To Fred L. Annable
with best regards from
L M Klauber

BULLETINS

OF THE

Zoological Society of San Diego

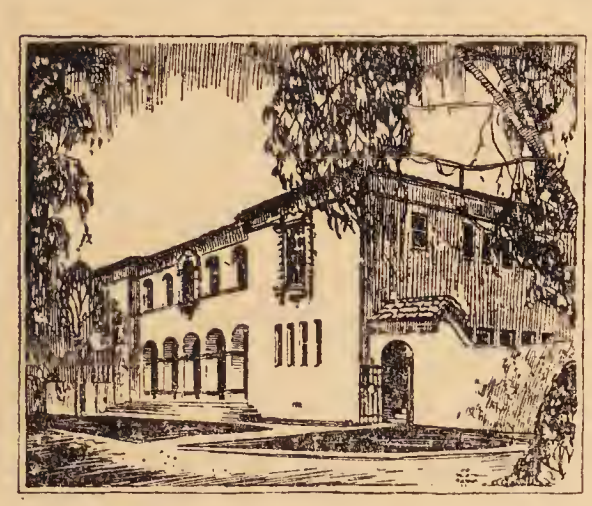
No. 21

HERPETOLOGICAL CORRELATIONS

I. Correlations in Homogeneous Populations

By L. M. KLAUBER

Consulting Curator of Reptiles, Zoological Society of San Diego



SAN DIEGO, CALIFORNIA

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INTRODUCTION

The problems of correlation which present themselves in herpetology are many and varied. In all directions there are attractive vistas suggesting interesting questions for investigation—such problems, for example, as the correlation of different elements of scalation with body size, the correlation between the numbers of ventrals and subcaudals, between rattle sequence-number and rattle width in a species of rattlesnake, or between the right and left femoral pores of a lizard. The possible combinations of these variable characters, which can be tested in pairs for a significant correlation (or its absence), are very great in number; and in addition we have the fields of partial or multiple correlations in groups of related characters. Furthermore we have to decide whether the studies shall be made by families, genera, species, or of territorially concentrated, homogeneous populations. Altogether, the possibilities are so numerous that we can do little more, in a study not restricted to some particular problem or species, than to select a few random pairs of characters for examination.

In the furtherance of co-ordination and clarity, I have divided this study into two parts; the present one discusses correlations in homogeneous localized populations—that is, populations which are geographically so restricted that they are presumed to be freely interbreeding, and without regional or ecological differentiation—while later I hope to offer a second series of calculations giving some statistics of more inclusive groups of organisms.

The fact of the existence of correlation between certain characters in example populations should not be too greatly generalized. Because a significant correlation is found to be present between, let us say, the numbers of ventrals and subcaudals in *Crotalus ruber* is no proof that such a correlation is universal; and even if it be demonstrated in several species of rattlesnakes we are not safe in assuming its presence in genera other than *Crotalus*. Even the proof of a correlation often lacks finality; instead, we can only determine the numerical probability that a correlation evident in a sample really exists in the population which the sample represents. We must be wary of both accidental and spurious correlations. Care must be taken to guard against heterogeneity or stratified samples, so that a correlation, as determined, is not merely a cumbersome proof of sexual dimorphism or territorial variation. And when we are assured of the existence of a correlation of considerable degree between certain pairs of characters there remains the all-important problem of the reason for the interrelationship and, particularly, the differentiation between cause and effect. Often a correlation between two factors is the result of a common influence upon both by a third.

The question naturally arises as to the value of correlation studies, aside from the usual curiosity an investigator feels respecting any scientific fact. One practical value is the greater insight correlation gives into the character and extent of bilateral asymmetry in an organism. While an R x 2 table will afford an idea of the extent and significance of asymmetry, if there be any, only a correlation table and a calculation of the statistics of correlation will fully illustrate the interdependence of the variation on the two sides. For an R x 2 table only shows differences in summation —that is, by class totals, and thus lends itself to a study of means and variances. A correlation table, on the other hand, gives a complete picture of the extent of bilateral divergence in each separate specimen; for we may find important individual unbalances without there being any appreciable net differences between the means or dispersions of the two sides. And even to determine the significance of the differences (if any be present) between the means or dispersions, we must calculate the correlation coefficient—since it is involved in the necessary formulas—unless the more cumbersome method of paired differences be employed.

Secondly, in evaluating differences based on the summation of groups of characters, one should naturally give greater weight to such differences if exemplified by several independent characters, than to the same number of correlated characters. For example, if a difference between two snakes be demonstrated in one character, a corresponding difference might well be expected in a second correlated character; and the weight given this second character should be less than that given a second independent character. This is important in determining the phylogenetic position of an intermediate species or subspecies in its relationship to two others.[1] This type of investigation may occasionally provide clues to multiple-factor inheritance. Correlation studies will indicate how closely the value of one variate may be calculated from another, for this is inherent in the correlation procedure.

The preparation of correlation tables will usually cause aberrant or freak specimens to stand out sharply; by this means mistakes in counting, sexing, or recording, and even misidentifications will often be disclosed. Also, a study of correlations will sometimes permit a combination of key characters in such a way as to cause an accurate determination in a higher proportion of the specimens being keyed than by the use of single characters separately. Such a combination of characters has been called a "summation of characters" by Van Denburgh (1920, p. 5) or a "character index" by Hubbs and Whitlock (1929, p. 470. See also Hubbs, Hubbs and Johnson, 1943, p. 4).

Lastly, correlations may be of interest in studies of clines, or territorial or ecological variations. Thus, if pairs of characters are found to be without correlation in homogeneous local populations, but correlation be evident in samples representative of more widely distributed populations,

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[1] Klauber, 1943b, p. 61.

we have an indication that such variations are more the result of external pressures than of a mere selective sieving of variations already existing in the population.

Thus, correlation studies may prove important in phylogeny and genetics —in the study of geographical variation and the inheritance of characters.

METHODS

The quantitative measure of the degree of correlation between a pair of characters, that is, the correlation coefficient r, and the method of its determination will be found discussed in all statistical texts.[2] Primarily it constitutes a measure of the extent to which one variable is linked with, or follows the fluctuations of, another. The calculations required, although tedious, may be co-ordinated, and the possibility of error reduced, by the use of standardized printed forms, and these I have employed, both for raw-score computations, where the samples were small, and for correlation tables, where more specimens were available and grouping became necessary. In determining the significance of r, I have used the customary formula: $t = r[(N-2)/(1-r^2)]^{1/2}$, which, being equally applicable to small or large samples, has placed the calculations on a uniform basis.[3] This tests the probability, P, that r is zero in the population which the available sample represents. However, Fisher's z-transformation has been used to find the significance of the difference between any two correlation coefficients, when such a computation has been required. It was also employed when correlation coefficients were to be combined, as well as in the computation of confidence limits.[4] To avoid the necessity of frequent interpolations in the t-tables, curves were prepared giving the probability of the significance, P, to an accuracy of three figures, for any value of t up to 15, with degrees of freedom from 1 to 30, and by larger steps to 120. In calculating variances and covariances, Sheppard's correction was usually not necessary, since most of the variates considered in these studies take only integral values; however, the correction has been used in the case of a broad grouping.[5] Certain equations using the relationships between the correlation coefficients and the standard deviations of sums or differences may occasionally be employed to advantage in the place of correlation tables. These equations have been listed in connection with a study of

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[2] For example: Fisher, p. 168; Simpson and Roe, p. 222; Croxton and Cowden, p. 651; Arkin and Colton, p. 74. The quantity r^2, called the coefficient of determination, represents the proportion of the total variance of the dependent character which is accounted for by the variation of the independent character: Ezekiel, p. 139; Croxton and Cowden, p. 660.

[3] Simpson and Roe, p. 235; Kenney, Vol. II, p. 157; Baten, p. 279; Treloar, p. 162.

[4] Fisher, p. 202; Simpson and Roe, p. 242; Croxton and Cowden, p. 683; Tippett, p. 175. The older method of indicating the probable or standard error of r as a measure of its significance is no longer to be considered satisfactory except under rather specialized circumstances. Hagood, p. 621.

[5] Yule and Kendall, p. 221; Peters and Van Voorhis, pp. 100, 397.

body and tail lengths of snakes.[6] In the same paper (p. 9) will be found a brief discussion of spurious correlation, an effect which must be avoided in determining the correlation between two variates, one of which is a part of the other, as, for example, the tails of a series of snakes and their lengths over-all.

In the determinations which I have made, it is realized that not all the variates are normally distributed nor the relationships linear. To this extent r may not always be an entirely adequate or proper measure of the relationship. However, as has been shown,[7] most of the variates of lepidosis in snakes approach normality in distribution, and under such circumstances r constitutes a satisfactory practical measure.[8] Where possible, the number of categories, grouping, etc., have been made to conform to the recommendations in recent statistical texts.[9] Occasionally the constants of the regression equation have been given as a further indication of the nature of the relationships.

In a paper such as this, it is impossible, for reasons of space limitation, to present the original data from which the correlation coefficients were computed, since every pair of characters would require a separate table for each subspecies tested. Besides, such data lack sufficient permanent value to warrant publication. However, in the discussion which follows, I shall occasionally include the basic tables in order to supply a graphic illustration of some particular type of relationship, more illuminating than that entailed in a mere statement of the coefficient of correlation. As examples of the character of original data which form the basis of correlation calculations, Tables 1 and 2 are presented, the first setting forth a relationship in which a considerable degree of correlation is evident ($r = +0.57$); the second, one in which there is virtually none ($r = -0.06$).

Reference to the specimens in Table 1 as the "San Patricio" series of *Crotalus cinereous* relates to the locality in Texas where they were collected. This and other series of specimens, such as the Platteville and Pierre series of *Crotalus viridis viridis*, which have been employed in previous studies, will be found described elsewhere.[10] Similar territorial designations for other collections of specimens will be used throughout the present discussion.

The fundamental difference between Tables 1 and 2 lies in the tendency, evident in Table 1 (which shows the relationship between the labials on the opposite sides of the head in a series of *Crotalus cinereous*), of the variates to cluster along a diagonal line. For it will be observed that higher

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[6] Klauber, 1943a, p. 7.

[7] Klauber, 1941, p. 7.

[8] Kenney, Vol. II, p. 160; Treloar, pp. 104, 152.

[9] Treloar, p. 103; Peters and Van Voorhis, p. 100; Yule and Kendall, p. 449.

[10] San Diego Society of Natural History, Occ. Pap. No. 1, p. 2, 1936.

TABLE 1

San Patricio Series of *Crotalus cinereous*:
Correlation between the Sum of the Labials on the Right and Left Sides of the Head

Labials on the Left	Labials on the Right								
	29	30	31	32	33	34	35	36	Total
29	1	2	1	2	....	....	....	....	6
30	6	2	4	4	....	....	....	....	16
31	....	5	8	9	3	1	....	....	26
32	1	5	9	19	8	....	....	....	42
33	....	.	3	5	9	6	2	2	27
34	....	....	4.	6	3	3	2	....	18
35	....	....	....	1	1	1	....	....	3
36	....	....	....	....	....	....	....	1	1
Total	8	14	29	46	24	11	4	3	139

Calculated coefficient of correlation, $r = +0.57$.

NOTE:—The figures in the body of this and subsequent tables represent the number of specimens falling within each classification. For example, there are 19 snakes with 32 labials on the right and 32 on the left; 5 with 32 on the right and 33 on the left, etc.

TABLE 2

San Diego County Series of *Crotalus ruber*:
Correlation of Minimum Scales between the Supraoculars with the Infralabials on the Left Side of the Head

Infralabials on the Left	Scales between the Supraoculars						
	4	5	6	7	8	9	Total
15	....	1	....	....	....	....	1
16	....	6	3	4	6	....	19
17	1	9	29	27	12	....	78
18	1	13	35	30	14	1	94
19	1	4	18	10	1	....	34
20	....	....	4	5	....	....	9
21	....	....	1	....	....	....	1
Total	3	33	90	76	33	1	236

Calculated coefficient of correlation, $r = -0.06$.

values of the labials on the right side of the head tend to match with higher values on the left, and correspondingly the lower values also match. This, of course, is what is meant by correlation. On the other hand, in Table 2, while variations of the same type are evident in each character separately, no co-ordination seems present; the variations appear quite independent of each other and the spread is circular, instead of grouping about a diagonal.

The coefficient of correlation r is so devised that it can take values only from $+1$ (perfect positive correlation) through zero to -1 (perfect negative correlation). A negative correlation indicates that higher values of one variable tend to match with lower values of the other.

Throughout the present paper I shall consider the correlation coefficient, as determined from the sample, virtually as if it were a population parameter. Such is not really the case; however, as most of the samples studied are relatively large, usually with N greater than 100, the optimum estimate of the population value of r differs only in minor amount from the value of r in the sample. Table 3 shows the differences between the two at $N = 50$ and $N = 100$, for various values of the sample r, as deduced from Fisher's formula, cited by Peters and Van Voorhis (p. 153). It will be seen that, when N exceeds 50, the difference between the sample statistic and the estimated population parameter is negligible from a practical standpoint, being quite overshadowed by other uncertainties and assumptions.

TABLE 3

Relationship Between a Sample r
and the Optimum Estimate of the Population r

Sample r	Population r	
	$N^* = 50$	$N^* = 100$
0.100	0.099	0.100
0.200	0.198	0.199
0.300	0.297	0.299
0.400	0.397	0.399
0.500	0.496	0.498
0.600	0.596	0.598
0.700	0.696	0.698
0.800	0.797	0.799
0.900	0.898	0.899

* N refers to the number in the sample, not the population.

Of greater importance than these slight differences between the sample r and the population optimum estimate, are the confidence limits of the population parameter. The value of P, which appears in the tables throughout this discussion, as calculated in each case by a t-test, states the probability that the population correlation is not zero, or, in other words, that correlation is really present; but, beyond giving the value of r, for the sample, it does not define the probable extent of the population correlation, which is best stated in terms of confidence limits. In the present study, where the existence of fairly high and important correlations are indicated by the sample, the 95 per cent (occasionally 99 per cent) confidence limits, as deduced by using Fisher's z-transformation, will be given. These limits are those which, in 95 cases (or 99) out of 100, may be

expected to contain the true (but unknown) population parameter. The effects of sample size and confidence percentages on the confidence limits are indicated by the example ranges set forth in Table 4.

TABLE 4

Example Confidence Limits

	95 per cent		99 per cent	
Sample r	$N = 50$	$N = 100$	$N = 50$	$N = 100$
0.100	− 0.101—0.368	− 0.098—0.291	− 0.269—0.443	− 0.160—0.347
0.200	− 0.083—0.453	0.004—0.381	− 0.171—0.522	− 0.059—0.434
0.300	0.024—0.534	0.110—0.469	− 0.066—0.595	0.048—0.516
0.400	0.137—0.610	0.221—0.553	0.048—0.664	0.161—0.595
0.500	0.257—0.683	0.337—0.634	0.172—0.728	0.280—0.670
0.600	0.386—0.753	0.457—0.712	0.305—0.789	0.407—0.742
0.700	0.524—0.819	0.584—0.788	0.456—0.846	0.541—0.811
0.800	0.671—0.882	0.716—0.861	0.619—0.900	0.684—0.877
0.900	0.829—0.942	0.855—0.932	0.799—0.952	0.837—0.939

Where N is relatively high (say above 100) and r is not high (say below 0.8), it may be sufficiently accurate to use as the standard error of r, the formula $(1 - r^2)/(N - 2)^{1/2}$ and assume the distribution to be normal. For example, with $N = 100$ and $r = 0.5$ the 95 per cent confidence limits, by Fisher's method, are 0.337 to 0.634; by the test involved in the ratio of r to its standard error, computed from this approximate formula, the limits are 0.351 to 0.649. At other values of r (with the same N and confidence limits) the comparisons are as follows: $r = 0.2$; exact method, 0.004 to 0.381; approximation, 0.010 to 0.390: $r = 0.8$; exact method, 0.716 to 0.861; approximation, 0.729 to 0.871. It will be observed that the approximate values, where N is 100 or more, give a rather good idea of the confidence range.

The use of the word "error", in connection with such terms as "standard error" or "probable error", should not be confused with the synonym "mistake" by those unaccustomed to statistical terms. The standard error is merely the standard deviation of a sampling statistic; in other words, a measure of dispersion. But this has nothing to do with errors of counting or recording, which are true mistakes. The latter do creep in, even in the most careful work. Fortunately, their effects are likely to be unimportant —except when stating the over-all range of a variate—if samples are large, provided the source of the error (mistake) is such as to produce random, rather than directionally biased, deviations. Sometimes differences in counts result from differences in interpretation rather than mistakes in counting. In any case the herpetological worker must recognize the existence of these mistakes; he has only to check the counts published by some previous

investigator, working with the same material he is now using, to find some that differ from his own. In making this comment I am not in any way exempting my own scale-count records; I know they contain their full share of mistakes.

