is 120, with the samples varying between 117.4 and 122.9. Thus, there is every reason to recommend the  $M \pm 3\sigma$  statistic as a population indicator as compared to the over-all range. Admittedly the samples I have used in this test (100 individuals) are relatively large, but similar advantages in the use of this statistic will be found in the case of smaller samples. For example, in Table 26 I have built a sample up to 25 specimens, by adding one randomly selected individual at a time, all the while recording the trend in the over-all range and in the statistic  $M \pm 3\sigma$ .

The population used is that shown in Table 13, that is, a homogeneous series of snakes having an average number of 40 body blotches, with a standard deviation of 4. All data are calculated from the sample as it grows, the population being assumed unavailable, as would be the case in actual practice. Thus, both  $M$  and  $\sigma$  change as each specimen is added; and in each calculation the factor  $[N/(N-1)]^{1/2}$  is used in securing the optimum population value of  $\sigma$ .

TABLE 26

Changes in the Range and in  $M \pm 3\sigma$   
as a Sample Increases from 1 Specimen to 25.  
Body Blotches. Mean = 40,  $\sigma = 4$ .

	Specimen Count	Overall Range		Range $M \pm 3\sigma$
Population Parameter		Min.	Max.	
Population Parameter	40	23	57	28.0-52.0
Specimen No. 1.....	44	44	44	44.0-44.0
2.....	43	43	44	42.0-44.0
3.....	41	41	44	38.1-47.3
4.....	37	37	44	32.0-50.5
5.....	34	34	44	27.2-52.4
6.....	44	34	44	28.1-52.9
7.....	41	34	44	29.2-51.9
8.....	44	34	44	30.0-52.0
9.....	35	34	44	28.2-52.3
10.....	33	33	44	26.3-52.9
11.....	39	33	44	27.0-52.2
12.....	37	33	44	27.1-51.5
13.....	42	33	44	27.6-51.5
14.....	38	33	44	27.8-51.0
15.....	33	33	44	26.9-51.2
16.....	31	31	44	25.3-51.7
17.....	38	31	44	25.7-51.3
18.....	36	31	44	25.8-50.8
19.....	42	31	44	26.1-51.0
20.....	42	31	44	26.4-51.0
21.....	42	31	44	26.7-51.1
22.....	40	31	44	27.0-50.9
23.....	45	31	45	26.9-51.4
24.....	40	31	45	27.2-51.2
25.....	32	31	45	26.4-51.4

NOTE: In determining the range  $M \pm 3\sigma$ , the estimated standard deviation of the population was calculated from the sample.

We see that the extreme or over-all range never approaches closely to that of the population. Even after 25 specimens are accumulated the range is only from 5 above the mean to 9 below, a notable unbalance in itself. But the statistic  $M \pm 3\sigma$  reaches a figure quite close to the population parameter after the accumulation of only 5 specimens, and remains consistently close to that parameter as long as specimens are added. So once more the consistency of a statistic which is a multiple of the standard deviation is demonstrated. However, it should be noted that these strictures upon the relative values of statistics of the over-all range as compared to some multiple of the standard deviation, are only pertinent when applied to variates having a substantially normal distribution, or at least one which is fairly symmetrical. The over-all range may be a better criterion in strongly skewed distributions.

These statistics of populations and samples are primarily necessary in taxonomic work to demonstrate the validity of differences—namely the chances that two supposed species overlap in a particular character and the extent of such overlap. I shall illustrate a typical case of overlap and how it becomes increasingly evident as more specimens are added to the available collections, that is, as the samples increase in size.

Table 27 represents the results of sampling two populations coincidentally, the same number of specimens being added to each. The populations sampled have similar characteristics, except with respect to their averages. They represent ventral scale counts in two species of snakes, both having standard deviations of 4; but the mean of one population is 200 scutes and of the other 184. Thus, the difference between the means is 4 times the standard deviation of either. The vertical columns in the table are cumulative samples; that is, the first column shows the first sample drawn, the second, the first plus the second, etc. To conserve space individual drawings are shown up to Sample 5, then by twos, threes, fives, etc. The interesting feature of this test is that one does not get the feeling that there is a probable overlap between the two forms until the seventh specimen of each has become available; and an actual overlap did not occur until the drawing of the eighteenth specimen. This is somewhat typical of our knowledge of rarer forms, which are often first thought to be quite well separated, and are so noted in keys, but which later are shown to overlap, when additional specimens have become available. The probability that such an overlap would eventually be evident might have been predicted by calculation as early as Specimen 5. Of course these remarks on the gradual evidence of an overlap have little to do with the validity of the two species, since even with the overlap, the difference between the means is sufficient to warrant recognition. According to Ginsburg's criterion<sup>5</sup> the small overlap (2.28%) would indicate full species. However, the discussion of the extent of divergence, its measure and significance, and

<sup>5</sup> Zoologica, Vol. 23, pp. 253-286, 1938.

TABLE 27. Simultaneous Sampling of Two Populations. Ventral Scutes:  $M_1 = 184$ ,  $M_2 = 200$ ;  $\sigma = 4$ .

	Populations		Sample Step													
	1	2	1	2	3	4	5	6	7	8	9	10	11	12	13	14
167-174	862															
175	793															1
176	1350											1	1	1	1	1
177	2157		1	2	2	2	2	2	3	3	3	4	4	4	5	5
178	3238											1	1	2	2	2
179	4766									1	1	2	2	3	4	4
180	6049								1	1	1	1	3	3	6	6
181	7529								1	1	1	1	1	2	6	7
182	8802								1	1	1	1	2	5	7	9
183	9667	1						1	4	4	5	7	7	9	11	16
184	9974	3						1	2	2	3	3	4	4	7	8
185	9667	9				1	1	2	2	2	2	2	2	4	4	5
186	8802	22	1	1	1	1	1	2	2	2	2	2	2	4	8	11
187	7529	51						1	1	1	2	2	2	2	5	7
188	6049	111										1	1	2	2	4
189	4766	227										1	1	2	4	5
190	3238	438						1	1	1	1	1	2	2	3	5
191	2157	793														1
192	1350	1350						1	1	1	1	1	1	1	1	2
193	793	2157							1	1	1	1	1	1	2	3
194	438	3238														2
195	227	4766														3
196	111	6049						1	1	1	2	2	3	4	5	7
197	51	7529									1	1	1	3	5	7
198	22	8802							1	2	3	5	5	9	11	12
199	9	9667								2	2	3	4	7	10	12
200	3	9974								1	1	1	1	2	3	4
201	1	9667											1	2	5	6
202		8802								2	2	3	3	5	6	11
203		7529								2	2	2	3	4	5	8
204		6049								3	4	4	6	8	11	15
205		4766											2	2	3	3
206		3238													1	1
207		2157									1	1	2	3	5	5
208-217		3005														
Total of Each Sample			1	2	3	4	5	7	10	15	20	25	35	50	75	100

its interpretation in taxonomy and nomenclature is quite beyond the scope of this paper.

#### SAMPLING OF ALTERNATIVE ATTRIBUTES

The examples thus far given all concern normally distributed discrete variates, principally those of scutellation. We frequently have in herpetology situations in which a character is present or absent, or in which either of two values or positions may be taken. For example, individuals of a species (e.g. *Trimorphodon vandenburghi*) may have a divided or undivided anal plate; in other species the rostral may or may not separate the internasals; there may be 23 or 25 scale rows; or there may be one or two preoculars (neglecting lateral asymmetry). The significance of differences in situations of this kind is usually determined by the use of 2x2 contingency tables. I think it will be of interest to show the extent of variations occurring in some random samples selected from very large populations having known proportionalities of distribution of such alternatives. For this purpose I have drawn 10 random samples, each comprising 10 individuals, from a population of which 90 per cent have 25 scale rows and 10 per cent 23. The experiment was then repeated with 10 samples each containing 100 individuals. Finally, similar samples were drawn from a second population of which half the individuals had 25 scale rows and the other half 23. Of course, the reference to scale rows is only made to give a suggestion of reality; the attributes might as well have been referred to as positive and negative, or white and black. The results are given in Table 28. The considerable variations from the population percentages are readily apparent. The first series of samples of 10 has resulted in a quite unusual distribution, in having no less than seven samples without any 23 scale-row individuals.

TABLE 28  
Sampling Alternative Attributes.

Sample Number	Population Composition 90% with 25 rows, 10% with 23.				Population Composition 50% with 25 rows, 50% with 23.			
	Samples of 10		Samples of 100		Samples of 10		Samples of 100	
	25	23	25	23	25	23	25	23
1	10	0	91	9	4	6	49	51
2	10	0	91	9	6	4	49	51
3	10	0	89	11	5	5	45	55
4	9	1	94	6	4	6	49	51
5	10	0	90	10	5	5	53	47
6	10	0	92	8	7	3	50	50
7	10	0	92	8	8	2	49	51
8	7	3	91	9	4	6	46	54
9	9	1	87	13	7	3	54	46
10	10	0	94	6	5	5	43	57
Total	95	5	911	89	55	45	487	513

## SUMMARY

The purpose of this paper is to emphasize, by illustrative examples of random sampling, the validity of various sample statistics in estimating population parameters. The consistency of estimates of the mean is shown; and also that of multiples of the standard deviation. The statistic  $M \pm 3\sigma$  is shown to be superior to the over-all range in judging from samples, the probable composition of a population with respect to extreme individuals. The desirability of homogeneity in samples is indicated by sampling heterogeneous populations.



### III. THE CORRELATION BETWEEN SCALATION AND LIFE ZONES IN SAN DIEGO COUNTY SNAKES

This is an inquiry to determine whether there are any consistent differential trends in the characters of snakes living under desert conditions and the same species found in more humid situations. The inquiry deals with scalation, especially ventral scale counts.

This is not a taxonomic study. I shall not here attempt to determine whether such differences as may be found are worthy of subspecific recognition; for sometimes these problems of nomenclature, through the necessity of adhering to rather artificial groupings, tend to relegate into the background certain interesting variations and trends.

The differences to be found within a species, in adjacent regions of divergent ecological character, are usually small in extent. Therefore, statistical methods are required to determine whether the differences are probably real or merely the result of sampling fluctuations.

In this study comparisons are made between snakes collected on the coastal and desert sides of the mountains in San Diego County, California. The territory involved has been discussed in two previous papers<sup>1</sup> and the ecological data will not be repeated. Suffice it to say that as we go eastward from the coast to the desert the following zones are crossed successively: (1) coast, (2) inland valleys and mesas, (3) western slope foothills, (4) mountains, (5) desert foothills, and (6) desert. The rainfall is about 10 inches per annum at the coast; it increases with altitude to about 50 inches in the higher mountains (above 5000 ft.), and then falls rapidly to about 2 inches in the desert. The vegetation changes appropriately. However, it is to be noted that the territory is highly irregular and the mountains do not comprise a uniform barrier between the coast and desert. Passes below 4000 ft. are available; and in the Campo-Jacumba area there is a broad plateau in which the coastal foothills gradually merge into the desert foothills without the interposition of a truly mountain zone. Under such conditions one would not expect to find an extreme or clear-cut difference between the snakes of the first four zones, which I shall group under the term cismontane, and those of the last two desert zones, referred to as transmontane. We are dealing essentially with average differences; much overlapping is to be expected.

Twenty-six species of snakes are found in San Diego County (Klauber, 1939, Table 16); however, of these, only 13 have a sufficiently wide range, in both the cis- and transmontane regions, to be the subject of this investigation. The others are either almost, or entirely, restricted to one region or the other. For example, although *Crotalus viridis oreganus* is found down the eastern slope as far as San Felipe, La Puerta, and Jacumba,

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<sup>1</sup> A Statistical Survey of the Snakes of the Southern Border of California. Bull. Zoöl. Soc. of San Diego No. 8, pp. 1-94, 1931; Studies of Reptile Life in the Arid Southwest. Bull. Zoöl. Soc. of San Diego, No. 14, pp. 1-100, 1939.

it does not reach the most extreme desert conditions, and therefore the few specimens available from the transmontane region do not exhibit the full effect of desert conditions. These zonal limitations are illustrated in Fig. 2 of the 1931 report.

The following species are sufficiently widespread on both sides of the mountains to warrant investigation:

1. *Leptotyphlops humilis* (coastal subspecies *humilis*; desert subspecies *cabuila*.)
2. *Lichanura roseofusca* (coastal subspecies *roseofusca*; desert subspecies *gracia*.)<sup>2</sup>
3. *Coluber flagellum frenatus*.
4. *Salvadora grahamiae* (coastal subspecies *virgultea*; desert subspecies *hexalepis*.)
5. *Arizona elegans occidentalis*.
6. *Pituophis catenifer* (coastal subspecies *annectens*; desert subspecies *deserticola*).
7. *Lampropeltis getulus californiae*.
8. *Rhinocheilus lecontei*.
9. *Hypsiglena ochrorhynchus*.
10. *Tantilla eiseni*.
11. *Trimorphodon vandenburghi*.
12. *Crotalus ruber*.
13. *Crotalus mitchellii pyrrhus*.

Thus, within the territory under consideration there are 13 species to consider, of which 4 have already been divided into desert and coastal subspecies. Two others probably warrant such a segregation. Four families (Leptotyphlopidae, Boidae, Colubridae and Crotalidae) are represented.