CHARACTER DEFINITION

One of the difficulties in the study of quantitative herpetology is the lack of standardization in definitions. For example, how does one decide where ventrals stop and gulars begin; shall certain head scales be called preoculars or loreals; how are the first and second temporals defined; how does one segregate postoculars from suboculars? These and many similar uncertainties will readily occur to anyone having had experience in making extensive series of scale counts. It is true that many of these terms will be found defined by illustrations in various herpetological papers; but most of such illustrations, for the sake of clarity, are drawn to show simple situations in which these puzzling questions of allocation do not arise. What is needed is a decision respecting border-line cases, made by some authoritative committee.

Failing in the availability of such decisions, it is important that the quantitative herpetologist lay down his own rules, in order that there will be consistency in his results. This involves a set of definitions. And he must also guard against differences in counts which might be the result of biased methods, such as viewing the sides of the head of a snake from different relative positions. This is especially necessary in counting the infralabials, which, being usually obscured by the overhang of the supralabials, often leave doubt as to whether certain scales at the commissure should or should not be included. A continuous bilateral error may be introduced if the two sides are viewed from different angles.

In the present survey I have considered a wide variety of characters in the hunt for examples of interdependent variation. While many are characters long standard in herpetological studies, others have been less often used. The search for new and different criteria, wherewith to distinguish species or races, is by no means a frivolous one, for they may tend to validate differences of major importance previously concealed by superficial resemblances and the coincidence of the better known characters. If such new differences are significant they are of distinct value, for the significance test itself involves the criterion of narrowness of dispersion and therefore of stability. However, in developing new differences, the certainty with which they may be defined is of importance, so that separate observers would agree upon interpretation, counts, or measurements. Permanence is another important feature; in the reptiles this seriously interferes with quantitative color measurements, such as are used in bird and mammal studies.

The more the scales on a snake's head are broken up into recognizable series, the more characters there are to investigate, not only with respect to counts, but also intersections, contacts, and suture proportions. In snakes

such as the rattlers, whose heads are largely sheathed with small scales, we have, besides the better known series such as the labials, internasals, loreals, oculars, canthals, etc., such groups as the scales contacting the rostral, the scales bordering the genials, the minimum scales between the supraoculars, the scales contacting the supraoculars from the postcanthal to the postocular, the scales bordering the pit, the scales between the pit and the supralabials and nasals, the number of gulars between the genials and the first ventral, and the number of gulars in the row between the last infralabial and the opposite ventral. And to whatever extent it may be shown that these scale groups are uncorrelated with each other, so they are less likely to vary in the same direction in different species or subspecies, and are thus the more likely to serve as independent difference indicators. Some species develop an especial variability in certain scale groups without corresponding trends in others, as, for example, the internasals in *C. viridis;* the scales before the pit in *C. exsul,* and, to a lesser extent, in *C. ruber;* and the scales around the rostral in *C. mitchellii.*

Most colubrids are not so well-supplied with variables as the rattlers, especially on the head; however, when taken in pairs for correlation studies, even the simplest afford a considerable field for investigation. As for the lizards, they far exceed any snakes in countable variables, and when these characters are taken in pairs for correlation studies, the possible combinations are very great indeed. As the scale counts which I have accumulated are largely those of snakes, the lizard studies have been restricted to a few examples.

BILATERAL CORRELATION

The most elementary case of correlation is that involving a study of the nature of the concomitant variation of any countable or measurable character which exists separately on the two sides of the body, that is, a determination of the extent of bilateral asymmetry.

In the simplest cases we have a bilateral variant which can only assume one of two values, or be present or absent. In such instances the result may be given in terms of the tetrachoric coefficient of correlation. For example, Table 5 sets forth the results of a study of the presence of divided first infralabials in two series of rattlesnakes.

Thus, we see in these two cases that the lateral correlation is quite high; there are relatively few specimens in which the condition on one side of the head fails to match that on the other.

Another variable character of the same nature is involved in the contact, or lack of contact, between the postnasal and upper preocular in certain rattlesnakes. In a series of *Crotalus cinereous* from Texas, out of 268 specimens, 108 show no contact, for either the postcanthal meets the loreal, or an upper loreal is interposed. In 140 specimens the postnasal does contact the upper preocular. Of the non-symmetrical specimens totaling 20, 8 have the contact on the right but not on the left, while 12 have it on

TABLE 5

Correlation in the Condition of the
First Infralabials in Two Series of Rattlesnakes

A. *Crotalus cinereous* from Southeastern California

	Right Side		
Left Side	Divided	Entire	Total
Divided	15	6	21
Entire	6	43	49
Total	21	49	70

$r^* = 0.82$

B. *Crotalus ruber* from San Diego County

	Right Side		
Left Side	Divided	Entire	Total
Divided	347	3	350
Entire	6	31	37
Total	353	34	387

$r^* = 0.95+$

* Values of r were determined from the Chesire-Saffir-Thurstone computing diagrams.

the left but not on the right. This gives a tetrachoric correlation of over 95 per cent.

In *Crotalus ruber* some individuals have a small scale contacting the rostral between the prenasal and the first supralabial. Out of 286 specimens from San Diego County, 48 have this scale on both sides, 16 on the right but not on the left, 9 on the left only, while in the remaining 213 the scale is absent on both sides. The tetrachoric correlation coefficient in this distribution is above 95 per cent.

Taking a case from among the colubrids, we have the following data on the preoculars in a series of 195 specimens of *Thamnophis o. ordinoides* from northwestern Oregon: 58 specimens have an upper preocular present; 108 have none. The remaining 29 specimens are asymmetrical; 12 have an extra preocular on the right only, while 17 have it only on the left. This gives 0.89 as the tetrachoric correlation coefficient. As an example among the lizards we have the following: In 159 specimens of *Dipsosaurus dorsalis lucasensis* from the Cape Region of Lower California, 103 have two scale rows between the rostral and nasal on both sides; 38 have one row. The other 18 are asymmetrical; 7 have two rows on the right and one on the left, while the remaining 11 have one on the right and two on the left. This gives a coefficient of 0.92.

Thus, we learn that asymmetry is relatively infrequent in these example cases, and the tetrachoric correlation is uniformly high. If there were no correlation the number of asymmetrical cases would always be at least twice one of the symmetrical sets, which is not the condition in any of the series tested, the unbalanced pairs being always greatly in the minority. For example, take the case of the extra scale touching the rostral in *Crotalus ruber*. In this instance the distribution was as follows: No extra scale, 213; one extra scale, 25; extra scales on both sides, 48; total, 286. Assuming the same over-all proportion of extra scales (21.2 per cent) and a purely random selection (zero correlation), the distribution would have been as follows: No extra scale, 178; one extra scale, (asymmetrical) 95; extra scales on both sides, 13; total, as before, 286. It will be observed that the asymmetrical cases have grown at the expense of the other two. Or, take as another example, the divided first infralabials in *Crotalus ruber*. The following table gives the distribution as actually found (from Table 5, Section B), the correlation coefficient being over 95 per cent, and as the distribution would be with the same proportion of undivided scales (9.18 per cent), but with zero correlation:

	Both sides divided	One side divided, the other undivided	Neither side divided	Total
As found	347	9	31	387
Zero correlation	319	65	3	387

Thus, it is shown that the condition of one side greatly affects the other; it tends to match with it, which is merely another definition of correlation.

Variable characters which can take only one of two values on either side of the body, or are present or absent, are not plentiful. Of much more frequent occurrence are characters which can assume any of a number of values. These lend themselves to correlation analysis to determine the prevalence of asymmetry. One might use the method of paired differences to determine whether there is a significant difference between the means of the sides, but a correlation table gives a better picture of concomitant variation—that is, whether a count on one side tends to be high when the count on the other is high; and the correlation coefficient, calculated from the table, affords a measure of bilateral uniformity. This study of bilateral symmetry is a special case of correlation, the more general case involving the investigation of concomitant variation in two different characters, instead of the same character on opposite sides of the body.

To illustrate the character of interdependent variations, which constitute the raw materials for the study of bilateral correlation, three typical cases are set forth in Tables 6 to 8. Two of these represent head shields, the other body rings.

TABLE 6

Borego Series of *Phyllorhynchus decurtatus perkinsi*: Correlation between the Loreal Scales on the Right and Left Sides of the Head

Left Side	Right Side 0	1	2	3	4	5	Total
0	....	2	....	....	....	..	2
1	....	19	10	....	....	....	29
2	...	11	204	21	1	....	237
3	..	2	30	41	2	....	75
4	....	....	1	6	4	1	12
5	....	....	..	....	....	....	....
Total	....	34	245	68	7	1	355

Calculated coefficient of correlation, $r = +0.649$

TABLE 7

Borego Series of *Phyllorhynchus decurtatus perkinsi*: Correlation between the Total Scales in the Ocular Ring on the Right and Left Sides of the Head

Left Side	Right Side 5	6	7	8	9	Total
5	1	....	....	....	....	1
6	...	2	4	1	....	7
7	...	4	72	55	3	134
8	...	2	52	134	5	193
9	....	....	2	6	9	17
Total	1	8	130	196	17	352

Calculated coefficient of correlation, $r = +0.425$

TABLE 8

San Diego County Series of *Lampropeltis getulus californiæ* (Pure Ringed Phase Only): Correlation between the Body Rings Counted on the Right and Left Sides of the Body

Left Side	Right Side 21	22	23	24	25	26	27	28	29	30	31	32	Total
23	1	....	2	2	1	....	....	....	....	....	....	....	6
24	....	....	1	....	1	4	1	....	....	....	....	....	7
25	....	1	1	2	2	4	3	1	....	....	....	....	14
26	....	....	....	3	4	1	....	2	1	....	....	....	11
27	....	....	....	....	4	4	8	....	1	2	....	....	19
28	....	....	....	1	2	2	6	6	2	3	1	....	23
29	....	....	....	....	1	....	1	4	1	1	....	1	9
30	....	....	....	....	....	1	....	1	2	1	....	....	5
31	....	....	....	....	....	....	....	....	....	1	....	....	1
32	....	....	....	....	....	....	....	....	2	....	1	....	3
33	....	....	....	....	....	....	....	....	....	1	....	1	2
Total	1	1	4	8	15	16	19	14	9	9	2	2	100

Calculated coefficient of correlation, $r = +0.686$

Using Table 6 as an example, it will be noted how much more completely a correlation table indicates the character of bilateral diversity than does an R x 2 table, involving a mere summation of totals, such as the following representing the same data:

Number of Loreals	Right Side	Left Side
0	....	2
1	34	29
2	245	237
3	68	75
4	7	12
5	1	....
Total	355	355

Space limitations prevent the presentation of all of the tables used in the investigation of bilateral correlation, but in Table 9 there are set forth the results of calculations involving a variety of characters and species. These have been selected as examples of characters which are subjected to sufficient variation so that a bilateral unbalance is frequent in individual specimens.

With respect to some of the particular characters tested, certain explanatory comments are pertinent. Lateral scale rows will be found discussed in Bull. Zool. Soc. San Diego, No. 17, p. 8; in the present instance they have been counted at mid-body. The canthals are considered to be the minimum scales between the internasals and supraoculars, along the upper edge of the canthus rostralis. The scales bordering the supraoculars are counted from the postcanthal to the postocular, but without including either. Pre- and postoculars do not vary enough in most snakes to warrant a study of correlation so that suitable examples are rare. Where the supralabials do not contact the orbit and suboculars are present, it is often difficult to segregate pre-, post-, and suboculars in a uniform manner; in such cases it is desirable to study the entire ocular ring, concerning which count there can be no question. The scales touching the parietals are counted from the mid-dorsal line to the postocular, but do not include the latter. The temporals often fall into arrangements which render allocations difficult, hence it is necessary to make rather arbitrary rules in counting. The scales between the lip and ventrals comprise a line of gulars, which begins with the last infralabial and ends at whatever ventral is contacted, the latter not being counted.

With respect to bilateral asymmetry in blotches or rings, it is sometimes not appreciated how often, in some species, they are broken or branched at the mid-dorsal line, so that the counts on the two sides of the body differ. To make the counts objectively, one should tally each side from a lateral view, without the other being visible.

All basic data in Table 9 are from original sources, except the costal counts in *Lepidochelys olivacea,* which are taken from Deraniyagala, 1939, p. 137; and the counts of the femoral pores of all the lizards (except *C. t. tessellatus*) which were kindly supplied me by Mr. J. R. Slevin of the California Academy of Sciences.

It will be seen from the results in Table 9 that, as might well be expected, the correlations are always positive and significant; they are relatively high but far from perfect. The lowest correlation is that of the scales contacting the parietals in *Lampropeltis g. californiæ,* the highest in the lateral scale rows in *Crotalus v. viridis.* There is no question as to the presence of a basic tendency toward bilateral uniformity, as evident in every one of these diverse characters. The over-all, weighted-average correlation of all pairs of characters is 0.614, with 95 per cent confidence limits of 0.604 to 0.625. In making this computation only one figure representing scale rows (the Platteville) was included. I realize that these final figures result from combining unlike things, but nevertheless they are of some interest.

Another character which may be investigated for bilateral symmetry is the incomplete lateral scale rows in snakes, measured either by the ratio of the length of the suppressed row to the body length, or by the serial number of the ventral scute opposite which the suppression occurs. Dr. James A. Oliver has kindly supplied me with the data on the incom-

plete rows of 13 male *Leptophis diplotropis* from Tehuantepec, Oaxaca. These snakes, in reducing from 15 to 11 rows, combine the fifth row with the sixth, and the third row with the fourth. I found the bilateral correlation to be 0.912 in the first instance and 0.910 in the second.

Dr. Henry S. Fitch determined the lengths of lateral scale rows in garter snakes as percentages of total head and body length (exclusive of tail). From his original notes, which he courteously allowed me to use, I found the following bilateral correlations in 107 male and 94 female *Thamnophis o. biscutatus* from the immediate vicinity of Klamath Falls, Oregon:

Row dropped	Male	Female
Fourth	0.903	0.903
Sixth	0.840	0.741

The low figure for the sixth row in the females is produced in part by one freak specimen.

Studies of these and other series indicate an increased variability in length, and a decreased correlation, the shorter the suppressed row. In a species of snake having a row which is absent in some specimens and present in others, that is, approaching total elimination, the lengths of the row, when present, on the two sides may be quite different. For example, in *T. o. biscutatus* the fifth lateral row is sometimes present and sometimes not. An investigation of 25 male specimens having this row present on both sides, at least to some extent, shows a bilateral correlation of 0.739.

Besides the correlation table and the calculation of the coefficient of correlation, there is another method whereby the extent of bilateral differences in these characters may be shown, namely, by tabulating the number of specimens wherein the counts on the two sides differ by 0, 1, 2, etc. Such data are presented in Table 10 covering some of the characters listed in Table 9. While supplying less information than is furnished by a complete correlation table, as in Tables 6 to 8, such a tabulation does give a good summary of the extent of bilateral unbalance. It will be observed that, as might be expected, the differences between the sides are likely to be higher where the character means are higher. Relatively large differences occur, for example, in the body rings of *L. g. californiæ* ($M = 26.91$) and the femoral pores of *C. t. tessellatus* ($M = 21.22$); for in these cases a difference of one between the counts of the two sides is proportionately less important than in characters wherein the count on each side is smaller, as is the case, for instance, in the canthals of *C. v. viridis* ($M = 2.35$) or the loreals of *P. d. perkinsi* ($M = 2.16$). In the latter a difference of one between the sides is almost half the mean, while in the cases of the body rings and femoral pores it is less than 10 per cent. Where differences of one are relatively large, proportionate to the total count, the specimens with no bilateral unbalance outnumber those which are asymmetrical; but where such a difference is relatively of smaller moment, the specimens with some unbalance outnumber those which are evenly matched on the two sides.