These thirteen species may be subdivided into three groups: (1) those which range across the lowlands of the Cahuilla Basin (or Salton Sink), where the most extreme desert conditions are found; (2) those which, while they are not found in this basin, occur in suitable rocky or mountainous areas on the far, or eastern, side of the basin; and (3) those whose ranges terminate at the base of eastern slope of the coastal range—that is, the ranges end at the lower edges of the rocky slopes or but a slight distance beyond. The segregations are as follows:

- (1) Snakes which occur in the level plains of the Cahuilla Basin:

*C. f. frenatus*  
*S. g. hexalepis*  
*A. e. occidentalis*  
*P. c. deserticola*  
*R. lecontei*

<sup>2</sup> Pure examples of this subspecies are not found in San Diego County,

(2) Snakes absent in the Cahuilla Basin but recurring beyond:

- L. b. cabuillae*
- L. r. gracia*
- L. g. californiae*
- H. ochrorhynchus*
- C. m. pyrrhus*

(3) Snakes whose ranges terminate at the eastern base of the coastal mountains:

- T. eiseni*
- T. vandenburghi*
- C. ruber*

All but one of the species listed are definitely, and in most cases strikingly, lighter in color in the desert than in the coastal region. The exception is *Lampropeltis getulus californiae*.

In the case of the five species inhabiting the plains of the Cahuilla Basin I have utilized Imperial County, as well as San Diego County, material in securing the averages. Riverside County and Lower California material has been excluded to avoid the risk of complicating the results with possible north-south variations, which might distort the east-west conclusions, except that, in the case of three species, I have included several Riverside County desert specimens because of lack of adequate material from transmontane San Diego County. All of the species in the second group with the exception of *L. g. californiae* are rock-dwellers, which explains why they do not occur in the flat, sandy Cahuilla Basin, but do have a resumption of range beyond.

A few remarks on particular species are necessary. The desert subspecies *Lichanura roseofusca gracia* has not been collected in San Diego County, although it may occur in the Santa Rosa mountains. The specimens from the eastern slope of the coastal mountains, which have been used in these statistics as representing the transmontane population, are either *L. r. roseofusca* or *roseofusca-gracia* intergrades.

In the case of *Lampropeltis* I have utilized only the statistics of the ringed pattern-phase, thus avoiding possible confusion resulting from the peculiar pattern dimorphism to which this snake is subject.<sup>3</sup> The striped phase does not occur as far down the eastern slope as does the ringed phase; nor is it found in as large a proportion of the total population on the eastern as on the western slope.

Among the snakes herein discussed there is rather definite evidence of intergradation, either across the mountains or through the mountain passes, upon the part of every species except one. Thus we are dealing with an intraspecific trend, rather than a difference between pairs of

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<sup>3</sup> A Further Study of Pattern Dimorphism in the California King Snake. Bull. Zoöl. Soc. of San Diego, No. 15, pp. 1-23, 1939.

TABLE 1  
VENTRAL SCUTES: COMPARISON BETWEEN DESERT AND COASTAL SPECIMENS

	Number of Specimens		Mean		Difference between means	Coefficient of divergence, per cent	t.	Significance of difference P.
	Trans-montane	Cis-montane	Trans-montane	Cis-montane				
<i>Leptotyphlops bunnilis cabuilaie</i> and <i>L. b. bunnilis</i> , both sexes*	40	56	293.50	271.98	21.52	7.61	17.37	.001-
<i>Lichanura roseofusca roseofusca</i> , males	12	41	235.83	231.63	4.20	1.80	2.39	.019
females	13	31	233.23	233.06	0.17	0.07	0.11	.912
<i>Coluber flagellum frenatus</i> , males	27	21	196.81	193.71	3.10	1.59	2.79	.006
females	20	19	194.90	195.74	-0.84	0.43	0.70	.496
<i>Salvadora grabanaie bexalepis</i> and <i>S. g. virgultea</i> , males	8	30	201.38	193.30	8.08	4.09	6.09	.001-
females	7	25	204.57	193.88	10.69	5.36	5.72	.001-
<i>Arizona elegans occidentalis</i> , males	36	10	220.97	215.00	5.97	2.74	4.07	.001-
females	19	15	233.84	223.87	9.97	4.36	6.17	.001-
<i>Pituophis catenifer deserticola</i> and <i>P. c. annectens</i> , males	32	57	238.97	227.81	11.16	4.78	12.14	.001-
females	27	60	244.74	232.20	12.54	5.26	11.18	.001-
<i>Lampropeltis getulus californiae</i> , males	13	82	237.08	232.90	4.18	1.78	2.75	.007
females	7	80	239.14	235.24	3.90	1.64	1.99	.049
<i>Rhinocbeilus lecontei</i> , males	17	35	210.76	207.29	3.47	1.66	3.89	.001-
females	13	30	207.62	203.73	3.89	1.89	3.42	.001-
<i>Hypsiglena ocrorbyncbus</i> , males	22	43	186.00	174.09	11.91	6.61	12.70	.001-
females	4	32	192.75	179.47	13.28	7.04	5.69	.001-
<i>Tantilla eiseni</i> , males	3	18	180.67	169.06	11.61	6.64	5.89	.001-
females	3	13	194.00	176.31	17.69	9.54	5.96	.001-
<i>Trimorphodon vandenburghi</i> , males	12	14	233.42	228.36	5.06	2.19	3.14	.004
females	6	12	244.00	235.67	8.33	3.48	3.16	.006
<i>Crotalus ruber</i> , males	27	97	197.48	193.29	4.19	2.15	6.72	.001-
females	20	72	199.80	196.46	3.34	1.69	4.16	.001-
<i>Crotalus mitchelli pyrrbus</i> , males	13	41	179.00	178.68	.32	0.18	0.30	.769
females	7	28	178.00	179.71	-1.71	0.96	1.72	.095

\*Dorsals.

species. The only exception is *Pituophis catenifer*. The evidence continues to multiply that the two supposed subspecies, *P. c. annectens* and *P. c. deserticola*, meet or overlap, but do not intergrade in eastern San Diego County.

The results of the investigation of the number of ventral scutes are given in Table 1. Since sexual dimorphism is present in nearly all these forms, the sexes are treated separately, except in the case of *Leptotyphlops humilis*. Also in this species the dorsals, rather than the ventrals are used, since they can be more accurately counted, and therefore are more often employed in taxonomic work.

From this tabulation of the thirteen forms we find that there is an almost universal tendency toward a higher number of ventrals in the desert specimens, as compared to those which were collected in the more humid<sup>4</sup> cismontane region. No less than ten out of the thirteen forms show this trend in both sexes; and in every instance the significance is beyond the usually accepted level of  $P = 0.05$ , meaning less than one chance in 20 that the result has occurred through an accident of random sampling. In the majority of cases the probability is below one in a thousand, leaving no doubt as to the reality of the trend.<sup>5</sup>

The exceptions are three in number: *Lichanura roseofusca*, *Coluber flagellum frenatus*, and *Crotalus mitchellii pyrrhus*. In the first two we find that the males follow the usual trend, that is, the desert males have more ventrals than the coastal. The females show no significant territorial variation in *Lichanura*; while in *C. f. frenatus* the desert females average lower than those from the coastal side of the mountains, although the difference is below the usually accepted level of significance.

The last species which fails to follow the trend of the majority is the rattlesnake *C. m. pyrrhus*. Here the desert males average slightly higher than the coastal, and the desert females somewhat lower, but the differences are below the significance level. It may be seriously doubted whether larger samples would reverse the condition noted in this species. Of the 13 forms listed in this study *C. m. pyrrhus* is the only one, besides *Trimorphodon*

<sup>4</sup> The difference in humidity is the outstanding difference between the two regions; however I do not claim to have shown that this is the cause of the observed difference in ventral scale counts, which might result from any of a number of secondary environmental characteristics, of which temperature is outstanding.

<sup>5</sup> As several of the samples are rather small, especially in the case of some species which are not plentiful in the desert region, I have in all cases used the *t*-test and the method of pooling, in determining the significance of the difference. The equation is

$$t = (M - M') \left[ \frac{NN'(N + N' - 2)}{(N + N')(Nv + N'v')} \right]^{-1/2}$$

where *M* and *M'* are the means of the two samples, *N* and *N'* the numbers of specimens in each of the samples, and *v* and *v'* are the variances (standard deviations squared) of the samples. The *t*-table is entered at *N* + *N'* - 2 degrees of freedom. (R. A. Fisher, *Statistical Methods for Research Workers*, Seventh Edition, 1938, p. 128; J. F. Kenney, *Mathematics of Statistics*, part 2, 1939, p. 140; P. R. Rider, *An Introduction to Modern Statistical Methods*, 1939, p. 91.)

*vandenburghi*, which inhabits only a limited zone in the cismontane area; for although both may rarely be found in the coastal and inland valleys zones, their infrequency shows that they are more or less strays. Their headquarters are in the foothill zones on both sides of the mountains. Thus it may be said, in possible explanation of the deviation of *C. m. pyrrhus* from the trend followed by the majority of forms, that it has never been fully subjected to the coastal influence.

It will be observed that the three smallest snakes, *Leptotyphlops humilis*, *Hypsiglena ochrorhynchus*, and *Tantilla eiseni*, have the highest coefficients of divergence.<sup>6</sup> This is probably evidence of the trend, frequently observable, that slowly moving forms exhibit greater differences per unit of distance than more widely wandering species.

Of the three colubrids which fail to attain a significance of  $P = .001$  —, or greater than one in a thousand, two have not been fully influenced by zonal extremes; *L. g. californiae* is quite rare in the desert, and *T. vandenburghi* is virtually absent along the coast. Even so, both would probably attain a significance of  $.001$  with larger samples, since, if the coefficient of divergence remains unchanged, the significance increases with the size of the sample.

Although a general tendency can be shown to exist in some genera (the rattlesnakes are an example) for larger species and subspecies to have higher scale counts, this is not a causative factor in increasing the number of ventrals in these desert specimens. In several cases desert specimens run somewhat smaller in size than in the cismontane region, as is the case, for example, in *Crotalus ruber* and *Coluber flagellum frenatus*. The reverse is true of *Leptotyphlops*; in other forms the inhabitants of the two areas do not differ conspicuously in size.

The trend shown definitely to exist in the ventrals in at least ten of thirteen species is not repeated in any other characteristic, the following having been tested by the same method: scale rows, caudals, supralabials, infralabials, body blotches, and tail rings. Some have no variations at all, such being true of several species in the case of scale rows and labials; for many colubrids have little or no intraspecific variation in these characters. Many show differences below the level of significance, which I have taken at  $P = .05$ . But even where there is significance in one species, there is no consistent trend throughout the thirteen forms or even a majority of them.

Thus in the case of the dorsal scale rows we find that *C. ruber* has a significantly higher average on the coast, while *C. m. pyrrhus* has a correspondingly higher average in the desert. The others either have no differences, or such differences as there are fall below the level of significance.

With respect to the caudals the following show significant differences: *Salvadora*, *Lampropeltis*, *Rhinocheilus*, and *Hypsiglena* average higher in

<sup>6</sup> Defined as the difference between the means divided by half the sum of the means.

the desert than in the cismontane region, thus following the trend in the ventrals; *Pituophis*, on the other hand, has the opposite trend, for the coastal subspecies has a higher average. The study of the caudals is somewhat handicapped by lack of specimens; for many specimens have incomplete tails, thus always reducing the number below those available for the study of ventrals. Larger series may show more definite trends; but they are not likely to be as consistent as is found to be the case in the ventrals.

The labials are constant in a number of species, as is often the case in the colubrids. Only *Trimorphodon* shows a significant difference, the coastal specimens having the greater number of supralabials. As to the infralabials *A. e. occidentalis*, *T. vandenburghi*, and *C. ruber* average significantly higher in the coastal region, while the contrary is true of *Pituophis*.

As regards pattern, those species which have rings or blotches—as differentiated from the striped forms—do exhibit differences, although not always above the level of significance. Thus *Rhinocheilus* and *Pituophis* have markedly fewer blotches in the desert than along the coast. However, the opposite is true in *Arizona* and *Trimorphodon*, although in both these cases the differences are somewhat below the significance level. Desert *Hypsiglena* also has a higher number of blotches than the cismontane form. Thus we see that the lightening of color in the desert individuals, which is universal in all 13 forms except *Lampropeltis*, is not secured by reducing the number of blotches, although this is the case with *Pituophis*, in which both fewer blotches and reduced pigment contribute to the lighter tone. Rather, it is effected by a reduction of pigment in blotches, ground color, or both.

It is worthy of note that the trend in ventrals, which has been shown to exist, is evident in that character which is relatively the most consistent of the really variable scale counts, that is, the ventrals have the lowest coefficients of variation.

I wish to acknowledge my indebtedness to Charles Shaw for making scale counts, Mrs. Elizabeth Leslie for statistical computations, and C. B. Perkins for his usual pertinent suggestions. Scale counts of particular specimens were received from Dr. R. B. Cowles, Charles M. Bogert, David Regnery, and J. R. Slevin.



## IV. THE RATTLESNAKES LISTED BY LINNAEUS IN 1758.

## INTRODUCTION

Linnaeus' descriptions of reptiles were so brief and so frequently based on composite material that, unless the type specimens are still extant, linking them with known species is often difficult and sometimes impossible. Yet, as the tenth edition of the *Systema Naturae*, 1758, is the foundation of all nomenclature, it is important that attempts be made to solve these problems of identification.

Linnaeus listed three species of rattlesnakes in the tenth edition: *horridus*, *dryinas*, and *durissus*. In the twelfth edition he added two more; these are not difficult to assign, being the species now known as *Sistrurus miliarius* and *Lachesis muta*, the latter not a rattlesnake. But the first three have been the source of much confusion among taxonomists, and even now there is not complete agreement respecting the proper applications of these names. It has occurred to me that the large collections of specimens at present available might justify a re-examination of the problems involved, since we can now more accurately define the scale-count ranges of the several species which may have been the real subjects of Linnaeus' descriptions. We likewise have new statistical methods of determining degrees of difference.