TABLE 9

Bilateral Correlation between Right- and Left-side Counts

Character	Species	Series or Locality	*N*	*r*	95 per cent Confidence Range
Lateral scale rows	*Crotalus v. viridis*	Platteville	833	0.885	0.869–0.899
	Crotalus v. viridis	Pierre	673	0.880	0.862–0.896
	Crotalus v. oreganus	Pateros	615	0.791	0.759–0.819
	Crotalus v. oreganus	S. D. County	613	0.834	0.808–0.857
Canthals	*Crotalus v. viridis*	Pierre	377	0.535	0.459–0.603
Scales bordering rostral	*Crotalus ruber*	S. D. County	232	0.756	0.695–0.807
Scales anterior to pit	*Crotalus ruber*	S. D. Coutny	100	0.552	0.399–0.675
Scales bordering supraoculars	*Crotalus ruber*	S. D. County	100	0.326	0.138–0.491
Scales between lip and ventrals	*Crotalus ruber*	S. D. County	100	0.324	0.136–0.489
Loreals	*Lichanura r. roseofusca*	S. D. County	100	0.515	0.355–0.646
	Phyllorhynchus d. perkinsi	Borego	355	0.649	0.584–0.706
Preoculars	*Thamnophis hammondii*	S. D. County	398	0.522	0.446–0.590
Postoculars	*Pituophis c. annectens*	S. D. County	265	0.660	0.586–0.723
Complete ocular ring	*Lichanura r. roseofusca*	S. D. County	101	0.546	0.393–0.670
	Phyllorhynchus d. perkinsi	Borego	352	0.425	0.335–0.507
Scales touching parietals	*Lampropeltis g. californiæ*	S. D. County	100	0.291	0.101–0.461
First temporals	*Lampropeltis g. californiæ*	S. D. County	539	0.613	0.557–0.663
	Phyllorhynchus d. perkinsi	Borego	353	0.311	0.214–0.403

TABLE 9
(Continued)

Character	Species	Series or Locality	N	r	95 per cent Confidence Range
Second temporals	*Phyllorhynchus d. perkinsi*	Borego	351	0.309	0.211–0.400
Total temporals	*Phyllorhynchus d. perkinsi*	Borego	350	0.296	0.196–0.389
Scales between lip and ventrals	*Lampropeltis g. californiæ*	S. D. County	100	0.439	0.266–0.585
Body rings	*Lampropeltis g. californiæ*	S. D. County	100	0.686	0.566–0.778
Lamellæ on fourth toe	*Cnemidophorus t. tessellatus*	Gila Valley	133	0.726	0.634–0.798
Femoral pores	*Cnemidophorus s. sackii*	Progresso, Guat.	154	0.595	0.482–0.688
	Cnemidophorus t. tessellatus	Gila Valley	154	0.759	0.683–0.819
	Cnemidophorus h. hyperythrus	Cape Region	51	0.689	0.510–0.811
	Dipsosaurus d. lucasensis	Cape Region	51	0.508	0.270–0.687
	Sceloporus f. smaragdinus	Guatemala	105	0.665	0.542–0.760
Costal scutes	*Lepidochelys olivacea*	Ceylon	378	0.655	0.593–0.709

NOTES:—*N* is the number of specimens; *r* is the calculated coefficient of correlation. Values of *P*, the probability that any correlation is zero, are not given. With three exceptions *P* is below 0.0001; these exceptions are (1) scales between the lip and ventrals in *C. ruber* ($P = 0.001$); (2) scales bordering the supraoculars in *C. ruber* ($P = 0.0009$); (3) scales touching the parietals in *L. g. californiæ* ($P = 0.0033$); thus all values of *r* are highly significant.

TABLE 10

Extent of Bilateral Differences

Character	Species	Series	Mean	Difference between Sides 0	1	2	3	4	Total
Canthals	*C. v. viridis*	Pierre	2.35	285	88	4	...	....	377
Loreals	*L. r. roseofusca*	S. D. County	4.49	41	52	7	....	....	100
Loreals	*P. d. perkinsi*	Borego	2.16	268	83	4	....	....	355
Preoculars	*T. hammondii*	S. D. County	1.74	344	53	1	....	....	398
Postoculars	*P. c. annectens*	S. D. County	3.60	191	70	4	....	....	265
Ocular ring	*L. r. roseofusca*	S. D. County	9.30	49	45	7	...	....	101
Ocular ring	*P. d. perkinsi*	Borego	7.62	218	126	8	....	....	352
First temporals	*P. d. perkinsi*	Borego	2.58	206	143	4	....	....	353
Second temporals	*P. d. perkinsi*	Borego	3.33	227	106	15	3	....	351
Body rings	*L. g. californiæ*	S. D. County	26.91	22	35	29	11	3	100
Lamellæ	*C. t. tessellatus*	Gila Valley	20.05	71	56	6	....	....	133
Femoral pores	*C. t. tessellatus*	Gila Valley	21.22	49	75	23	6	1	154
Costal scutes	*L. olivacea*	Ceylon	6.76	215	142	18	3	....	378

CORRELATION IN LABIALS

It may be wondered why I have left until the last the most obvious of the bilateral correlations—that between labials. For no one who has tabulated the scale counts of large numbers of snakes can have failed to observe, in many species, that a deviation from the mode on one side of the head is likely to be duplicated on the other. But in the case of the labials we have two counts on either side of the head, and the possibility of vertical as well as horizontal correlation is introduced; that is, do fewer supralabials on the right correspond to fewer on the left, and likewise to fewer infralabials on the right? Which is the stronger tendency, bilateral or vertical symmetry? I have assigned the investigation of these questions to a separate section to avoid confusion with other, less complicated correlations; for a different method, that of partial correlation, lends itself to the solution of these problems.

The rattlesnakes afford useful material for the investigation of the relative magnitudes of lateral and vertical correlations in labials, since there is enough variation in these scales, even within a homogeneous series, to provide a well distributed correlation table.[11]

The simplest method of comparing vertical with lateral correlation is to compare the correlation between the sum of the supralabials and the sum of the infralabials, with the correlation between the sum of the labials on the right hand side of the head with the sum of those on the left. Table 11 shows the results of such studies in a number of homogeneous series of rattlers.

[11] For examples of such distributions see Bull. Zool. Soc. San Diego, No. 17, p. 17, Table 7, 1941.

TABLE 11

Labial Correlations in Homogeneous Series of Rattlesnakes

Series	Vertical Correlation			Horizontal Correlation		
	N	*r*	*P*	*N*	*r*	*P*
Zacatecas *nigrescens*	92	0.299	0.004	92	0.421	0.0001–
San Patricio *cinereous*	139	0.310	0.0002	139	0.566	0.0001–
San Lucan *lucasensis*	289	0.385	0.0001–	289	0.394	0.0001–
Mojave *scutulatus*	100	0.477	0.0001–	100	0.581	0.0001–
Platteville *viridis*	827	0.429	0.0001–	827	0.595	0.0001–
Pierre *viridis*	672	0.401	0.0001–	672	0.617	0.0001–
Bonesteel *viridis*	79	0.525	0.0001–	79	0.494	0.0001–
Timberlake *viridis*	96	0.461	0.0001–	96	0.654	0.0001–
Pateros *oreganus*	614	0.458	0.0001–	614	0.579	0.0001–
S. D.-Imperial *laterorepens*	148	0.370	0.0001–	148	0.510	0.0001–
Arizona *klauberi*	109	0.194	0.109	109	0.422	0.0001–

NOTE:—By vertical correlation is meant the correlation between the sums of the supralabials and the sums of the infralabials, while horizontal correlation is that between the sum of the supra- and infralabials on one side of the head and the corresponding sum on the other.

It will be observed that significant correlations are found in all cases except one, this being the vertical correlation in *klauberi,* which is found somewhat below the usually accepted level of significance. In all except one series (Bonesteel *viridis*) the horizontal correlation is higher than the vertical, usually considerably higher.

Using Fisher's z-transformation we find the weighted average correlations of the four *viridis* series to be:

Vertical Correlation			Horizontal Correlation		
N	r	95% confidence limits	N	r	95% confidence limits
1674	0.424	0.384 to 0.463	1674	0.605	0.573 to 0.634

The difference between these two correlation coefficients is highly significant (P much below 0.0001).

The weighted average correlation coefficients of all eleven series tested, totalling 3165 rattlesnakes, is, for the vertical pairs, 0.411, and for the horizontal, 0.565. It is my opinion that most homogeneous series will approximate these degrees of correlation. There can be no question but there is a stronger tendency of the laterally opposite labials to vary together than of the labials on the same side of the head to do so.

In order that the character of the symmetry indicated by these figures may be visualized there are set forth in Tables 12 and 13 the detailed tabulations for the Pateros series of *C. v. oreganus.*

Having determined these relationships between the sums of the labials, the question naturally arises as to what would be disclosed by treating each set of labials separately. But since each set is evidently related, at least to some extent, to all three of the others, we must determine how each pair would vary if the other two remained constant. This is the method of partial correlation, the formulas for which will be found available in any statistical text.[12] This method has been used in investigating the labials of two large series of *Crotalus v. viridis,* the Platteville and Pierre, with the results set forth in Table 15. As a matter of interest the raw data for the Platteville series of 827 specimens are presented in Table 14. This permits one to visualize the differences in the adherence of the variates to the tabular diagonals. All correlations are, as expected, positive. It will be observed that the closest correlations are those between the supralabials and between the infralabials; that is, the horizontal or bilateral correlations.

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[12] For example, see Fisher, p. 191; Simpson and Roe, p. 245; Croxton and Cowden, p. 739.

TABLE 12

Pateros Series of *Crotalus v. oreganus*:
Correlation between Supralabials and Infralabials

Sum of Infralabials	Sum of Supralabials 26	27	28	29	30	31	32	33	34	35	Total
28	1	....	....	....	....	1	....	....	....	....	2
29	1	....	1	5	7	1	1	....	....	....	16
30	....	2	6	17	18	5	....	2	....	....	50
31	....	3	12	21	42	18	5	1	....	....	102
32	....	1	11	25	56	36	28	2	....	....	159
33	....	....	6	20	40	41	32	7	2	1	149
34	....	....	1	7	26	21	20	11	2	....	88
35	....	....	....	3	5	12	12	6	....	....	38
36	....	....	....	....	....	2	2	4	....	1	9
37	....	....	....	....	....	....	1	....	....	....	1
Total	2	6	37	98	194	137	101	33	4	2	614

Calculated coefficient of correlation, $r = +0.458$

TABLE 13

Pateros Series of *Crotalus v. oreganus*:
Correlation between Labials on the Right and Left Sides of the Head

Sum of the Labials on the Left	Sum of the Labials on the Right 27	28	29	30	31	32	33	34	35	36	Total
27	....	1	....	....	....	....	....	....	....	....	1
28	1	....	1	4	2	....	....	....	....	....	8
29	....	2	7	18	10	4	1	....	....	....	42
30	....	3	16	31	38	17	3	2	....	....	110
31	....	2	11	37	52	40	16	6	....	....	164
32	....	....	....	21	49	60	21	12	1	....	164
33	....	....	....	1	20	33	23	10	1	....	88
34	....	....	....	....	2	4	14	4	2	....	26
35	....	....	....	....	....	1	6	3	....	1	11
36	....	....	....	....	....	....	....	....	....	....	0
Total	1	8	35	112	173	159	84	37	4	1	614

Calculated coefficient of correlation, $r = +0.579$

These judgments, from a visual examination of the raw data contained in Table 14, are validated by the calculated correlations as shown in Table 15.

TABLE 14

Platteville Series of *Crotalus v. viridis*:

Labial Correlations

		Right Supralabials							Left Supralabials							Right Infralabials							
		12	13	14	15	16	17	18	12	13	14	15	16	17	18	13	14	15	16	17	18	19	Total
Left Supralabials	12	....	2	5	....	....	....	....															7
	13	3	4	35	7	1	....	....															50
	14	1	23	119	83	11	....	....															237
	15	....	9	122	185	51	4	....															371
	16	....	....	22	66	44	5	1															138
	17	....		1	7	11	2	....															21
	18	....	....	....	....	....	3	....															3
Right Infralabials	13	1	2	3	1	....	....	....	2	2	2	1	....	....	....								7
	14	....	9	28	12	6	....	....	1	8	25	19	2	....	....								55
	15	1	15	96	98	18	1	....	1	17	84	97	28	2	....								229
	16	2	11	129	135	39	5	....	2	17	88	160	48	5	1								321
	17	....	1	41	77	36	5	1	....	4	31	71	45	9	1								161
	18	....	....	7	20	19	3	....	1	2	6	20	14	5	1								49
	19	....	....	....	5	....	....	....	....	....	1	3	1	....	....								5
Left Infralabials	13	....	3	1	1	....	....	....	....	2	3	....	....	....	....	....	2	2	1		....	....	5
	14	....	4	30	14	1	....	....	2	7	19	19	2	....	....	4	11	25	9		....	....	49
	15	2	18	117	101	18	2	....	4	22	91	114	24	2	1	3	28	98	98	27	4	....	258
	16	1	10	107	138	52	3	....	1	15	83	141	63	8	....	....	11	78	140	69	12	1	311
	17	1	3	41	82	38	6	1		4	38	85	35	9	1		3	24	64	53	26	2	172
	18	....	....	8	12	8	3	....	....	....	3	12	13	2	1		....	2	9	11	7	2	31
	19	....	....	....	....	1	....	....	....	....	....	....	1	....	....	....	....	....	....	1	....	....	1
Total		4	38	304	348	118	14	1	7	50	237	371	138	21	3	7	55	229	321	161	49	5	827

TABLE 15

Partial Correlations in Labials of *Crotalus v. viridis*: Platteville Series (827 Specimens) and Pierre Series (672 Specimens)

	Unadjusted Correlations			Adjusted Correlations		
	Platteville	Pierre	Series Combined	Platteville	Pierre	Series Combined
Horizontal Correlations						
Between supralabials	0.483	0.498	0.490	0.404	0.432	0.417
Between infralabials	0.454	0.480	0.466	0.372	0.410	0.390
Combined labials	0.469	0.489	0.478	0.388	0.422	0.403
Vertical Correlations						
Right side	0.319	0.268	0.296	0.144	0.057	0.105
Left side	0.309	0.307	0.308	0.133	0.123	0.128
Sides combined	0.314	0.288	0.302	0.139	0.090	0.117
Diagonal Correlations						
Right supralabial to Left infralabial	0.307	0.279	0.295	0.121	0.111	0.117
Left supralabial to Right infralabial	0.307	0.337	0.321	0.121	0.175	0.145
Diagonals combined	0.307	0.308	0.307	0.121	0.143	0.131

I have not entered the results of the significance tests on the values of r set forth in Table 15 to avoid complicating the comparisons of the correlations. All values are found highly significant (P lower than .01) except the adjusted vertical correlation on the right side of the Pierre series, in which case it is not evident that the value found ($r = 0.057$) differs significantly from zero, P being 0.139.

The results of these investigations agree with those previously derived (Table 11), that is, a proof that bilateral correlation is considerably higher than vertical. While the vertical correlation is higher than the diagonal in the Platteville series, the contrary is found to be the case in the Pierre series.

The final partial correlations of the two rattlesnake series taken together to produce a weighted average result, are of particular interest. With their appropriate 95 per cent confidence limits they are:

	N	r	95 per cent confidence limits
Between supralabials	1499	0.417	0.374 – 0.458
Between infralabials	1499	0.390	0.346 – 0.432
Combined horizontal	2998	0.403	0.373 – 0.433
Vertical	2998	0.117	0.081 – 0.152
Diagonal	2998	0.131	0.096 – 0.166

The significances of the differences between these correlation coefficients are as follows:

	t	P
Between the supralabials and the infralabials	0.88	0.38
Between the combined horizontals and the verticals	12.00	0.0001–
Between the combined horizontals and the diagonals	11.40	0.0001–
Between the verticals and the diagonals	0.55	0.58

We see that the horizontal correlations—supralabials and infralabials—do not differ significantly from each other, but do differ very significantly from either the vertical or diagonal correlations. The vertical and diagonal correlations in turn, do not differ significantly from each other. We conclude that in these rattlesnakes the lateral linkage is definitely closer than the vertical.

The labials of several colubrids have been investigated in a similar manner—first unadjusted, then adjusted by the method of partial correlations. Three series (of those available in ample numbers) were found to have a sufficient variation to warrant study, these being the Borego series of *Phyllorhynchus decurtatus perkinsi* (337 specimens) from eastern San Diego County, 226 specimens of *Pituophis catenifer annectens* from coastal San Diego County, and a group of *Thamnophis sirtalis concinnus* (236 specimens) from the Pacific northwest. The latter series is not territorially homogeneous, but is included for purposes of comparison. The results are presented in Table 16. It will be seen that they indicate the same trends observable in *Crotalus viridis viridis*. Since, in the present instance, we are dealing with separate species, no attempt has been made to combine the series. The following remarks apply to the partial, or adjusted, correlation coefficients.

All horizontal correlations are significant; of the verticals *concinnus* is not, while *perkinsi* and *annectens* are. No diagonal correlation is significant.

The infralabial correlations are higher than those of the supralabials; in *perkinsi* and *annectens* the differences between them are highly significant ($P = 0.0017$ and 0.0007, respectively); in *concinnus* the difference is below the usually accepted level ($P = 0.11$). This may result from the wider variation in the infralabials than the supralabials, a condition in the colubrids which is less marked in the rattlesnakes.

In all three colubrid cases both the supralabial and infralabial correlations are significantly different from the corresponding vertical or diagonal correlations, although in *annectens* the supralabials are just on the border line of a significant difference from the combined vertical correlation ($P = 0.059$). In this subspecies the vertical correlations are exceptionally high and differ significantly from the diagonal ($P = 0.0001 -$). In *perkinsi*, also, the combined verticals are significantly higher than the diagonals ($P = 0.037$), but not to so marked a degree.

The principal conclusion derived from both rattlesnakes and colubrids is that the horizontal, or bilateral, correlation is definitely higher than the vertical.

TABLE 16

Partial Correlations in Labials of Example Colubrids

	Unadjusted Correlations			Adjusted Correlations		
	Perkinsi	*Annectens*	*Concinnus*	*Perkinsi*	*Annectens*	*Concinnus*
Number of specimens	337	226	236	337	226	236
Horizontal Correlations						
Supralabials	0.422	0.402	0.290	0.408	0.381	0.289
Infralabials	0.585	0.622	0.425	0.589	0.618	0.421
Combined	0.508	0.521	0.359	0.504	0.509	0.357
Vertical Correlations						
Right	0.227	0.268	0.076	0.167	0.253	0.057
Left	0.151	0.257	0.067	0.091	0.230	0.066
Combined	0.189	0.263	0.071	0.129	0.242	0.062
Diagonal Correlations						
R. supra to L. infra	0.202	0.194	0.099	0.062	−0.058	0.052
L. supra to R. infra	0.116	0.182	0.024	−0.030	−0.054	−0.072
Combined	0.159	0.188	0.062	0.016	−0.056	0.010

There are, of course, cases of limited variability, in which horizontal labial correlations may be investigated by the use of a four-fold table. The following tabulation of the infralabials in 296 specimens of *Diadophis amabilis similis* from San Diego County illustrates such a situation:

Left Side	Right Side 7	8	Total
7	15	9	24
8	8	264	272
Total	23	273	296

This gives a tetrachoric coefficient of +0.89.

In most situations of this kind, where there is a sufficient variability to give some dispersion between two values, a third value will usually appear occasionally, thus preventing the use of a simple four-fold table.

This study suggests a query concerning the effect of correlation on the proportion of snakes which adhere to the mode in any combination of characters, a subject already mentioned in another connection (p. 15). For example, the labial mode in the Pierre series is 15-15 supralabials and 16-16 infralabials. If we assume the same total number of counts of 15 and

16 as were actually found in this series, but a purely random distribution of these counts, about one snake in 33—$(311 \times 312 \times 262 \times 241)/672^4$—would adhere to the mode. Actually there are 32 out of 672, or about one in 21, with 15-15 and 16-16 labials. We see that correlation has increased the frequency of what might be termed a normal arrangement.

Of course, if we introduce further modal specifications, so that our prairie rattlesnake fashion-plate must also have 27 scale rows, 177 ventrals (or 184 if a female), 26 subcaudals (20 if a female), 43 body blotches, and 10 tail rings (7 if a female), we greatly increase the rarity of specimens adhering to the mode. Taking the actual occurrence of modal counts in the Pierre series of 672 specimens, rather than the calculated frequency of the mode derived from the theoretical dispersion-curve of each character, we find that only one specimen in 33,729 would be a perfect fit. This calculation neglects the effect of correlation, which would somewhat raise the frequency of perfect fits, although not greatly, as several of these characters are uncorrelated. No specimen in our available series of 672 fits the modal specification in these characters; the nearest male misses the subcaudals, body blotches, and tail rings by one count each. A female is correct in all scale counts, but misses the body blotches by 3 and the tail rings by one. These figures give some indication of the wide variety of different ways in which these numerical characters may be combined.

BILATERAL UNBALANCE

Thus far, in our consideration of bilateral symmetry, we have treated concomitant variation specimen by specimen. Another phase of the same problem is the question of whether there is ever a net unbalance in the population, that is, a substantially higher average count on one side of the body than the other. The answer, surprisingly, seems to be definitely affirmative, there being differences of such magnitude as not to be attributable to the chance selection of the particular specimens comprising the available sample. Of course, small differences in averages are always to be expected, for it would be virtually impossible that the means of paired, but not perfectly correlated, variables should be equal; the question is: are such differences sufficient in magnitude to be worthy of notice and are they significant, i.e., not chargeable to the chance composition of the sample?

Table 17 presents the results of an investigation of the extent of net asymmetry in several of the characters of which the bilateral correlation was previously determined. The extent of divergence is expressed in terms of the coefficient of divergence, which is defined as the difference between the means, divided by half their sum. The significance of the difference is determined by the usual method of finding the ratio of the difference between the means, to the standard error of the difference, this being satisfactory where the samples are relatively large and the numbers in the two groups are equal, as in this case. I have used the formula for the standard error of the difference which includes the factor r, since in all

TABLE 17

Bilateral Unbalance in Scale Counts

Character	Species	Series	Number of Specimens	Mean			Standard Deviation		Significance of Difference*	Coefficient of Divergence†
				Right	Left	Difference	Right	Left		
Supralabials	*C. v. viridis*	Platteville	827	14.706	14.796	−0.090	0.854	0.929	0.005	0.61
	C. v. viridis	Pierre	672	14.829	14.924	−0.095	0.887	0.930	0.007	0.64
	P. d. perkinsi	Borego	337	6.139	6.104	0.035	0.434	0.424	0.16	0.57
	P. c. annectens	S. D. County	226	8.274	8.221	0.053	0.541	0.454	0.15	0.64
	T. s. concinnus	Northwest	236	7.127	7.157	−0.030	0.333	0.364	0.27	0.42
Infralabials	*C. v. viridis*	Platteville	827	15.896	15.838	0.058	1.046	0.973	0.11	0.37
	C. v. viridis	Pierre	672	15.862	15.766	0.096	0.994	1.005	0.016	0.61
	P. d. perkinsi	Borego	351	8.405	8.516	−0.111	0.655	0.653	0.0011	1.31
	P. c. annectens	S. D. County	226	12.832	12.898	−0.066	0.715	0.687	0.10	0.51
	T. s. concinnus	Northwest	236	9.809	9.780	0.029	0.453	0.463	0.35	0.30
Canthals	*C. v. viridis*	Pierre	377	2.366	2.329	0.037	0.539	0.557	0.17	1.58
Loreals	*P. d. perkinsi*	Borego	355	2.144	2.186	−0.042	0.609	0.645	0.134	1.94
Preoculars	*T. hammondii*	S. D. County	398	1.726	1.749	−0.023	0.468	0.462	0.31	1.32
Postoculars	*P. c. annectens*	S. D. County	265	3.577	3.615	−0.038	0.686	0.691	0.28	1.06
Ocular ring	*P. d. perkinsi*	Borego	352	7.625	7.619	0.006	0.627	0.625	0.86	0.08
First temporals	*L. g. californiæ*	S. D. County	539	1.494	1.447	0.047	0.515	0.512	0.009	3.20
	P. d. perkinsi	Borego	353	2.663	2.490	0.173	0.535	0.569	0.0001−	6.71
Second temporals	*P. d. perkinsi*	Borego	351	3.294	3.359	−0.065	0.625	0.633	0.10	1.95
Total temporals	*P. d. perkinsi*	Borego	350	5.943	5.903	0.040	0.819	0.870	0.45	0.68
Body rings	*L. g. californiæ*	S. D. County	100	26.800	27.030	−0.230	2.195	2.220	0.19	0.85
Lamellae, 4th toe	*C. t. tessellatus*	Gila Valley	133	20.075	20.037	0.038	1.070	1.022	0.58	0.19
Femoral pores	*C. t. tessellatus*	Gila Valley	154	21.071	21.377	−0.306	1.691	1.740	0.004	1.44
Costal scutes	*L. olivacea*	Ceylon	378	6.749	6.778	−0.029	0.930	0.988	0.52	0.43

* Calculated by the formula which takes account of *r* in determining the standard error of the difference between the means.

† Defined as the difference between the means divided by half their sum, expressed in per cent.

cases here under consideration there is correlation between the paired variables. [13]

It will be observed in Table 17 that, in several instances, there is a significant difference between the counts on the two sides, using $P = 0.05$ as the significance level. Yet in some of these cases the coefficient of divergence shows the difference to be so small as to be of little practical interest. In four cases the divergence is both significant and exceeds 1 per cent; these are *P. d. perkinsi* infralabials and first temporals; *L. g. californiæ* first temporals; and *C. t. tessellatus* femoral pores. The *Phyllorhynchus* case seems so remarkable that it warrants further investigation. Here we have a coefficient of divergence in the infralabials of 1.31 per cent and in the first temporals of 6.71 per cent, and both are highly significant. The first temporals are higher on the right than on the left; the reverse is true of the infralabials. The first temporals were defined as the scales touching the oculars in the area between the supralabials and the parietals.

In order that these differences could not be charged to some source of consistent error, such as the angles at which the heads were examined on the two sides, all specimens were re-examined by a single observer (Charles E. Shaw) using a binocular microscope, and the results given are premised on this verification.

The specimens of *Phyllorhynchus* hitherto discussed were collected in the Borego area of eastern San Diego County. Some 43 specimens are available from the desert bordering the Coachella Valley in Riverside County, some miles to the northeast of the San Diego County locality. An investigation of these shows that the lateral divergence evident in the Borego specimens is continued in Riverside in one of the two characters. The unbalance in the infralabials is reduced to insignificance in the Coachella series, but the discrepancy in the first temporals is continued in the Coachella specimens; the coefficient of divergence is 5.93 per cent, with the right temporals exceeding the left, as in San Diego County. I think we may conclude that it is possible for a definite lateral unbalance in scalation to become established in a local homogeneous population and occasionally to be carried into an adjacent population.

INTERCHARACTER CORRELATIONS IN SCALATION

Thus far we have discussed bilateral correlation, involving the reciprocal relationship between the values of the same variable on opposite sides of the body. We now proceed to investigate correlations between pairs of different characters. As before, the study, for the present, will be limited to territorially homogeneous series, to avoid introducing ecological complications and the effects of clines, which tend to produce correlations that might be absent in homogeneous groups. Initially the investigation will be limited to characters of scalation, to avoid the problems introduced by ontogenetic change.

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[13] $\sigma_{1-2} = (\sigma_1^2 + \sigma_2^2 - 2r\sigma_1\sigma_2)^{1/2} N^{-1/2}$

I shall first discuss the correlations found in a number of pairs of characters in the rattlesnakes, using, primarily, examples derived from the Platteville *viridis* series. However, with respect to some of the more important pairs, confirmatory evidence will be sought in other series; and in the case of some characters, in which species other than *C. viridis* show wider dispersions (for example, the scales before the pit in *C. ruber*), the illustrations will be drawn from such other species. These studies will be followed by similar investigations of the more limited characters available in the colubrids and other non-crotalids.

The rattlesnake scale-character combinations are, in fact, so extensive that it appears desirable, for the sake of clarity, to divide the correlations investigated into three groups: (1) paired body scale-counts; (2) paired head scale-counts; and (3) one body count correlated with one head count. The possible combinations are so numerous that no attempt will be made to check them all. In the Platteville series alone, there are some 62 combinations possible in ten characters, two of which (ventrals and subcaudals) have marked sexual dimorphism, thus requiring the sexes to be treated separately. Other species of rattlers, having variable scale-groups which are constant in *viridis*, would greatly increase the number of these possible pairs. It is obviously necessary to restrict the investigation to a few combinations, such as those involving particularly important scale-counts, or others in which the relationship appears of special interest.

The first group of combinations, that of body scale counts, includes pairs of the following: dorsal scale rows, ventrals, and subcaudals. The first may be further subdivided into counts at various locations on the body, such as at the neck, at midbody, just anterior to the vent, and at the center of the tail. Points of suppression of incomplete rows may be included. The ventrals and subcaudals are sexually dimorphic, which requires segregation of the sexes whenever either of these characters is involved.

I may say, in passing, that I did give consideration to the possible presence of sexual dimorphism in the dorsal scale rows, but found the differences small, although in some instances significant. The maximum coefficient of divergence only slightly exceeds one per cent. The males in some cases average more rows than the females, whereas in others the contrary is true. While it was decided to make no sexual segregation, as far as scale rows are concerned, the results of calculations on several series are given, as a matter of interest, in Table 18. It will be noted that some of the series involved in these tests are not territorially restricted. This is of no importance in a difference test, provided the sexes are represented with substantially equal proportions in the several areas included. Furthermore, sexual dimorphism in scale rows, even if important, would not affect the correlation coefficients derived from the dorsal-ventral or dorsal-subcaudal pairs, as the sexes are treated separately anyhow, but it would affect such correlations as dorsals-supralabials, dorsals-canthals, etc. A similar investi-

TABLE 18

Sexual Dimorphism in Dorsal Scale Rows

Species	Area or Series	Males			Females				
		N	*M*	σ	*N*	*M*	σ	*P*	*CD*
C. cinereous	All areas	386	25.736	1.011	285	25.498	0.913	0.0017	0.93
C. cinereous	Arizona	124	25.919	0.964	98	25.646	0.914	0.029	1.06
C. lucasensis	Cape San Lucas	168	27.398	0.832	125	27.688	1.169	0.019	−1.05
C. ruber	All areas	176	28.602	0.960	138	28.667	1.002	0.56	−0.23
C. scutulatus	All areas	239	25.510	1.031	144	25.578	1.194	0.58	−0.26
C. v. viridis	Platteville	441	26.531	0.999	392	26.390	1.007	0.044	0.53
C. v. viridis	Pierre	342	26.506	1.031	331	26.535	1.011	0.71	−0.11
C. v. oreganus	San Diego Co.	292	25.376	0.881	278	25.507	0.880	0.077	−0.51
C. cerastes	All areas	193	21.979	1.138	160	22.163	1.134	0.13	−0.83

NOTES: All standard deviations are the optimum estimates of the population parameters. The value of *P* gives the significance of the difference between the means, in terms of the probability that the samples were drawn from the same population. The coefficient of divergence is the difference between the means divided by half their sum, expressed as a percentage. Where the value is negative the females exceed the males.

gation was made to determine possible sexual dimorphism in the labials, with results no more consistent or important than those of the dorsal scale rows.[14]

Returning to the correlations between body characters, the first investigated was that between dorsal scale rows and ventrals, the statistics of the two large series of *C. v. viridis* being as follows:

	Platteville Series			Pierre Series		
	N	*r*	*P*	*N*	*r*	*P*
Males	443	0.014	0.76	342	0.026	0.63
Females	392	0.024	0.63	332	0.030	0.59

These results are consistent in indicating a probable absence of correlation.

The existence of correlation in these relatively important characters was investigated in two other series, the San Lucan *C. lucasensis* and the San Diego County *C. ruber*, using a somewhat different method, that is, by determining the mean ventral count for each value of the dorsals. The results are as follows:

	Number of Specimens			Mean Ventrals		
Scale rows	27	29	31	27	29	31
C. ruber, males	18	105	6	196.28	193.64	193.60
females	12	74	6	199.08	196.57	197.17
C. lucasensis, males	132	32	....	187.32	188.81	....
females	79	31	....	193.23	193.23	....

There is evident here no consistent trend, there being some indication of a negative correlation in *ruber* and a positive in *lucasensis* males, but neither is significant. As is usually the case in dealing with scale rows, the investigation is handicapped by the limited variation in this character; that is, the material is heavily concentrated in one category, 29 rows in the case of *ruber* and 27 in *lucasensis*. Furthermore, the distribution is clearly not normal, owing to the concentration on odd numbers, so that the use of the coefficient of correlation is not entirely justified. However, the conclusion may be drawn that there is no correlation between dorsal scale rows and ventrals in these typical species of rattlesnakes.

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[14] See Klauber, 1943a, Table 2, p. 13.

Only one series, the Platteville *viridis,* was investigated for a correlation between scale rows and subcaudals. Again no significant correlation was found, the figures being as follows:

	N	*r*	*P*
Males	441	0.052	0.27
Females	390	−0.063	0.22

The remaining correlation to be tested between these body characters is that of ventrals to subcaudals. This is not as important among the rattlers as the colubrids, because of the foreshortened tail of the former to accommodate the rattles, and it will, therefore, be given a more complete treatment when the colubrids are discussed. However, an investigation has been made on a number of rattlesnake series, with results shown in Table 19.

TABLE 19

Correlation between Ventral and Subcaudal Scales in Rattlesnakes

Species	Series	Males			Females		
		N	*r*	*P*	*N*	*r*	*P*
C. lucasensis	San Lucan	150	0.193	0.018	117	0.076	0.41
C. ruber	S. D. County	153	0.076	0.35	100	−0.084	0.41
C. v. viridis	Platteville	441	0.082	0.085	392	0.004	0.94
C. v. viridis	Pierre	341	0.034	0.53	331	0.054	0.33
C. v. viridis	Bonesteel	45	0.257	0.088	34	0.037	0.84
C. v. viridis	Timberlake	52	0.245	0.080	28	0.125	0.51
C. v. viridis	Series combined	879	0.082	0.015	785	0.031	0.39
C. v. oreganus	S. D. County	279	0.235	0.0001	287	0.097	0.102
C. v. oreganus	Pateros	324	0.182	0.001	288	0.040	0.50
C. v. oreganus	Series combined	603	0.207	0.0001−	575	0.068	0.103

It will be noted that the female correlations are quite low and none is significant. However, as only one out of eight is negative, I am inclined to think that there may be a very slight positive correlation. As to the males, there appears no question but that there is a positive correlation in *oreganus,* the 95 per cent confidence limits for the two series combined being 0.130 to 0.289. The combined *viridis* groups indicate a lower coefficient, as does *lucasensis* also, and the *ruber* sample shows no significant correlation. It may be concluded that correlations of about +0.2 will be found between ventrals and subcaudals in the males of many rattler species.

Another possible set of correlations, involving only body scales, is that of the scale rows at different parts of the trunk. These are of interest, as the complete scale row formulas have been often used in classification since Ruthven's pioneer work on the garter snakes in 1908.[15] Taking *C. ruber* as the best available species, because of its high dispersion in dorsal scale

[15] See Philip J. Clark and Robert F. Inger, Copeia, 1942, pp. 163 and 230.

rows, I have determined the correlations between the scale rows, in 100 specimens from San Diego County, at four different points: At the neck (narrowest point); at mid-body, or slightly anterior thereto, where the maximum is reached; just ahead of the anus; and at the mid-point of the tail. The results in terms of r follow:

	Mid-body	Anus	Mid-tail
Neck	0.215	−0.049	−0.022
Mid-body	.....	−0.069	0.154
Anus	.....	.....	0.210

Only two of these correlations are significant, the neck to mid-body ($P = 0.032$) and the anal to mid-tail ($P = 0.036$). I was rather surprised to find the other contiguous pair (mid-body to anal) without significance. These correlations might be adjusted by the method of partial correlation, but this is not worthwhile in view of the low correlations found.