The confusion primarily relates to the correct names to be assigned to five species and subspecies of rattlesnakes; these are the timber (or banded) rattlesnake of the eastern United States, the canebrake rattler (a southeastern subspecies of the timber rattler), the Florida diamondback, the Central American rattlesnake, and the South American rattlesnake, the last two being subspecies of the Neotropical rattlesnake. I am constrained, for the moment, to refer to these by their common names, since to use the technical names would involve the confusion I am trying to explain. Besides the three initiated by Linnaeus, another technical name, that of *terrificus* Laurenti, 1768, must also be considered.

## PAST USAGES

Some past allocations have been as follows:

(a) The timber rattlesnake (to which the name *b. horridus* is now usually assigned) was identified as *durissus* by Holbrook, 1842, and by Duméril, Bibron, and Duméril, 1854.

(b) The Florida diamondback (now generally known as *adamanteus*) was called *durissus* by Boulenger, 1896, and in the Mission Scientifique, 1909; and *terrificus* by Le Conte, 1853.

(c) The Central American rattlesnake (now usually called *durissus*) was assigned to *horridus* by D., B., and D., 1854, and Günther, 1902; and to *terrificus* by Boulenger, 1896.

(d) The South American rattlesnake (to which the name *terrificus* is usually applied) was referred to as *durissus* by Jan, 1859.

*Dryinas* has been adjudged so vague that the name was dropped at an early date and has not been used for many years.

I have mentioned the decisions of only a few herpetologists; the list and confusion could be greatly extended.

#### LINNAEUS' METHOD AND TYPE SPECIMENS

Linnaeus, in describing the snakes in the *Systema Naturae*, generally used a schedule comprising five parts, especially if the type specimen was contained in one of the collections to which he had access, as was the case with the rattlesnakes. These parts are:

(1) The sex and number of ventrals and subcaudals of the type specimen.

(2) A primary reference, in which a more complete description of the type, either by himself or some other author, may be found.

(3) Secondary references which Linnaeus assigned to the same species. However, these often lead to confusion, since they may refer to species other than that of the type, or they may refer to composite or indefinitely described material. When there is a conflict, these secondary references must obviously yield to 1 and 2. It is important that the primary reference be not confused with the secondary; it can usually be identified through the scale counts, as well as by its initial position. Sometimes all references have an equal value, but such is not the case with the three rattlesnakes. The primary reference may contain still others, which may be considered tertiary.

(4) A habitat. Since this is expressed more as an over-all range than a type locality, as we know the latter today, the statement is usually too broad to be of any service in assigning names. For example, the habitats of all three rattlesnakes are given in the tenth edition simply as "America," and therefore do not facilitate the problems of identification.

(5) A description, usually including color notes. These are all too brief; they sometimes involve descriptions of specimens other than the type, and it is often clear that the specimens described were much faded. Sometimes the descriptive notes on the type specimen are supplanted by natural history notes culled from other references.

None of the three types of Linnaeus' rattlesnakes is now available for study. The type of *horridus* was contained in the King Adolf Fredrik Museum, most of the material from which was eventually transferred to the Royal Museum in Stockholm. Andersson, 1899, p. 5, states that *horridus* is one of the types now missing. He mentions (p. 27) two jars labeled *Crotalus horridus*, one containing a head, which is not that of a rattler; and the other the tail of a rattlesnake, which presumably is not that of the type of *horridus*, since it has more rattles than the type had,

and more subcaudals as well. I communicated with the Royal Natural History Museum in 1935, hoping the rattle might be a complete string which could be analyzed, but Count Nils Gyldenstolpe replied that the string was incomplete, and that there were no new developments with regard to the lost type of *horridus*, only the jars and their contents mentioned by Andersson remaining.

Lönnberg, 1896, states that the types of both *dryinas* and *durissus* are also lost (pp. 18 and 27). These specimens were originally contained in two collections which were available to Linnaeus for study, the first the Adolf Fredrik Collection (not the same assemblage as the Adolf Fredrik Museum) and the second the Claudius Grill Collection, also referred to as the Surinam Collection. Both collections were eventually transferred to the Zoological Museum of the Royal University at Upsala, but the two rattlesnakes have disappeared. Thus our investigation must be restricted to the original descriptions supplied by Linnaeus. In fact, it must be clear that the uncertainties respecting the proper applications of the Linnean names are present only because the types are gone. Were they available, they would take precedence over the inadequate and conflicting descriptions upon which we must now depend.

#### STUDIES OF SCALE COUNTS

The rattlesnakes scale counts given by Linnaeus are as follows:

- |      |                   |           |
|------|-------------------|-----------|
| 192. | <i>horridus</i> . | 167-23:2. |
| 195. | <i>Dryinas</i> .  | 165-30.   |
| 196. | <i>Durissus</i> . | 172-21:3. |

In each case the figure preceding the name is the sum of the ventrals and subcaudals.<sup>1</sup> If there are two figures, separated by a colon, representing the subcaudals, it is to be understood that the first indicates the number of entire scales, and the second those which are divided. Only two other scale counts are made available by Linnaeus; in the primary reference the supralabials of *dryinas* are given as 14-14, and the infralabials 14-14 also. All three types are stated to be males.

Before matching these scale counts against the known dispersions of present day species and subspecies by the methods of mathematical statistics, we can narrow the field by some general considerations of the characters and ranges of the forms which are now recognized as valid. Hereafter I shall use the scientific names in their customary modern assignments (Klauber, 1936).

Of the more than forty species and subspecies of rattlesnakes now recognized, many can be eliminated from consideration on one of two counts: Either their ranges are so restricted or were so inaccessible to the

<sup>1</sup> It is interesting to note that Linnaeus listed the snakes in each genus in the order of their total ventral plus subcaudal scales, beginning with the lowest number, in effect a sort of numerical index.

early eighteenth century traveler as virtually to exclude the possibility of their being in the three collections which contained these types; or their ventral and subcaudal scale counts are so widely different from those of the three types as to preclude their being the species described. The first criterion practically eliminates all species except those found along the eastern coasts of North and South America, or territories not far inland; the second excludes many other forms.

I think we may exclude *C. viridis* and all of its subspecies on the score of geographic inaccessibility. In fact, it seems to me highly significant that no amphibian or reptile specimen from what is now the United States was contained in any of the three collections which included the three rattlesnake types. In the tenth edition of the *Systema Naturae*, Linnaeus described six land reptiles (other than *C. horridus*) whose ranges center in the United States. Using their present-day names these are: *Eumeces fasciatus*, *Coluber constrictor*, *Natrix sipedon*, *Thamnophis sirtalis*, *Celydra serpentina*, and *Terrapene carolina*. I omit *Bufo marinus* as being primarily Neotropical. The type descriptions of all of these were based on Kalm, Catesby, or Edwards, with the exception of *C. serpentina* (about the original of which type Linnaeus was not definite) none being described from specimens in the three Swedish collections containing the rattlers. This would leave one to infer that the chance that, of all the reptiles in these collections, only one or more of the rattlers came from the United States, is somewhat remote; at least it would take rather strong evidence to balance the probability that they did not. In the twelfth edition of the *Systema Naturae*, Linnaeus described fourteen additional land reptiles from the United States, but all except one were premised on Catesby's descriptions; thus up to 1766 no U. S. specimens had reached these collections which Linnaeus studied, although many Neotropical forms were included therein. Nevertheless I have not excluded the timber rattler and Florida diamondback as possibilities. But at least we are justified in eliminating such western forms as *viridis* and its subspecies.