We now proceed to the second group of characters whose interrelations are to be tested, namely, those involving only head scales.

The following remarks are explanatory of some of the terms used: The scales on the crown are the total scales on the top of the head anterior to a line connecting the forward ends of the supraoculars. These scales, also referred to as scales before the supraoculars, are clearly defined in some species, such as *C. scutulatus;* however, they can hardly be considered an important character in *C. ruber,* or *C. viridis,* since it is often impossible to determine just where, in the frontal area, the count should stop. The intersupraoculars comprise the minimum series of scales bridging the gap between the supraoculars. The internasals are the scales contacting the rostral between the nasals, regardless of size. The canthals are the scales along the upper edge of the canthus rostralis, between the internasals and the supraoculars. The scales before the pit are those anterior to the pit which lie above the supralabials and below the nasals, loreals, and lower preoculars. The scales around the supraoculars are those touching that scale, from the postcanthals to the postoculars, but including neither of these.

When a scale character which is present separately on each side of the head (*e.g.*, loreals), is to be paired with another also present on each side, the two sides are tabulated separately. On the other hand, where such a dual character is to be paired with another, of which only one count per specimen is available (*e.g.*, intersupraoculars), then the sum of the two counts of the first character (one from either side), is treated as a single variate.

It is to be remembered that the supralabial-infralabial relationship has already been covered in the discussion of bilateral symmetry; this will not be repeated.

The correlations of a number of head characters, taken in pairs, are set forth in Table 20. I have selected, particularly, pairs in which, because of contiguity, some correlation might reasonably be expected.

TABLE 20

Correlations between Head Scales in *Crotalus*

Species	Series	Paired Characters	*N*	*r*	*P*
C. v. viridis	Platteville	Supralabials (sum) and internasals	400	0.094	0.061
C. v. viridis	Platteville	Supralabials (sum) and scales of crown	831	0.135	0.0001
C. v. viridis	Pierre	Supralabials (sum) and scales of crown	100	0.070	0.70
C. v. viridis	Platteville	Supralabials (sum) and intersupraoculars	830	0.113	0.0001
C. v. viridis	Pierre	Supralabials (sum) and intersupraoculars	100	0.247	0.009
C. scutulatus	Mojave	Supralabials (sum) and intersupraoculars	100	0.086	0.39
C. ruber	San Diego County	Supralabials and scales before pit	200	0.021	0.98
C. v. viridis	Platteville	Infralabials (sum) and scales of crown	832	0.125	0.0003
C. v. viridis	Platteville	Infralabials (sum) and intersupraoculars	827	0.001	0.98
C. ruber	San Diego County	Infralabials and gulars between commissure and ventrals	200	0.266	0.0002
C. v. viridis	Platteville	Internasals and canthals (sum)	833	0.164	0.0001–
C. v. viridis	Platteville	Internasals and intersupraoculars	831	0.107	0.002
C. ruber	San Diego County	Canthals (sum) and intersupraoculars	100	–0.052	0.61
C. ruber	San Diego County	Canthals (sum) and scales contacting rostral	100	0.349	0.0003
C. ruber	San Diego County	Canthals and scales before pit	200	0.150	0.034
C. ruber	San Diego County	Canthals and loreals	200	0.059	0.41
C. v. viridis	Platteville	Scales of crown and intersupraoculars	830	0.415	0.0001–
C. v. viridis	Pierre	Scales of crown and intersupraoculars	671	0.315	0.0001–
C. scutulatus	Arizona	Scales of crown and scales contacting supraoculars (sum)	100	0.305	0.002
C. ruber	San Diego County	Scales of crown and scales contacting supraoculars (sum)	100	0.013	0.90
C. ruber	San Diego County	Intersupraoculars and scales contacting supraoculars (sum)	100	0.323	0.001
C. ruber	San Diego County	Intersupraoculars and scales contacting rostral	100	0.428	0.0001–
C. ruber	San Diego County	Scales before pit and loreals	200	0.150	0.034

Of the 23 pairs tested, 7 show no significant correlation; of those which remain, all are positive and 6 have values of r in excess of 0.3. These are the canthals and the scales contacting the rostral, the intersupraoculars and the scales contacting the supraoculars, the intersupraoculars and the scales contacting the rostral in C. *ruber;* the scales of the crown and the scales contacting the supraoculars in C. *scutulatus*; and the scales of the crown and intersupraoculars in the two series of *viridis*. With one exception (intersupraoculars and scales contacting the rostral) these pairs comprise contiguous groups of scales. It is naturally to be expected that such a correlation would be evident—that individual snakes with larger (and therefore fewer) scales than the average on one part of the head, would also have larger scales on other parts. We conclude that a moderate correlation is evident between many pairs of head scales.

We come now to the final group of paired rattlesnake characters—those in which one of each group is on the body, the other on the head. The possible combinations are very numerous and only four will be tested, these being the relations between scale rows or ventrals on the one hand, and supra- or infralabials on the other.

I have previously indicated that the dorsals of snakes may either be studied as such, or as series of laterals.[16] In the present instance, since I use as one variate the sum of the supralabials, or the sum of the infralabials, I shall also take the total dorsals, rather than the laterals, even though the former are not normally distributed (because of the predominance of odd totals) while the latter approach normality.[16] For that matter, there seems to be no correlation between the unbalance in the laterals and unbalance in the labials, as shown by the contingency tables derived from the Platteville series of *viridis*, and set forth in Table 21. It requires no computation to show that no significant correlation is indicated in this table.

TABLE 21

Platteville Series of *Crotalus v. viridis*:
Correlation of Unbalance in Laterals and Labials

Distribution of Supralabials	Distribution of Laterals		
	Equal	Unequal	Total
Equal	394	27	421
Unequal	382	24	406
Total	776	51	827
Distribution of Infralabials			
Equal	388	21	409
Unequal	388	30	418
Total	776	51	827

[16] Bull. Zool. Soc. San Diego, No. 17, p. 8, 1941.

Proceeding with the investigation of the correlation between scale rows and labials, five homogeneous series of rattlesnakes were investigated, with the results set forth in Table 22. There seems no doubt that there is a moderate correlation between scale rows and labials in these snakes, for only in the *nigrescens* series is none evident. If the series which I have tested be combined, the weighted average correlation coefficients are, for the scale rows to supralabials, 0.175; and, to the infralabials, 0.164. The difference between the two is not significant ($P = 0.70$). The 95 per cent confidence limits are 0.133 to 0.217, and 0.121 to 0.206, respectively.

TABLE 22

Correlations between Scale Rows and Labials in *Crotalus*

		Supralabials			Infralabials		
Species	Series	*N*	*r*	*P*	*N*	*r*	*P*
C. m. nigrescens	Zacatecas	92	0.158	0.124	93	0.022	0.833
C. lucasensis	San Lucan	285	0.154	0.009	289	0.254	0.0001
C. v. viridis	Platteville	833	0.188	0.0001–	830	0.190	0.0001–
C. v. viridis	Pierre	673	0.165	0.0001–	672	0.113	0.003
C. c. laterorepens	San Diego-Imperial Cos.	150	0.154	0.051	147	0.151	0.064
Series Combined		2033	0.175	0.0001–	2031	0.164	0.0001–

A test was made on the correlation between ventrals and labials in the Platteville series of *C. v. viridis*. Because of sexual dimorphism in the ventrals, the sexes must be treated separately. The results were as follows:

	Males			Females		
	N	*r*	*P*	*N*	*r*	*P*
Supralabials	441	–0.016	0.74	391	0.053	0.28
Infralabials	440	–0.008	0.87	390	0.131	0.009

A significant correlation is evident in only one of the four pairs, the ventrals-infralabials in the females. To verify this result the same pair of characters was then tested in three other series of *C. v. viridis*, but none proved significant, the results being:

Series	*N*	*r*	*P*
Pierre	279	0.003	0.97
Bonesteel	34	–0.215	0.22
Timberlake	44	0.054	0.73

It may therefore be concluded that the significant result in the Platteville series is a situation out of the ordinary, and usually no real correlation exists between the ventrals and either supralabials or infralabials, in territorially homogeneous groups of *Crotalus v. viridis*.

Summarizing the intercharacter correlations in the rattlesnakes we find no indication of correlation between scale rows and ventrals. Correlation is occasionally present between ventrals and subcaudals, especially in the males. Significant correlations are often found between different series of head scales, particularly contiguous groups. A correlation is evident between scale rows and labials, but not between ventrals and labials.

We now turn to some similar examples of correlations between different scale-count characters in forms other than rattlesnakes. In general, these, especially colubrids, offer a less fruitful field, since there are fewer variable series on the head to investigate; and the variations in many of the characters (scale rows and labials, for example) are held within narrower limits than in the genus previously discussed. Only the subcaudals are a more variable character in most colubrids than in the rattlesnakes, whose tails are shortened to accommodate the rattles. As was the case in the previous discussion, the present investigation is limited to homogeneous series from restricted localities, to avoid the possible effects of territorial—but nevertheless intrasubspecific—variation.

The most important correlation to be investigated is that between ventrals and subcaudals. Certain assumptions might lead one to expect a correlation between these characters. From one viewpoint it would be logical to infer a positive correlation, since, whatever the cause of a high number of ventrals in a particular snake, the same cause might be expected to produce a higher than average number of subcaudals, thus resulting in a positive correlation. On the other hand, one might presume a tendency toward a constant total number of scales on the ventrum; that is, ventrals plus subcaudals. If this were the case, a high number of ventrals would tend to reduce the number of subcaudals, and vice versa. Such an effect would lead to a negative correlation.

In an investigation of the ventral-subcaudal correlation, it is important that the sexes be segregated, if sexual dimorphism be present, which is usually the case. The male subcaudals in most genera are higher than in the females, and if the sexes are not segregated (or many specimens are inaccurately sexed) and the females have more ventrals than the males, as for example, in *Lampropeltis* and *Phyllorhynchus*, then a negative correlation will be in evidence, even if the sexes separately manifest no correlation. Similarly, if the males have more ventrals than the females, as in *Thamnophis* and *Rhinocheilus*, then combining the sexes will produce a positive correlation. On the other hand, in genera in which there is little or no difference between the sexes in ventrals (but sexual dimorphism be present in the subcaudals) inaccurate sexing may tend to reduce the correlation coefficient below its true value.

One of the best ways to pick up questionable cases of sexing is to enter both sexes in a single ventral-subcaudal correlation table, using two colors to distinguish the sexes. The area of overlap (if there be one) will be readily apparent, and doubtful cases will stand out prominently—much

more so than if the two characters be investigated separately. This is a matter of sufficient interest to warrant the presentation of Tables 23 to 25 showing such correlations for three typical situations.

Table 23 covers a case in which the males exceed the females in subcaudals, but have fewer ventrals, this being the more usual situation in colubrid genera. The particular subspecies selected, *Phyllorhynchus decurtatus perkinsi*, is notable for the wide divergence between the sexes (this is, in fact, a generic characteristic), so that there is no overlap of the areas which they occupy in the table. However, it is to be observed that there would be an overlap were either character considered separately, so the value of such a dual tabulation becomes apparent. It will be noted that, were there any inaccurate sexing, the misplaced specimens of either sex would fall along a diagonal line from upper right to lower left, the improperly sexed specimens producing a salient into the area occupied by the other sex. The result would be a fictitious negative correlation, higher values of either character matching with lower values of the other. Whether there is any correlation in *Phyllorhynchus* when the sexes are properly segregated, as in Table 23, will be discussed later.

Of course, the chance of inaccurately sexing a *Phyllorhynchus*, without discovering the fact as soon as the results are tabulated, is remote; unfortunately, few genera have so marked a sexual divergence. Table 24 shows the same data for a series of *Diadophis amabilis similis* from San Diego City and its environs. This series is restricted to a small area around San Diego Bay; it was found that when specimens from the inland valleys and foothills were included, territorial differentiation became evident, thus interfering with the homogeneity necessary for this particular investigation.

In Table 24 it will be observed that there is considerable overlap between the sexes and more scattering is evident than in Table 23. A few specimens are decidedly aberrant. In a situation such as this, a special effort must be made to avoid the inaccurate sexing of specimens falling in the intermediate area in the table, for mere location is no longer a sure indication of faulty sexing, as was the case with *Phyllorhynchus*.

Table 25 shows the same data covering a series of *Thamnophis hammondii* from San Diego County. In this species the males exceed the females in both ventrals and subcaudals, so that the relative positions of the two groups in the table are different from those of the two previous tables. It will be readily apparent that inaccurate sexing in such a case would tend to result in a fictitious positive correlation, for improperly placed individuals in this case will cause salients along the upper-left to lower-right diagonal.

Ordinary errors of counting will also produce inaccurate results; yet in the long run they will be less serious than errors in sexing, since they are likely to be of a random nature and will tend to cancel each other, which is not true of errors in sexing. Also, a few freak specimens may quite materially change the correlation coefficient. For this reason, if high

TABLE 23

Borego Series of *Phyllorhynchus decurtatus perkinsi*:
Correlation of Ventrals and Subcaudals, showing Sexual Divergence.

Ventrals	Subcaudals 24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	Total Males	Total Females
164															1					1	
165																					
166																					
167													1	1		1				3	
168													2				1			3	
169										1	1	1	3	3	3	1				13	
170												2	3	2	3	1	1		1	13	
171										1	1		2	3	3	2	2	1		15	
172									1			1	2	6	1	1	2	1	1	16	
173												1	3	4	6	4	2	1		21	
174										1	1		4	2	6	5	6	1		26	
175											2		2	7	4	6	5		1	27	
176													5	5	2	4	4		1	21	
177													2	3	4	3	2	3		17	
178												1	4	3	3	4	1	1		17	
179															5	2	1	1		9	
180													1				1			2	
181					1	1									1	1				2	2
182				1		2	1								1	1	1			3	4
183			1	1		1	2	1													6
184				1	3	2				1											7
185	1			2	1	1	1	1	4	1											12
186			1	4	2	6	1	1													15
187			1	2	7	6	2	2	3												23
188		1			3	10	5	2	1	1											23
189		1	1		3	1		3	2	1											12
190			1		1	2	6		2		1										13
191				1	2	2	3	2													10
192					1	1	2														4
193			1		2	1				1											5
194			1						1												2
195						1	1	1	1												4
196							1														1
Total Males									1	3	5	6	34	39	43	36	29	9	4	209	
Total Females	1	2	7	12	26	37	25	13	14	5	1										143

TABLE 24

Series of *Diadophis amabilis similis* from Vicinity of San Diego: Correlation of Ventrals and Subcaudals, showing Sexual Divergence.

Ventrals	Subcaudals 46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	Total Males	Total Females
178													1									1	
179																							
180																							
181																	1					1	
182												1										1	
183																							
184										1		2										3	
185										1	1	1	1									4	
186										1	1	2	1	2			1					8	
187										1	2		2		1	1		1				8	
188									1		2	5			1	1	1					11	
189								1			2	2	1		2	1	1					9	1
190											1		3	1	3		1	3				11	1
191							1							3			1	2	1			7	1
192										1	3	1		3	2		2					11	1
193		1								1			1	2		1					1	6	1
194							1	1			1	2	4	1	5			1				16	
195				2					1		1	1		3	1	1						5	5
196						2	1		1	11						1						3	4
197				1		1	1		1	1	1												6
198			1	2		2	2	2				13										3	10
199							1	1	1	1	1												5
200				1		1	2		1		1		1		1								8
201					1	2	2	1	1	2													9
202	1		1			1	3	2	1	1	2												12
203					2	1			1														4
204	1						1	2	2		2				1								9
205						1	2			1	1												5
206						2		1	2														5
207						1	1	1	1	1													5
208						1				1			1										3
209									1														1
210								1															1
211																1							1
212																							
213																							
214																							
215																1							1
Total Males							1	1	2	7	12	18	14	15	15	6	8	7	1		1	108	
Total Females	2	1	2	6	3	15	17	12	13	9	10	3	2		2	2							99

TABLE 25

San Diego County Series of *Thamnophis hammondii*:
Correlation of Ventrals and Subcaudals, showing Sexual Divergence.