Returning to other species which may be omitted from consideration on the score of rarity or geographical inaccessibility, I think we can exclude both *molossus* or *scutulatus*, which, although they are found in the vicinity of Mexico City are rare so near the southern limits of their ranges. Neither reaches the east coast of Mexico.

*C. triseriatus* and *S. catenatus* are eliminated on the score of scale counts. The likeliest candidates remaining are the following:

- C. d. durissus* ..... Central American Rattlesnake
- C. d. terrificus* ..... South American Rattlesnake.
- C. unicolor* ..... Aruba Island Rattlesnake.
- C. adamanteus* ..... Florida Diamondback Rattlesnake.
- C. cinereus (atrox)* ..... Western Diamond Rattlesnake.
- C. b. horridus* ..... Timber Rattlesnake.
- C. b. atricaudatus* ..... Canebrake Rattlesnake.

I have included *C. unicolor* as a possibility because the color description of Linnaeus' *dryinas* fits it well, although the chance that he had access to such an island form appears remote. However, *unicolor* may also occur on the mainland (Klauber, 1936, p. 197).

I now proceed to analyze the relative chances that the three species described by Linnaeus represent each of the seven species and subspecies listed as being possibilities. This analysis is made by taking the statistics of these forms, as deduced from scale counts now at hand, and calculating, by the *t*-test, the significance of the difference between the population mean and Linnaeus' scale count. The formula is  $t = (M - X) / \sigma$ , where *M* is the population mean, *X* is Linnaeus' count, and  $\sigma$  is the optimum estimate of the standard deviation of the population, as calculated from the specimens available to me, by the formula  $\sigma = s [N / (N - 1)]^{1/2}$ . *N* is the number of specimens contained in the sample, and *s* the standard deviation of the sample. The *t*-table is entered at the degrees of freedom equal to *N* - 1. Having determined separately a probability for each scale count given by Linnaeus (these being the ventral and subcaudal counts in the case of all three species described, together with the labials in the case of *dryinas* only) these probabilities are then combined into a single aggregate probability by the chi-square method of Fisher.<sup>2</sup>

This scheme involves the following assumptions: That the scale counts (and sexes) as given by Linnaeus are accurate and were made by the same methods as those used today; that the dispersions of these characters are substantially normal, as seems to be the case (see Sec. 1 of this series); and finally that the scale counts included in my samples represent the areas from which Linnaeus' specimens were derived, so that the tests are not adversely affected by intransubspecific trends or clines.

With respect to the scale counts, aside from obvious slips, Linnaeus seems to have been quite accurate. When we compare Andersson's checks on Linnean types we find that there is seldom a difference of more than one in either the ventrals or subcaudals. Usually when there is a difference, Andersson's results are one higher than Linnaeus'. If there are any counts especially to be doubted they are the 14-14 of both supralabials and infralabials in the type of *dryinas*. This is a uniformity rarely met with in actuality.

Admittedly these conditions render conclusions somewhat hazardous; nevertheless, by this method we will be making the best use of the tenuous numerical data which Linnaeus has supplied. Table 1 sets forth the statistics resulting from studies of the species and subspecies considered to be possible solutions.

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<sup>2</sup> R. A. Fisher: Statistical Methods for Research Workers, Seventh Edition, pp 104-106, 1938.

TABLE 1

## STATISTICS OF SCALE COUNTS

Subspecies	Ventrals			Subcaudals		
	N	M	$\sigma$	N	M	$\sigma$
<i>C. d. durissus</i> .....	52	175.27	3.92	51	30.14	1.91
<i>C. d. terrificus</i> .....	18	170.39	3.26	18	28.44	2.18
<i>C. unicolor</i> .....	12	158.67	2.10	12	28.67	1.30
<i>C. adamanteus</i> .....	35	170.49	2.73	35	29.49	1.34
<i>C. cinereous</i> .....	147	178.63	3.24	147	25.88	1.47
<i>C. b. horridus</i> .....	154	167.66	3.29	154	24.69	1.82
<i>C. b. atricaudatus</i> .....	24	171.04	3.52	25	26.72	1.86

Subspecies	Supralabials			Infralabials		
	N	M	$\sigma$	N	M	$\sigma$
<i>C. d. durissus</i> .....	192	14.83	1.05	192	16.42	1.17
<i>C. d. terrificus</i> .....	68	13.88	0.91	68	15.29	1.01
<i>C. unicolor</i> .....	38	12.74	0.76	38	13.21	0.66
<i>C. adamanteus</i> .....	142	14.20	0.91	140	17.60	0.98
<i>C. cinereous</i> .....	543	15.59	0.93	541	16.41	1.04
<i>C. b. horridus</i> .....	724	13.61	1.02	722	14.78	1.03
<i>C. b. atricaudatus</i> .....	115	14.09	0.92	114	15.58	0.94

NOTES: N is the number of specimens available for study, restricted to males in the case of the ventrals and subcaudals. The data on labials is of interest only for comparisons with the Linnean *dryinas*. M is the average scale count, and  $\sigma$  is the population standard deviation estimated from the sample. The *C. cinereous* statistics were limited to material from Texas and northeastern Mexico, as specimens from farther west have higher average scale counts, and Linnaeus' specimens are presumed to have come from near the coast. To have used western scale counts would have eliminated *cinereous* at once.

We next test the differences between these statistics derived from the studies of present-day specimens, and the scale counts given by Linnaeus, using the formulas<sup>3</sup> previously mentioned, and arrive at the set of probabilities in Table 2, high numbers indicating close agreement, and low numbers wider divergence.

<sup>3</sup> The labials are treated as if there were one count per specimen since it can be shown that there is bilateral correlation in these characters.

TABLE 2

Aggregate Probability, P, of the Identity of Linnaeus' Types  
with Various Subspecies.

Modern Designation	Linnaeus' Designation		
	<i>Horridus</i>	<i>Dryinas</i>	<i>Durissus</i>
<i>Durissus</i> .....	.003	.027	.006
<i>Terrificus</i> .....	.22	.41	.16
<i>Unicolor</i> .....	.001-	.02	.001-
<i>Adamanteus</i> .....	.002	.003	.001-
<i>Cinereous</i> .....	.001-	.001-	.05
<i>Horridus</i> .....	.96	.06	.41
<i>Atricaudatus</i> .....	.32	.08	.37

Thus we see that, premised on scale counts alone, Linnaeus' *horridus* is in closest agreement with the modern *horridus*, next, to the subspecies *atricaudatus*, with *terrificus* the third possibility in order; *dryinas* most nearly resembles *terrificus* first, *atricaudatus* second, with *horridus* third; while Linnaeus' *durissus* adheres closest to modern *horridus*, with *atricaudatus* second, and *terrificus* third. It is of interest to note that if we eliminate chances below 1 in 10, *dryinas* is the only name definitely fixed; it could refer only to the subspecies we now call *terrificus*. We now carry these probabilities forward and introduce the effects of the other information supplied by Linnaeus, discussing each of his types separately.