	Subcaudals																										
Ventrals	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	Total Males	Total Females
148										1																		1
149																												
150																												
151																												
152																												
153											1		1															2
154									1	1																		2
155					1	1		1																				3
156	1						1		1		1	1	1															6
157						2	1	2	2	1		2																10
158				1		1	2		5	2	2	2		1														16
159				1		3		1	2	2	3	2	1	11													1	16
160			1			2	3	3	2	3		1	4					1									1	19
161				1	2	2	2	4	3	4	3	1		1								1					1	23
162	1			1	4	1	3	2	3	4	2	3		1	1					5							5	26
163			1	1		1	2	1	3	2	1	1					2		1		2		3	1			9	13
164								2	4	2	2	1	1	1		1	3	1	2	1	1	1		3			14	12
165								1	2	2		1		1	1	1	3	2	1	2	1	1	1				13	7
166										1				1	1	3	2		5	3	2	2	1	2			22	1
167				1	1		1			1					1	3	5	3	5	4	3	1	2				27	4
168								1								2	1	2	2	6	3	2		1			19	1
169												1	1	1	1	3	4	6		1	5	2	3			1	29	
170														1		2	1	1	2		2		2				11	
171																1	3	1		2	1	1				1	10	
172											1								2	1	2	1					7	
173										1								1	1	1		1		1			6	
Total Males										1	1	1	2	4	4	16	24	18	21	26	22	13	12	8		2	175	
Total Females	2		2	6	8	13	15	18	28	26	15	15	7	6	1													162

accuracy is desired, it may be advisable to omit juveniles, for such freaks are usually juveniles which would not survive. Whether they should be omitted depends on the purpose of the test. [17]

These tables also illustrate a method whereby it may be possible to segregate more completely two forms (or the sexes of a single form), by using two characters, where a single character alone would not involve so definite a differentiation. For example, from Table 23 we observe that the ventrals of the males vary from 164 to 182, and the females from 181 to 196; and the subcaudals 32 to 42, and 24 to 34, respectively. Thus, both sets of characters overlap, and, were more specimens available, these overlaps would tend to increase. However, if we combine the characters by taking the differences between the ventrals and subcaudals, we find that the ventrals-less-caudals in the males vary from 126 to 144 and in the females from 151 to 168. Thus there is no overlapping, and there would probably be little or none even if the number of available specimens was considerably increased.

Similarly, in Table 24 the ventral and subcaudal overlaps separately are each about half the total range: ventrals, males, 178 to 195; females 189 to 215; subcaudals, males, 52 to 66; females 46 to 61. But the differences show much less overlap: males, 119 to 142; females, 134 to 158. Furthermore, the number of specimens falling within the questionable overlapping range will be considerably reduced. To secure this more efficient combined result differences should be used if the correlation (in the combined forms) is negative, as in Tables 23 and 24; or sums should be employed if the correlation is positive, as in the case of *Thamnophis hammondii*, Table 25. For examples of the practical use of combined characters to sharpen differences see Van Denburgh, 1920, and Hubbs, Hubbs and Johnson, 1943.

Table 26 sets forth the results of determinations of the correlation between ventrals and subcaudals in twenty-four territorially homogeneous series of snakes, involving, as the sexes are treated separately, forty-eight separate lots. Of these it will be noted that there is a significant correlation (using $P = 0.05$ as the upper limit of significance) in only eight out of forty-eight series, these being *D. a. similis* females, *P. d. perkinsi* males, *G. nasalis* females, *T. l. varians* males, both sexes of *S. o. annulata*, *S. m. linearis* females and *A. m. mokeson* females. Even where correlation is present it is relatively low (about 0.25 or below) except in three instances. It is consistent only in *S. o. annulata*, for this is the only species in which correlation is evident in both sexes. This may result from the beginning of a trend toward territorial differentiation. For, as I shall subsequently show, such differentiation does produce correlation in territorially widespread groups; and this small snake may show differentiation, even in as limited a territory as desert San Diego County.

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[17] The detection of aberrants and errors by a graphic study of tail lengths has been discussed in a paper on that subject. Bull. Zool. Soc. San Diego, No. 18, p. 15. Ventral-caudal tables may be co-ordinated with such investigations, as a double check on aberrants, although some cross-correlation is to be expected.

TABLE 26

Correlation between Ventrals and Subcaudals in Homogeneous Series of Snakes.

Series	Sex	*N*	*r*	*P*
Adelphicos quadrivirgatus sargii	M	76	0.173	0.14
(Volcan Zunil, Guatemala)	F	57	0.019	0.89
Geophis nasalis	M	113	0.109	0.90
(Volcan Zunil, Guatemala)	F	85	0.493	0.0001–
Diadophis amabalis similis	M	108	0.076	0.44
(Vicinity of San Diego)	F	99	0.234	0.02
Diadophis punctatus arnyi	M	233	0.010	0.13
(Tulsa, Oklahoma)	F	148	0.063	0.45
Aspidura guentheri	M	63	0.012	0.93
(Annasigala Estate, Ceylon)	F	58	0.113	0.40
Uromacer catesbyi	M	66	0.189	0.13
(Hispaniola)	F	7	0.328	0.47
Phyllorhynchus decurtatus perkinsi	M	209	0.219	0.0015
(Desert San Diego County)	F	143	0.115	0.165
Elaphe rufodorsata	M	33	0.205	0.25
(Soochow, China)	F	88	–0.010	0.95
Arizona elegans occidentalis	M	49	0.085	0.50
(Desert San Diego County)	F	22	–0.333	0.13
Pituophis catenifer annectens	M	114	0.086	0.36
(Coastal San Diego County)	F	119	–0.147	0.11
Lampropeltis getulus californiae	M	73	–0.023	0.85
(Coastal San Diego County)	F	75	0.086	0.46
Toluca lineata varians	M	70	0.259	0.031
(Acultzingo, Veracruz)	F	74	0.085	0.47
Sonora miniata linearis	M	41	–0.078	0.63
(Laguna Dam Island, Imperial County)	F	55	0.379	0.006
Sonora occipitalis annulata	M	141	0.267	0.0015
(Desert San Diego County)	F	67	0.274	0.023
Thamnophis hammondii	M	175	–0.053	0.48
(San Diego County)	F	162	–0.044	0.58
Thamnophis ordinoides ordinoides	M	77	0.032	0.78
(Vicinity of Portland, Oregon)	F	82	0.211	0.06
Thamnophis ordinoides biscutatus	M	112	0.104	0.27
(Klamath Falls, Oregon)	F	105	0.089	0.37
Thamnophis radix	M	104	0.065	0.51
(Cook County, Illinois)	F	72	0.076	0.52

TABLE 26
(Continued)

Series	Sex	*N*	*r*	*P*
Conopsis nasus	M	58	0.086	0.52
(Alvarez, San Luis Potosí)	F	66	0.036	0.77
Hypsiglena ochrorhynchus	M	35	0.281	0.10
(Coastal San Diego County)	F	27	−0.221	0.27
Micrurus nigrocinctus nigrocinctus	M	44	0.063	0.68
(Panama and Canal Zone)	F	38	0.123	0.47
Micrurus nigrocinctus divaricatus	M	44	0.293	0.054
(Honduras)	F	36	0.250	0.14
Agkistrodon mokeson mokeson	M	176	0.128	0.09
(Kansas)	F	134	0.205	0.017
Bothrops insularis	M	94	−0.103	0.32
(Queimada Grande Island, Brazil)	F	106	0.055	0.58

NOTE:—For the sources and other data on these series of snakes see Bull. Zool. Soc. San Diego, No. 18, p. 21, 1943.

Table 26 indicates that correlation between ventrals and subcaudals is neither usual nor, when it does occur, high, in the colubrid and other genera represented. It will be recalled that there was no correlation in the majority of rattlesnake series tested, although a slight correlation was indicated in some, especially the males. However, so brief a survey is not to be considered a proof that it may not be present to a considerable degree in some genera. In fact, it is to be noted that only 9 out of the 48 series show a negative correlation. I think we may conclude, although few of the series show significant correlations in themselves, there is a slight positive correlation between ventrals and subcaudals; but in any event the association is low in value and its presence can be demonstrated only in large series.

It should be emphasized that this statement has reference to homogeneous series; correlation is to be expected in collections representing entire species, or where sexual dimorphism is neglected. As an example, we may observe the effect of neglecting sexual dimorphism in a study of the ventral-subcaudal relationship. The following results were secured from two small samples of *Phyllorhynchus browni browni* from the vicinity of Tucson, Arizona, first treating the sexes separately, then combining them:

	N	*r*	*P*
Males	13	+0.095	0.76
Females	13	−0.010	0.97
Sexes Combined	26	−0.898	0.0001−

We see that separately the sexes show a very low and non-significant correlation between the ventrals and subcaudals, but when combined the correlation is high and significant. As is the case when the females have more ventrals and fewer subcaudals than the males, the correlation in the heterogeneous group is negative.

As an example of territorial heterogeneity, we take ten male specimens of *Hypsiglena ochrorhynchus* from the coastal slope in San Diego County, and a similar number from the desert slope. The results are as follows:

	N	*r*	*P*
Coastal specimens	10	+0.090	0.81
Desert specimens	10	+0.221	0.54
Both series	20	+0.793	0.0001–

Again we see that, while no significant correlation is evident in either homogeneous sample separately, the heterogeneous combination shows a high and significant positive correlation, for the desert specimens are higher than the coastal in both ventrals and subcaudals.

The question may be asked: Why should one be critical of these results of heterogeneity, since the fact remains that correlation is proven, which was the original purpose of the inquiry? However, it should be observed that in the first example we have merely demonstrated the existence of sexual dimorphism by a very cumbersome and laborious method; in the second, we have demonstrated the existence of correlated territorial trends or clines. This latter is a worthwhile subject for investigation, but should not be confused with simple character-correlation in homogeneous series.

A third case of heterogeneity is one in which a sample thought to be homogeneous is really a mixture of two species superficially much alike. For example, in coastal central California one must have some experience with the garter snakes to be always accurate in segregating *Thamnophis sirtalis infernalis* from *Thamnophis ordinoides atratus*. They overlap considerably in both ventrals and subcaudals, for which reason these characters cannot be used unfailingly; and generally one employs a combination of supralabials, proportionate tail length, eye diameter, and pattern in reaching a decision. But *T. s. infernalis* averages somewhat higher in both ventrals and subcaudals, so that correlation will result if mistakes be made in identification.

To show how such misidentifications can produce a high fictitious correlation, I present the statistics of two small series of males from Santa Clara County, first taking the species separately, and then combining them.

	N	*r*	*P*
T. s. infernalis	10	0.292	0.42
T. o. atratus	10	0.094	0.80
Species combined	20	0.758	0.0001

Thus it is seen that, although properly segregated samples show no significant correlation between ventrals and subcaudals, the mixture evidences a high and significant positive correlation.

Related to the ventral-subcaudal relationship is the location of the navel in young snakes, as measured by the number of ventral scutes between the navel and the anal plate. Dunn[18] gives the necessary counts of a brood of *Natrix sipedon*. I find no correlation between the total ventrals and the navel-to-anal count ($r = 0.086$, $P = 0.66$), but there is correlation between the subcaudals and the navel location ($r = 0.539$, $P = 0.0027$); thus the higher the number of subcaudals, the closer the navel is to the anal plate. But I suspect that this results from sexual dimorphism. Dunn did not segregate the sexes of his brood. If we make a tentative segregation based on the number of subcaudals, the correlation in each group, separately, disappears (males, $r = 0.120$, $P = 0.74$; females, $r = -0.184$, $P = 0.45$).

Ventrals and subcaudals are the only scale counts which, in many colubrid genera, have sufficient degrees of variation to involve possible correlations. Most of the characters upon which herpetological classification is based, are either invariant in homogeneous colubrid series or take, at best, only two or three values.

In the important character of dorsal scale rows, for example, many species are quite or almost without variation.[19] Occasionally there may be a fairly even division, in some areas, between two values; but it is exceptional in the colubrids, for the scale rows in a homogeneous series to take three or more possible values. *Pituophis* is such an exception. The same strictures apply to the various head scales, including the labials, oculars, loreals, and temporals. Occasionally some other head scales are sufficiently variable to permit a study of this type, such as the prefrontals in *Pituophis*. But I think the differences between genera are such as to preclude the possibility of attempting to find family trends, as was done in the case of the ventrals and subcaudals; rather, each genus must be considered separately to determine, for each pair of characters, whether there are sufficient degrees of variation to warrant an investigation of correlation.

In cases where both the variates take separate values on the opposite sides of the body, each side can be considered separately, or both sides may be combined into a single table. However, where a dual character is matched with one which can take only one value (supralabials with ventrals, for example) then the sum of the sides is used as a single entry representing the dual character.

Occasionally both characters take only one of two numerical values; in such instances a four-fold table may be employed. But these cases are comparatively few; for, as I have stated, where a variable is divided, with

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[18] E. R. Dunn: The Variations of a Brood of Watersnakes. Proc. Biol. Soc. Washington, Vol. 28, pp. 61-68, 1915.

[19] For examples see Bull. Zool. Soc. San Diego, No. 17, p. 10, 1941.

a fair degree of equality, between two numerical values, there are almost sure to be occasional appearances of third and even fourth values, thus eliminating the opportunity to use a 2 x 2 or R x 2 table. Of course, it is possible to revert to an R x C table and a chi-square determination of whether the arrangement is a random one. While this involves a simpler procedure than that of a correlation study and does not presuppose normality of distribution of the variates, it does not give as complete an answer respecting the interrelationship, since it tells only whether the distribution is random. Table 27, showing the relationship between infralabials and first temporals in *P. d. perkinsi,* is an example of a distribution in which a chi-square test supplies an adequate negative answer. Here $P = 0.91$, so there is no indication of other than a random or chance arrangement of the variates and no correlation is evident. Indeed, this result is indicated, without the formality of calculation, by the fact that the proportion of specimens having two temporals, relative to those with three, remains practically unchanged as the infralabials increase from 7 to 9.

TABLE 27

Borego Series of *Phyllorhynchus decurtatus perkinsi*:
Correlation between the Infralabials on One Side of the Head
and the First Temporals on the Same Side

First Temporals	Infralabials 6	7	8	9	10	Total
1	....	....	2	....	....	2
2	....	21	125	157	4	307
3	1	30	150	184	4	369
4	....	....	9	10	1	20
5	....	....	1	....	....	1
Total	1	51	287	351	9	699

Returning to correlation tests as such, Tables 28 to 30 present the results of investigating some of the many combinations possible in one boid and two colubrid genera. As previously mentioned, the selections had to be limited to characters having fairly wide variations, that is, taking not less than three (and preferably more) numerical values. All distributions are unimodal and probably approach normality, excepting the scale rows, in which odd numbers predominate. These boid and colubrid correlations in Tables 28 to 30 may be compared with the crotalid results set forth in Tables 19 to 22. It has been impossible, in the studies of the harmless snakes, to concentrate on a single species or genus as was done with the rattlers, since no colubrid species has so much variability in all characters of lepidosis. Of the forms of which I have adequate series of scale counts, and which likewise fulfill the requirement of having considerable character variations within homogeneous series, the three which supply the data for

Tables 28 to 30, *Lichanura roseofusca roseofusca, Pituophis catenifer annectens,* and *Phyllorhynchus decurtatus perkinsi,* are outstanding.

In these tables I have repeated the data on the ventral-subcaudal and supralabial-infralabial correlations previously discussed, in order that the tables may be complete in themselves. It has been necessary to segregate the sexes in every correlation pair if either character is sexually dimorphic to any considerable degree; this has not been necessary in *Lichanura* since the ventral counts do not exhibit a conspicuous sexual dimorphism. It will be observed that the pairs of characters in the three tables do not correspond. This is because some of the characters which have sufficient variability in one species to warrant study are constant, or substantially so, in the others. The possible character-combinations in *P. c. annectens* have been by no means exhausted in Table 30.

In these tables *N* represents the number of cases rather than the number of specimens; thus if there be two counts of both characters per specimen, *N* is double the number of specimens. The fact that *N* fluctuates slightly in a series, results from the lack of certain counts, either through blemishes on a specimen or a failure to make complete counts when the snake was available.

Of the characters peculiar to certain species, the variable prefrontals in *P. c. annectens* have already been mentioned. In determining these, all scales in the prefrontal area have been counted, including those often referred to as azygos. Another unusual variable is the loreals of *L. r. roseofusca*; in this genus a horizontal suture divides the loreals into an upper and lower group, each of which is variable. In pairing with other characters I have taken all the loreals on a side as a unit; but a check was made of the correlation between the upper and lower loreals taken separately.