#### HORRIDUS

The references are as follows:

- Mus. Ad. Fr. 1. p. 39.
- Bradl. Natur. t. 9. f. 1.
- Seb. Mus. 2. t. 95 f. 1.

The primary reference (Mus. Ad. Fr. p. 39 = Linnaeus, 1754, of my bibliography) is of little help. Unfortunately Linnaeus gives no color or pattern description of his type specimen and there is no figure. The rest of the description is so generalized that it would fit almost any species, although reference to a dorsal ridge suggests the Neotropical rattler, as does also mention of very blunt scales with turned-up edges on the snout. Two other specimens besides the type are mentioned, these being the specimens which Linnaeus later made the types of *dryinas* and *durissus*. From his study of these he concludes there may be more than one species of rattlesnake. Reference is made to Catesby (1743) and Kalm (1753) for discussions of the natural history of rattlesnakes, which tertiary references are premised on the snake which we now know as *horridus*.

The secondary references add to the confusion. Linnaeus refers only to figures in Bradley, 1721, and Seba, 1735. That in Bradley (plate 9, fig. 1) bears some resemblance to *horridus*, although it looks as if it had been made from a specimen which was once dried out and thus lost the outer skin and much of the pattern. The head is so badly done that the scales are not recognizable. The specimen is stated to have come from the West Indies, which is highly improbable, since *unicolor* on Aruba Island is the only West Indian form at present known. On the other hand, fig. 1 in plate 95 of vol. 2 of Seba is clearly not the timber rattler, for it has diamonds rather than bands. (Seba mentions in his text a chain of black blotches edged with white.) There is a dark line on the neck which may be a dorsal ridge or a paravertebral stripe, either of which is characteristic of *durissus* or *terrificus*, and the scales on the head suggest these subspecies, or *molossus*; at any rate, this Seba plate is not *horridus*. Yet when Linnaeus revised his allocation of Seba's plates in the twelfth edition of the *Systema Naturae* he did not change the assignment of plate 95, fig. 1 to this species. This should have considerable weight. Nor did Linnaeus make any other change in the entry under *horridus* in the last edition of the *Systema Naturae* (the twelfth, 1766) which he edited. In the thirteenth edition, 1789, edited by Gmelin, mention is made twice of triangular red-brown spots, strongly suggestive of *horridus*. But there is no assurance that this addition came from any study made by Gmelin of the type specimen; more probably it was derived from a statement in Boddaert, 1783. If *horridus*, 1758, were composite, and we consider Gmelin the first reviser, a fair case is made for the present application of the name *horridus* to the timber rattlesnake.

The conclusion with respect to Linnaeus' *horridus* is that the scale counts of the type fit the timber rattler well, and, in fact, fit best the subspecies which we now know as *b. horridus*, with *b. atricaudatus* second. The other data available are conflicting, but there are three items which rather strongly suggest other species: first, Seba's plate, which is certainly not *horridus*; secondly, the fact that this specimen, if *horridus*, must have been the only reptile from the United States among the considerable number in the King Adolf Fredrik Museum; and lastly, the dorsal ridge and blunt scales on the snout, as mentioned in the description. Therefore, while we may continue the present application of Linnaeus' name *horridus* to the timber rattler, because of lack of conclusive evidence that such an allocation is incorrect, there is reason to doubt that this type really belonged to that species. I must say that were no considerations of usage involved we should be more consistent in assigning *horridus* to the South American rattler than to the timber species, for although the scale counts favor the latter, South American males with 167 ventrals and 25 subcaudals are not particularly unusual. Also, *horridus* means "rough" as well as "horrible" and this is an apt description of the Neotropical form, with its prominent scale bosses. It should not be forgotten that of the 50 recognizable species of snakes contained in the King Adolf Fredrik Museum

more than half (26) were Neotropical in origin; and if the type of *horridus* really came from the United States it was the only snake in that collection which did.

#### DRYINAS

The primary reference is Amoen, acad. 1. p. 297.

There are no secondary references. The description is very brief: "Whitish with a few yellowish spots." This fits only *unicolor*, unless the specimen was badly faded, which is highly probable, in which case it might apply to almost any species.

The description in Amoen, acad. 1, p. 297 (= Linnaeus, 1749a) is somewhat confusing, in that it not only discusses this type, but other rattlesnake generalities, the description being really a summary of the knowledge respecting rattlesnakes available to the author. The tertiary references given in Linnaeus, 1749a, are of no assistance, since they suggest several different rattlesnakes, although *terrificus* more than any other. Three figures in Seba, 1735, are mentioned; of these, plate 95, fig. 1 has already been allocated to *horridus*, as previously stated.<sup>4</sup> Plate 95, fig. 2 and plate 96, fig. 1, are not definitely recognizable; the former has diamonds, and the latter large scales on the snout; both have indications of vertebral ridges, all of which characters suggest *durissus* or *terrificus*. Unfortunately Linnaeus does not mention fig. 4 of plate 45; this is the best rattlesnake plate in Seba, clearly recognizable as *durissus*. The primary reference states that the snake being described as *dryinas* occurs in Virginia and Brazil, and therefore confuses *horridus* and *terrificus*.

Using the probabilities of the four scale counts in combination, as previously developed, and remembering that the chances are against this having been the only United States specimen in the Adolf Fredrik Collection, I think the probability quite strong that the type of *dryinas* was a small, badly faded specimen of the South American rattler, or what we now call *terrificus*. The type specimens of at least eight other South American snakes were contained in this collection. *Durissus* would be a rather remote second choice. However, I do not state that we would be entirely warranted in reviving the long-disregarded name *dryinas*.

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<sup>4</sup> In the twelfth edition Linnaeus made it clear that the allocations of the Seba plates in the tenth edition (and in the primary references contained therein) were confused. He corrected them as follows:

*horridus* plate 95, fig. 1.  
*dryinas* plate 95, fig. 3.  
                   plate 96, fig. 1.  
*durissus* plate 95, fig. 2.

As he must have used care in making this correction, it is unfortunate that Seba's plates should be so poor and his descriptions so inadequate.

## DURISSUS

The references are as follows:

Amoen. acad. 1. p. 500.

Kalm. act. Stockh. 1752, p. 310, and 1753, p. 52, 185.

Gron. Mus. 2. p. 70. n. 45. Crotalophorus 174-22:3?

As developed in the statistical tables the scale counts favor *horridus* as first choice, *atricaudatus* second, and *terrificus* third. The color description "mixed white and yellow, black rhombic blotches with white discs (centers?)" best fits either *durissus*, or a faded *terrificus* or *adamanteus*.

In the more complete discussion in the primary reference, Amoen. acad. p. 500 (= Linnaeus, 1749b), Linnaeus reiterates the opinion that there are several species of rattlers, stating that this is the third that he is able to distinguish, the first being *horridus* and the second *dryinas*. He mentions particularly a supraocular and interocular white cross mark which suggests *durissus* or *viridis*, but not *adamanteus*, although some of the latter have lighter areas between the supraoculars than on the supraoculars themselves. The description is of a large snake four feet long, which eliminates the smaller species from consideration. This white cross mark, and the "*disco albis*" are the most important points in the description. "*Disco albis*" has been variously interpreted to mean both a white center in the blotches, or white edges. A light center would favor *durissus*; this was the translation given by Turton (1806); and Le Conte (1853).

The secondary references are definitely conflicting. Kalm deals only with *horridus*, which he discusses at length; and Gronovius contains a description of a specimen from Surinam which is, therefore, *terrificus*.

If we rule out *horridus* and *atricaudatus*, which, although they check well in scale counts with Linnaeus' type, evidently do not agree with his description, the conclusion is that Linnaeus' type specimen which he called *durissus* was probably a South American rattlesnake, or *terrificus* by our current nomenclature; however, it must have been badly faded. The fact that the collection containing the type of *durissus* was referred to as the Surinam Collection, as well as by the alternative name of the Claudius Grill Collection, lends weight to this view. Other rather remote choices would be *adamanteus* and *durissus*. If we were willing to assume that Linnaeus made a mistake in sexing this specimen, the subcaudals of the type would be fairly representative of *durissus*, but then the ventrals would be too low. The fact that Linnaeus described the tail as short and slender leads one to suspect that the type may have been a female. Assuming the accuracy of Linnaeus' counts and sexing, the few subcaudal scales are the strongest barrier to accepting this as a specimen of the Central American rattler, which we currently call *durissus*, for this species is notably long-tailed with a relatively high subcaudal count. A male with 24 subcaudals is by no means impossible, but certainly it would be highly improbable

as a single chance specimen. The final determination of the meaning of Linnaeus' *durissus* is every bit as uncertain as his *dryinas*—more so, in fact.

Do Amaral (1936) takes exception to my use of *durissus* as the specific name of the Neotropical rattler, although he had referred to the Central American snake as *C. terrificus durissus*. I pointed out that *durissus* could not be subsidiary to *terrificus* since it is the older name. Do Amaral then took the position that *durissus* is composite; and as it cannot be revived with a later date than 1758, he thought it should be abandoned. Hence he assigns *terrificus* Laurenti, 1768, as the specific name of the Neotropical rattler and proposes a new name, *terrificus copeanus*, for the Central American subspecies. Admitting the questionable identity of Linnaeus' *durissus*, it seems to me that do Amaral's suggestions will neither lead to less confusion as he states, nor are they in accordance with the rules of nomenclature. First, it is to be pointed out that Laurenti's *terrificus* is just as difficult to assign to a modern species as is *durissus*; in fact, more so, since no scale counts are given. The description, evidently based on Seba, fits the Central American subspecies even better than the South American, and, for that matter, applies almost as well to *adamanteus*. So if we are to abandon *durissus* because of indefiniteness, *terrificus* should also be abandoned. As to *copeanus*, this is a *nomen nudum*, for the presentation does not comply with Art. 25 of the International Rules. Besides, if *durissus* be abandoned as unrecognizable, both *boiquira* Lacépède, 1789, and *simus* Latreille, in Sonnini and Latreille, 1801, are available as names for the Central American snake. *Boiquira* is subject to some of the uncertainties that surround the original intentions of both *durissus* and *terrificus*, but *simus* is quite clear, both because of the description, involving black parallel lines on the neck, and the reference to Seba's plate 45, which is unmistakable.

Returning to *terrificus* there is another view which I think tenable; namely, that *terrificus* is a synonym of *horridus* regardless of what snake Linnaeus may have intended to attach the name *horridus* to, because Laurenti was merely repeating, with additions, Linnaeus' description of *horridus*, but preferred to use an alternative Latin word, *terrificus*. He included the other Linnean species, *dryinas* and *durissus*, and would hardly have omitted only *horridus*. Naturally he had no thought of our modern nomenclatorial rules and would have changed one of these names with as little hesitation as we would change a common or local name in English. This theory is suggested, first by his reference to the same Seba figure (plate 95, fig. 1) as Linnaeus used to illustrate *horridus*; and secondly, by the fact that he changed other Linnean names, when he thought it advisable, as for example, *Boa caninus* to *Boa thalassina*, and *Coluber laticaudatus* to *Laticauda scutata*. In these cases we know he was still referring to the Linnean species because of his mention of the Adolf Fredrik plates. Gmelin thought *terrificus* a synonym of Linnaeus' *horridus* (p. 1080). So I do not consider *terrificus* more worthy of retention than *durissus*.

## CONCLUSIONS

When we sum up the three conclusions separately arrived at, we find the indications rather strong that all three of Linnaeus' types were specimens of the Neotropical rattler, more probably belonging to the South American subspecies than the Central American. This introduces the question of why Linnaeus should have described three species from specimens at best representing only two subspecies. Of course, there is much pattern variation in the Neotropical rattler, and in addition two of the specimens were badly faded. There seems not much doubt that *dryinas* was a small faded South American rattler. This leaves *horridus* and *durissus*. For either of these to have been a timber or canebrake rattler requires us to overlook the fact that the other New World specimens in these Swedish collections were Neotropical rather than Nearctic in origin. In both cases there are details of description which are against either type having been a timber rattlesnake. However, if we must accept one, on the theory that Linnaeus would not otherwise have described three species, I think I should favor his *durissus*. To do otherwise is to neglect the evidence of Seba's plate 95, fig. 1, which is the only recognizable figure amongst the four cited by Linnaeus.

*Horridus* has been established as the type species of the genus *Crotalus*, which was placed in the official list of generic names in Opinion 92 of the International Commission on Zoological Nomenclature.

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## SUMMARY

Evidence deduced from scale counts fails to give certainty to the linking of the three species of rattlesnakes described by Linnaeus in 1758 with any of the forms known today. Identifications are doubtful because of the loss of the types, and the inadequacy of the original descriptions, together with the introduction of accessory matter and references which are conflicting. Were we considering an author less important than Linnaeus, and names less thoroughly established, it would be best to abandon them all as being unrecognizable. *Terrificus* Laurenti, 1768, is on no firmer ground. Under the circumstances, while the chances seem rather remote that the Linnean type of *horridus* could have come from the United States, it may be best to continue the name *horridus* as the specific name of the timber rattlesnake, for we cannot prove absolutely that such an identification is inaccurate. By similar reasoning the name *durissus* may be retained for the Neotropical rattler, with *terrificus* as the South American subspecies. *Dryinas*, not having been used for a long time, should be neglected, although we can come nearer to a positive identification of this specimen than either of the others.

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