TABLE 28

San Diego County Series of *Lichanura roseofusca roseofusca*: Correlations in Pairs of Scale Counts

	N	*r*	*P*
Scale rows and ventrals	81	0.121	0.28
Scale rows and subcaudals	70	0.112	0.49
Scale rows and sum of supralabials	92	0.195	0.06
Scale rows and sum of infralabials	93	0.205	0.05
Scale rows and total loreals	93	0.190	0.08
Scale rows and total oculars	100	0.164	0.10
Ventrals and subcaudals	72	−0.133	0.27
Ventrals and sum of supralabials	91	0.027	0.80
Ventrals and sum of infralabials	93	0.128	0.22
Ventrals and total loreals	91	−0.014	0.90
Ventrals and total oculars	99	0.025	0.81
Subcaudals and sum of supralabials	82	0.189	0.10
Subcaudals and sum of infralabials	83	0.316	0.004
Subcaudals and total loreals	79	0.237	0.035
Subcaudals and total oculars	81	0.256	0.021
Supralabials and infralabials	190	0.463	0.0001−
Supralabials and loreals (upper plus lower)	186	0.353	0.0001−
Supralabials and oculars	188	0.199	0.005
Infralabials and loreals (upper plus lower)	186	0.210	0.004
Infralabials and oculars	190	0.378	0.0001−
Loreals (upper plus lower) and oculars	189	0.192	0.008
Upper loreals and lower loreals	186	−0.355	0.0001−

TABLE 29

Borego Series of *Phyllorhynchus decurtatus perkinsi*: Correlations in Pairs of Scale Counts

	N	*r*	*P*
Ventrals and subcaudals, males	209	0.219	0.0015
Ventrals and subcaudals, females	143	0.115	0.17
Ventrals and sum of supralabials, males	207	−0.028	0.69
Ventrals and sum of supralabials, females	143	0.024	0.77
Ventrals and sum of infralabials, males	207	0.147	0.034
Ventrals and sum of infralabials, females	144	0.046	0.58
Ventrals and sum of loreals, males	210	−0.006	0.93
Ventrals and sum of loreals, females	145	0.100	0.23
Ventrals and sum of first temporals, males	208	0.127	0.067
Ventrals and sum of first temporals, females	143	0.010	0.91
Ventrals and sum of oculars, males	209	0.076	0.28
Ventrals and sum of oculars, females	143	−0.035	0.67
Subcaudals and sum of supralabials, males	206	−0.006	0.94
Subcaudals and sum of supralabials, females	142	0.010	0.91
Subcaudals and sum of infralabials, males	207	0.071	0.31
Subcaudals and sum of infralabials, females	142	−0.063	0.45
Subcaudals and sum of loreals, males	209	−0.089	0.20
Subcaudals and sum of loreals, females	143	0.001	0.99
Subcaudals and sum of first temporals, males	207	0.156	0.025
Subcaudals and sum of first temporals, females	141	−0.085	0.31
Subcaudals and sum of oculars, males	209	0.116	0.10
Subcaudals and sum of oculars, females	141	0.069	0.42
Supralabials and infralabials	674	0.192	0.0001−
Supralabials and loreals	700	0.097	0.10
Supralabials and first temporals	699	0.025	0.51
Supralabials and oculars	699	0.011	0.77
Infralabials and loreals	705	0.105	0.005
Infralabials and first temporals	699	−0.005	0.90
Infralabials and oculars	699	0.129	0.008
Loreals and first temporals	705	0.043	0.24
Loreals and oculars	705	0.034	0.37
First temporals and oculars	703	0.034	0.37
First temporals and second temporals	704	0.009	0.81

TABLE 30

San Diego County Series of *Pituophis catenifer annectens*: Correlations in Pairs of Scale Counts

	N	*r*	*P*
Scale rows and ventrals, males	158	0.089	0.27
Scale rows and ventrals, females	154	0.095	0.24
Scale rows and sum of supralabials	316	0.109	0.053
Scale rows and sum of infralabials	314	0.187	0.0006
Scale rows and prefrontals	203	0.207	0.003
Ventrals and subcaudals, males	114	0.086	0.36
Ventrals and subcaudals, females	119	−0.147	0.11
Supralabials and infralabials	643	0.243	0.0001−
Supralabials and loreals	648	0.012	0.76
Supralabials and preoculars	647	0.075	0.056
Supralabials and postoculars	648	0.237	0.0001−
Supralabials and first temporals	555	0.074	0.080
Sum of supralabials and prefrontals	206	0.219	0.0016
Infralabials and preoculars	646	0.153	0.0001
Infralabials and postoculars	646	0.197	0.0001−
Sum of infralabials and prefrontals	205	0.202	0.004
Loreals and preoculars	648	0.151	0.0001
Sum of loreals and prefrontals	206	0.082	0.24
Preoculars and postoculars	646	0.105	0.008
Sum of preoculars and prefrontals	206	0.318	0.0001−
Postoculars and first temporals	553	0.216	0.0001−
Sum of postoculars and prefrontals	205	0.127	0.07
Sum of first temporals and prefrontals	205	0.137	0.013
First temporals and second temporals	436	0.447	0.0001−

In studying the results of Tables 28 to 30 it is apparent that while many pairs show a correlation both low in value and lacking in significance, a preponderance of the determinations are positive. This can hardly be the result of chance and suggests that a positive correlation, although by no means of high value, is the rule. Since correlation can be shown to exist in widespread populations, it may be that these correlations result from slight differentiations already begun, under the topographic and ecologic variability which characterizes San Diego County.

In analyzing the results of these investigations, if we consider only those pairs which show a correlation both significant ($P = 0.05$ or less) and of an appreciable value ($r = 0.15$ or greater), and further eliminating the ventral-subcaudal and supralabial-infralabial pairs already discussed, we find that comparatively few remain for such consideration.

In *L. r. roseofusca* there is correlation between the scale rows and infralabials, and the same is true in *P. c. annectens,* a condition which was likewise found present in *Crotalus.* While in *Lichanura* and *Pituophis* the scale-row-supralabial correlation is not quite significant, within the limit I have set ($P = 0.05$), it is nearly so, and with larger samples would probably verify the condition usually found to exist among the rattlesnakes. I think we may conclude that there is a definite tendency toward correlation between scale rows and labials among snakes in general.

An interesting situation in *Lichanura* is the consistent correlation between the head scales when taken in pairs, that is, the supralabials, infralabials, loreals, and oculars. Also in this genus we have a negative correlation between the upper and lower loreals, as if an increase in one tended to crowd out the other.

Phyllorhynchus d. perkinsi is notable for the apparent lack of correlations which come within the arbitrary limits I have fixed. Only one (beyond the ventral-subcaudal and supralabial-infralabial pairs) is evident, this being the subcaudals and first temporals in the males only. This is probably a quite fortuitous result, as it is not validated in the females.

In *P. c. annectens* (aside from the pairs already discussed) the following show significant and important correlations:

Scale rows and prefrontals
Supralabials and postoculars
Supralabials and prefrontals
Infralabials and preoculars
Infralabials and postoculars
Infralabials and prefrontals
Loreals and preoculars
Preoculars and prefrontals
Postoculars and first temporals

As in *Lichanura,* and among the rattlesnakes, we see here a tendency of adjacent groups of head scales to be correlated, as, for example, loreals with preoculars, and postoculars with first temporals. There is often correlation between the labials and other head scales, but this is not universal.

The seeming inconsistency in the temporals, with *P. c. annectens* showing a rather high ($r = 0.447$) correlation between the first and second series, while *P. d. perkinsi* has none, is evidenced in several other snakes as shown by the following:

	N	*r*	*P*
Lampropeltis getulus californiæ (Western San Diego County)	1008	0.058	0.066
Arizona elegans occidentalis (Desert San Diego County)	152	0.130	0.110
Rhinocheilus lecontei lecontei (Western San Diego County)	130	0.432	0.0001–

Evidently the first and second temporals in homogeneous series of colubrids are sometimes correlated and sometimes not.

A group of head scales which will occasionally be found of use in differentiating species comprises the scales contacting each parietal, from the mid-dorsal line to the postocular. In a series of *Lampropeltis g. californiæ* from San Diego County, these scales were correlated with the first temporals with the following results: $N = 200$; $r = 0.152$; $P = 0.032$.

Another character sometimes used is the number of gulars between the commissure and the ventrals. The same specimens, correlating this character with the infralabials, produced the following: $N = 200$; $r = 0.119$; $P = 0.086$.

It has been mentioned that *Pituophis* is one of the few colubrid genera having sufficient scale-row variability to permit a study of scale-row correlations. In a series of 100 *P. c. annectens* from western San Diego County, the dorsal scale rows were counted at the neck, at mid-body, just anterior to the anus, and at mid-tail. The correlation coefficients of these pairs of counts were as follows:

	Mid-body	Anus	Mid-tail
Neck	0.516	0.458	0.142
Mid-body	....	0.548	−0.061
Anus	....	....	0.183

The three body counts are all correlated with each other to a marked degree, and all coefficients are highly significant (P below 0.0001). The count at mid-tail is not significantly correlated with any body count, although the anus to mid-tail pair approaches significance ($P = 0.07$).

These results differ considerably from those in a series of rattlesnakes (p. 37) in which the body correlations were less marked, and the anal-tail correlation was significant.

It can be shown by the method of partial correlation that the net partial coefficients between the three body counts in this series of gopher snakes, the mid-tail counts being neglected, are as follows: Neck to mid-body, 0.356; mid-body to anal, 0.409; neck to anal, 0.244. Although materially reduced in value, as compared to the unadjusted coefficients, all remain significant; however, they are not significantly different from each other, even though, as would be expected, the most widely separated counts are less closely correlated than those which are contiguous.

The correlation between the lengths of different dropped rows may be of interest. Dr. James Oliver has given me the counts on 13 male specimens of *Leptophis diplotropis* from Tehuantepec, Oaxaca, Mexico. In these snakes the fifth and sixth rows coalesce, and likewise the third and fourth. The number of the ventral scale opposite which each suppression occurs was recorded. It was found that there is a positive correlation ($r = 0.501$),

between the two points of suppression. Similarly in *Thamnophis ordinoides biscutatus* Dr. Henry S. Fitch has supplied me with the body positions at which the sixth and fourth lateral rows are suppressed. I find the correlation between the points of suppression to be 0.389 in the males and 0.596 in the females. All of these values are significant. There is no question that the positions of suppression of different lateral scale rows are correlated in these species. But there seems to be no correlation between points of suppression and total ventrals.

CORRELATIONS IN LIZARD SCALES

Lizard scale counts are not so often used in classification as those of snakes, probably because of the presence of other satisfactory characters for differentiation not found in the snakes. Also, in some of the series it is quite difficult to fix the terminations of the counts by definition, so that different investigators may not reach the same conclusion with respect to a single count, or specimen. There is often an irregularity of arrangement which makes accurate counting difficult. Nevertheless, one may hazard the guess that future lizard studies will tend to lean more heavily on numerical scale counts for validating differences.

The great number of variable scale characters in the lizards offers a fruitful field for correlation studies, since many pairs of variables are available in most species. As an example, the ventrals, when correlated with the sums of the lamellæ on the fourth toe in 120 specimens of *Cnemidophorus t. tessellatus* from the Gila Valley, Arizona, gave the result $r=0.162$, $P=0.077$. Here we have a low correlation of doubtful significance.

Table 31 shows correlations calculated from the scale counts of Galapagos lizards of the genus *Tropidurus,* as given by Van Denburgh and Slevin.[20] It will be observed that significant correlation of a moderate order is the rule, although not present in two of the pairs of characters in the James Island population. In two subspecies the scale rows show the highest correlation with the belly scales, but this is not the case with *T. delanonis* of Hood Island. This may be due to the fact that sexual dimorphism is indicated (especially in the crest) in this form, but not in the others.

Another series of scale counts is given by Boulenger.[21] I have calculated the correlations between five scale characters taken in pairs, using 20 specimens of each sex of *Lacerta laevis* from Damascus. The results are shown in Table 32. Of the ten combinations tested, only one, scales across mid-body and the gular scales in a longitudinal series, is significant at the 5 per cent level, when the sexes are treated separately, and this in the males only. When the sexes are combined (using Fisher's z-transformation) two combinations show significant correlations, the one already mentioned, and the collar plates and longitudinal gulars. But none of these correlations is

[20] Proc. Cal. Acad. Sci., Fourth Series, Vol. 2, pp. 133-202, 1913.

[21] Monograph of the Lacertidae, Vol. I, p. 305, 1920.

particularly high. I judge the irregularity in the arrangements of most of the scale series in lizards inhibits correlation except in groups of adjacent scales. This remark, however, applies only to territorially homogeneous series.

TABLE 31

Galapagos Lizards of the Genus *Tropidurus*:
Correlations in Pairs of Scale Counts

T. a. albemarlensis, James Island	*N*	*r*	*P*
Scale rows and crest	149	0.081	0.33
Scale rows and belly scales	155	0.326	0.0001–
Crest and belly scales	149	0.072	0.39
T. a. barringtonensis, Barrington Island			
Scale rows and crest	130	0.194	0.028
Scale rows and belly scales	129	0.343	0.0001
Crest and belly scales	130	0.217	0.013
T. delanonis, Hood Island			
Scale rows and crest	137	0.256	0.0027
Scale rows and belly scales	137	0.171	0.044
Crest and belly scales	137	0.263	0.0020

TABLE 32

Lacerta laevis from Damascus:
Correlations in Pairs of Scale Counts
(20 specimens of each sex)

Pairs of Scale Counts	Males	Females	Sexes Combined
Scales across mid-body and transverse ventral scutes	–0.057	–0.139	–0.099
Scales across mid-body and collar plates	0.132	0.111	0.121
Scales across mid-body and longitudinal gulars	0.586*	0.215	0.418*
Scales across mid-body and lamellæ on 4th toe	–0.190	0.142	–0.020
Transverse ventral scutes and collar plates	0.149	–0.254	–0.055
Transverse ventral scutes and longitudinal gulars	–0.144	–0.264	–0.205
Transverse ventral scales and lamellæ on 4th toe	–0.273	0.065	–0.108
Collar plates and longitudinal gulars	0.217	0.430	0.328*
Collar plates and lamellæ on 4th toe	0.236	0.054	0.147
Longitudinal gulars and lamellæ on 4th toe	0.006	0.197	0.103

* Significant at the 5 per cent level.

CORRELATIONS IN PATTERN

A correlation between the numbers of body and tail marks of blotched or ringed snakes is obviously to be expected. The extent of such correlations, found in seven example forms, is presented in Table 33. In this table, since the correlations are relatively high, compared with most of those hitherto discussed, I have likewise entered *a* and *b*, the coefficients of the regression equations, and *s*, the standard error of estimate. In these determinations the body blotches have been considered the independent variable and the tail rings dependent. Thus the regression equations are of the form

$$\text{tail rings} = a + b \text{ times body blotches},$$

the values of these coefficients being set forth in the table.

For purpose of graphic illustration, Table 34 is presented to show the nature of the correlation in *Lampropeltis getulus californiae*, one of the subspecies considered.

It would appear logical to expect the closest correlations between body and tail blotches in species wherein the tail blotches are most variable and therefore freer to follow variations in the body blotches. Since the tail variations will be greater numerically (assuming substantially equal co-

TABLE 33

Correlations between Body Blotches and Tail Rings

Series	*Sex*	*N*	*r*	*a*	*b*	*s*
Crotalus v. viridis	M	438	0.424	4.08	0.131	0.98
(Platteville series)	F	391	0.283	3.80	0.084	0.94
Crotalus v. oreganus	M	326	0.161	3.69	0.054	0.76
(Pateros series)	F	290	0.159	2.94	0.046	0.66
Phyllorhynchus d. perkinsi	M	207	0.346	2.29	0.120	1.27
(Desert San Diego County)	F	143	0.336	1.33	0.095	1.23
Arizona e. occidentalis	M	42	0.635	1.53	0.281	2.05
(Desert San Diego County)	F	22	0.519	5.18	0.206	2.03
Pituophis c. annectens	M	142	0.637	2.07	0.299	2.08
(Coastal San Diego County)	F	136	0.654	6.09	0.220	1.70
Lampropeltis g. californiae	M	92	0.621	1.45	0.244	0.81
(Ringed phase; coastal San Diego County)	F	93	0.468	2.69	0.177	0.78
Sonora o. annulata	M	149	0.469	2.64	0.216	0.89
(Desert San Diego County)	F	72	0.556	1.73	0.212	0.88

NOTE on the significance of *r*: All values of *P* are below 0.0001, with the exception of the value for the females of *A. e. occidentalis*, in which case $P = 0.014$, the males of *C. v. oreganus* wherein $P = 0.004$, and the females of the same series, in which $P = 0.007$.

TABLE 34

Coastal San Diego County Series of
Lampropeltis getulus californiae (Ringed Phase):
Correlation between Body Rings and Tail Rings

Males

Body Rings	Tail Rings 6	7	8	9	10	11	Total
20	1						1
21							
22		1					1
23	1	1					2
24		4	1	1			6
25		6	2	1			9
26		5	7	2			14
27	1	1	6	3	1		12
28		3	10	9			22
29		1	3	3			7
30				1	4		5
31			4	1		1	6
32				2	1		3
33			1	1	1		3
34							
35					1		1
Total	3	22	34	24	8	1	92

Calculated coefficient of correlation, $r = + 0.621$.

Females

Body Rings	Tail Rings 6	7	8	9	10	Total
22	3	1				4
23		1				1
24	6	7	2			15
25		9	4			13
26	3	6	7	2		18
27	1	3	8			12
28	1	5	5		1	12
29		4	3	1		8
30		2	2			4
31		1	1	2		4
32		1				1
33					1	1
Total	14	40	32	5	2	93

Calculated coefficient of correlation, $r = + 0.468$.

efficients of variation), the higher the number of tail marks, it might further be expected that the higher the ratio of tail rings to body blotches—virtually concomitant with greater proportionate tail length—the higher will be the correlation between the two sets of blotches. This is found actually to be the case, for the long-tailed snakes show a higher correlation between body and tail blothes than those with proportionately shorter tails. In fact, with three exceptions (*Phyllorhynchus* and *Pituophis* females, and *Sonora* males) all the determinations fall close to a value *r* found by multiplying the ratio of tail rings to body blotches by 1.9. Obviously, this relationship could not continue to be maintained indefinitely into the higher values, since, with a tail-blotch count somewhat more than half the body blotches, *r* would exceed unity, an evident impossibility. I regret not having available any large series of long-tailed, blotched snakes to test whether this relationship would be substantiated for higher values of the tail-length ratio. However, it is to be remembered that attenuated, blotched snakes are rather unusual, for most slim and long-tailed snakes are either striped or unicolor.[22]

The correlation between body blotches and tail rings in the rattlers is not of particular interest, because of their foreshortened tails, for which reason I have made calculations of only two series (Table 33). *C. v. viridis* has a considerably higher number of tail rings (about 70 per cent more) than *C. v. oreganus,* which accounts for the higher correlation in the former. The range of variation in the latter is so small that the rings cannot be expected to follow closely the variations in the body blotches.

I have made a few cross-correlations between scale counts and what might be considered the corresponding elements of pattern—that is, ventrals with body blotches, and subcaudals with tail rings. The results are shown in Table 35. It will be noted that there is a significant correlation between ventrals and body blotches in only one case out of fourteen (*L. g. californiae* males), and this is negative. Half the correlations found are negative, half positive. With such a divergence in trends I conclude that correlation between these characters is quite uncommon in homogeneous series.

On the other hand, ten out of fourteen correlations between subcaudals and tail rings proved significant, and most of them rather substantial in value. It should be observed that if, through error, any incomplete tails were included in a compilation of this kind, correlation would obviously result. But as errors of this nature would be infrequent in several blunt-tailed subspecies which I have tested, particularly *Phyllorhynchus d. perkinsi,* the results cannot be attributed to such errors, and I conclude that a positive correlation between subcaudal scales and tail spots or rings is probably of frequent occurrence and fairly high in value.

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[22] Bull. Zool. Soc. San Diego, No. 8, p. 46, 1931.

TABLE 35

Correlations between Scales and Pattern

Subspecies and Series	Sex	Ventral scales and body rings or blotches			Subcaudal scales and tail rings or spots		
		N	*r*	*P*	*N*	*r*	*P*
Phyllorhynchus d. perkinsi	M	100	0.117	0.24	206	0.167	0.017
(Borego series)	F	100	0.077	0.45	137	0.346	0.0001
Pituophis c. annectens	M	109	−0.020	0.84	136	0.223	0.009
(Coastal San Diego County)	F	84	−0.020	0.86	133	0.422	0.0001−
Pituophis c. deserticola	M	26	−0.077	0.71	26	−0.159	0.44
(Mohave Desert)	F	15	−0.143	0.61	15	0.548	0.035
Lampropeltis g. californiae	M	95	−0.303	0.003	89	0.404	0.0002
(Ringed phase, coastal San Diego County)	F	98	0.030	0.77	92	0.481	0.0001−
Rhinocheilus l. lecontei	M	38	−0.102	0.54	31	0.314	0.085
(Coastal San Diego County)*	F	27	−0.037	0.86	24	0.422	0.042
Sonora o. annulata	M	169	0.115	0.14	160	0.230	0.004
(Desert San Diego County)	F	79	0.103	0.36	75	0.382	0.0008
Hypsiglena ochrorhynchus	M	49	0.166	0.15	35	0.205	0.24
(Coastal San Diego County)	F	34	0.294	0.092	28	−0.162	0.41

* *Clarus* intergrades not included.

MORPHOLOGICAL CORRELATIONS

The correlation coefficient, as a measure of the relationship between body parts, or between some part and an over-all dimension, is not a satisfactory criterion, for the result will depend too much on the ontogenetic distribution of the specimens comprising the sample. Obviously, if all ages are represented, the value of r is sure to be high, for the sizes of body parts are certain to follow the growth of the organism, although not necessarily with a linear relationship. For example, the head-length to body-length relationship in certain colubrids follows an exponential curve, while the fang-to-body relationship in the rattlesnakes is parabolic. Strictly linear relationships, in fact, by no means predominate; and even when the relationship is linear the usual presence of a constant term in the equation makes it evident that the proportionate size of the part does not remain constant during life.

Relationships of this character vary so widely in their nature that no brief discussion can summarize them; each pair must receive a separate study. Such an investigation should start with a graphic layout which will show clearly both the trend of the realtionship and the extent of the scatter of the individuals about the regression line. If the line is not straight on rectangular co-ordinates, it may prove to be if plotted on logarithmic or semilogarithmic paper, which will serve as a clue to an equation that should give a close fit. If the relationship is linear, or can be transformed to a linear form, the equation and the standard error of estimate should be determined; these statistics will be of far more importance than the correlation coefficient r, with which this paper has been heretofore concerned.[23] Even if one is not interested in an algebraic analysis of the relationship, the graphic investigation is fully justified because of the insight it will give into the character of the ontogenetic trend, which may be of importance in evaluating taxonomic differences.

While admitting the lack of importance of these figures, examples of correlation coefficients showing the relationship between body parts are shown in Tables 36 to 38 to indicate the uniformly high values which are evident in such pairs of characters. Table 36 covers rattlesnakes only, Table 37 other snakes, and Table 38 amphibians.

It will be observed that limited age groups always involve lower correlations than a complete ontogenetic series. This does not necessarily result from a deviation from linearity in the complete series. What might be

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[23] Examples of studies of this type on rattlesnakes will be found in the Occasional Papers of the San Diego Society of Natural History, as follows: Head length to body length, No. 4, p. 5, 1938; head width to head length, *op. cit.*, p. 45; fang length to body length, No. 5, p. 23, 1939; fang length to head length, *op. cit.*, p. 27. See also tail length to body length, Bull. Zool. Soc. San Diego, No. 18, p. 51, 1943.

TABLE 36

Morphological Correlations in Rattlesnakes

Species	Series	Limitations	Characters	*N*	*r*
C. lucasensis	San Lucan	None	Log. weight and log. length	38	0.969
C. ruber	San Diego Co.	None	Log. weight and log. length	61	0.986
C. v. viridis	Platteville	None	Log. weight and log. length	818	0.990
C. v. viridis	Pierre	None	Log. weight and log. length	338	0.991
C. v. oreganus	San Diego Co.	None	Log. weight and log. length	114	0.983
C. v. viridis	Platteville	Adults	Log. weight and log. length	594	0.948
C. v. viridis	Pierre	Adults	Log. weight and log. length	223	0.973
C. v. oreganus	San Diego Co.	Adults	Log. weight and log. length	76	0.990
C. cinereous	San Patricio	Juveniles	Log. weight and log. length	139	0.739
C. v. viridis	Platteville	Juveniles	Log. weight and log. length	224	0.796
C. v. viridis	Pierre	Juveniles	Log. weight and log. length	118	0.877
C. v. oreganus	San Diego Co.	Juveniles	Log. weight and log. length	46	0.936
C. v. viridis	Platteville	Males	Log. weight and log. length	315	0.960
C. v. viridis	Platteville	Females	Log. weight and log. length	279	0.945
C. v. viridis	Pierre	Males	Log. weight and log. length	115	0.981
C. v. viridis	Pierre	Females	Log. weight and log. length	108	0.967
C. lucasensis	San Lucan	None	Head length and body length	247	0.831
C. v. viridis	Platteville	None	Head length and body length	833	0.989
C. v. viridis	Pierre	None	Head length and body length	715	0.988
C. v. viridis	Platteville	None	Head length and head width	233	0.982
C. v. viridis	Platteville	Adult males	Tail length and body length	312	0.905
C. v. viridis	Platteville	Adult females	Tail length and body length	281	0.809
C. v. viridis	Platteville	Juvenile males	Tail length and body length	124	0.853
C. v. viridis	Platteville	Juvenile females	Tail length and body length	102	0.702

TABLE 36 (Continued)

Species	Series	Limitations	Characters	N	r
C. cinereous	Arizona	Males	Tail length and body length	87	0.968
C. cinereous	Arizona	Females	Tail length and body length	95	0.959
C. lucasensis	San Lucan	Males	Tail length and body length	161	0.939
C. lucasensis	San Lucan	Females	Tail length and body length	140	0.935
C. ruber	San Diego Co.	Males	Tail length and body length	156	0.986
C. ruber	San Diego Co.	Females	Tail length and body length	104	0.974
C. v. viridis	Platteville	Males	Tail length and body length	452	0.978
C. v. viridis	Platteville	Females	Tail length and body length	392	0.954
C. v. viridis	Pierre	Males	Tail length and body length	364	0.985
C. v. viridis	Pierre	Females	Tail length and body length	342	0.959
C. v. oreganus	Pateros	Males	Tail length and body length	314	0.962
C. v. oreganus	Pateros	Females	Tail length and body length	266	0.942
C. v. oreganus	San Diego Co.	Males	Tail length and body length	354	0.982
C. v. oreganus	San Diego Co.	Females	Tail length and body length	354	0.962
C. v. viridis	Platteville	None	Fang length and body length	594	0.982
C. v. viridis	Platteville	Adults	Fang length and body length	526	0.895
C. lucasensis	San Lucan	Adults	Fang length and body length	274	0.924
C. ruber	San Diego Co.	Adults	Fang length and body length	35	0.919
C. v. viridis	Platteville	None	Fang length and head length	588	0.961
C. v. viridis	Platteville	Adults	Fang length and head length	519	0.887
C. lucasensis	San Lucan	Adults	Fang length and head length	273	0.903
C. ruber	San Diego Co.	Adults	Fang length and head length	35	0.893

NOTE:—All values of *P* are less than 0.0001.
All body lengths include the tail.

TABLE 37

Miscellaneous Morphological Correlations in Snakes

Species	Series	Sex	Character	N	r
Masticophis lateralis	San Diego Co.	Both	Head length and length over-all	23	0.982
Thamnophis hammondii	San Diego Co.	Both	Head length and length over-all	54	0.967
Lampropeltis g. californiae	San Diego Co.	Both	Head length and body length	79	0.989
Thamnophis o. biscutatus	Upper Klamath R.	Both	Head length and body length	18	0.990
Thamnophis o. hydrophyla	Rogue River Valley	Both	Head length and body length	27	0.956
Diadophis a. similis	San Diego Co.	Male	Tail length and body length*	133	0.964
Diadophis a. similis	San Diego Co.	Female	Tail length and body length*	134	0.972
Phyllorhynchus d. perkinsi	Borego	Male	Tail length and body length*	214	0.960
Phyllorhynchus d. perkinsi	Borego	Female	Tail length and body length*	148	0.970
Pituophis c. annectens	San Diego Co.	Male	Tail length and body length*	155	0.990
Pituophis c. annectens	San Diego Co.	Female	Tail length and body length*	144	0.988
Leptotyphlops h. humilis	San Diego Co.	Both	Diameter at mid-body and length over-all	57	0.793
Leptotyphlops h. cahuilae	Laguna Island	Both	Diameter at mid-body and length over-all	155	0.955

* For other values of the tail to body correlation see Bull. Zool. Soc. San Diego, No. 18, 1943.

TABLE 38

Miscellaneous Morphological Correlations in Amphibians

Species	Locality	Character	N	r
Hynobius tsuensis	Tsu-shima, Japan	Head and body	61	0.967
Siren intermedia nettingi	Herrin, Ill.	Body and tail	113	0.979
Pseudobranchus striatus axanthus	Alachua Co., Fla.	Body and tail	235	0.951
Bufo fowleri	Near Benton, Ala.	Body and foot	200	0.752
Bufo fowleri	Scraper, Okla.	Body and foot	169	0.898
Bufo woodhousii	Tulsa, Okla.	Body and foot	90	0.930
Bufo fowleri	Near Benton, Ala.	Length and width of parotoid gland	200	0.502
Bufo fowleri	Scraper, Okla.	Length and width of parotoid gland	169	0.558
Bufo woodhousii	Tulsa, Okla.	Length and width of parotoid gland	90	0.715

Measurements are from the following sources: *Hynobius*, Dunn, Proc. Amer. Acad. Arts and Sciences, Vol. 58, p. 492, 1923; *Siren*, unpublished data from M. G. Netting and C. J. Goin; *Pseudobranchus*, unpublished data from C. J. Goin; *Bufo* measurements from A. P. Blair.

called the group trend is often different from the growth trend.[24] Among birds and mammals, wherein each individual reaches a definite growth limit (although differing between individuals) the selection of a sample composed entirely of fully grown adults is a simple procedure. In such adult series the body-part correlations are found to be lower than if full ontogenetic series are included. Examples of a large number of such adult correlations have been given by Clark.[25]

In problems of this kind, where ontogenetic variation obscures the true correlation between two variables, such a correlation can be determined if both are clearly dependent on a third, as is the case with body parts or head scales. As an example I take various head measurements of 18 specimens of *Thamnophis o. biscutatus* from the upper Klamath River in Oregon (10 to 15 miles below Keno, Klamath County). These measurements were made by Dr. Henry S. Fitch, who has kindly permitted me to use them. In each specimen Dr. Fitch measured the length of head together with eleven other scale lengths, breadths, and contacts. In Table 39 are given the results of calculations of the correlations between head length and each of the other characters, and also between each pair of subsidiary characters. All correlations are quite high and significant, as would be expected with any characters which grow with an organism.

By the method of partial correlation we are able to calculate the adjusted correlation between two variables when a third variable with which both are correlated is held constant. In the present instance all of the characters are obviously dependent on head length, their high correlations therewith being evident from the top line in Table 39. In Table 40 are shown the adjusted correlations between the subsidiary pairs of characters with the head length variability eliminated; in other words, the correlations are those which might be expected between these subsidiary characters in a series of snakes all having the same head lengths, so that growth would no longer be a factor. Now the high intercharacter correlations have disappeared. Only four pairs out of 66 remain significant, these being length of jaw to length of rostrum, length of rostrum to interorbital breadth, length of posterior genials to inferior length of seventh supralabial, and interorbital breadth to anterior height of nasal. I suspect that even some of these are accidental—that is, the result of the chance composition of the sample series—and that true correlation between these scale dimensions, when the effects of growth have been eliminated, is unusual. For example, there would seem to be no logical relationship between the length of the posterior genial and the length of the seventh supralabial. This independence of characters is an important consideration in evaluating differences between homogeneous populations.

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[24] Occ. Pap. San Diego Soc. Nat. Hist., No. 3, p. 50, 1937; Bull. Zool. Soc. San Diego, No. 18, p. 19, 1943.

[25] Frank H. Clark: Correlation and Body Proportions in Mature Mice of the Genus *Peromyscus*. Genetics, Vol. 26, pp. 283-300, 1941.

TABLE 39

Unadjusted Correlations in Head Dimensions
(18 Specimens of *Thamnophis o. biscutatus* from Klamath River)

	Length of jaw	Length of frontoparietal	Length of rostrum	Length of anterior genials	Length of posterior genials	Interorbital breadth	Longitudinal diameter of eye	Inferior length of 7th supralabial	Posterior height of 7th supralabial	Anterior breadth or internasals	Anterior height of nasal	Anterior height of 1st supralabial
Length of head	.992	.966	.976	.946	.906	.946	.942	.954	.952	.894	.952	.897
Length of jaw		.964	.981	.946	.924	.943	.927	.956	.938	.884	.956	.890
Length of frontoparietal			.967	.924	.912	.933	.895	.925	.950	.874	.934	.830
Length of rostrum				.927	.922	.961	.919	.931	.929	.873	.929	.876
Length of anterior genials					.857	.895	.891	.934	.901	.801	.924	.866
Length of posterior genials						.876	.846	.933	.873	.860	.895	.760
Interorbital breadth							.914	.906	.913	.892	.849	.888
Longitudinal diameter of eye								.897	.864	.873	.857	.846
Inferior length of 7th supralabial									.914	.845	.914	.862
Posterior height of 7th supralabial										.802	.910	.822
Anterior breadth of internasals											.788	.817
Anterior height of nasal												.821

TABLE 40

Correlation in Head Dimensions Adjusted to Constant Head Size
(18 Specimens of *Thamnophis o. biscutatus* from Klamath River)

	Length of frontoparietal	Length of rostrum	Length of anterior genials	Length of posterior genials	Interorbital breadth	Longitudinal diameter of eye	Inferior length of 7th supralabial	Posterior height of 7th supralabial	Anterior breadth or internasals	Anterior height of nasal	Anterior height of 1st supralabial
Length of jaw	.175	.469*	.190	.453	.113	–.161	.266	–.156	–.047	.301	.000
Length of frontoparietal		–.431	–.126	.331	–.230	–.168	.049	.385	.085	.188	–.320
Length of rostrum			.048	.407	.532*	.066	.112	–.066	.369	–.196	.050
Length of anterior genials				.045	–.013	–.255	.331	.008	–.305	.241	.119
Length of posterior genials					.135	–.051	.537*	.079	.262	.246	–.287
Interorbital breadth						.207	.038	.125	.319	–.509*	.275
Longitudinal diameter of eye							–.008	–.310	.202	–.377	.009
Inferior length of 7th supralabial								.067	–.057	–.032	.044
Posterior height of 7th supralabial									–.361	.049	–.235
Anterior breadth of internasals										–.454	.074
Anterior height of nasal											–.244

* Significant at the 5 per cent level.

As further examples of morphological correlations in a series of adult reptiles, I present data on turtles, based on measurements made by Dr. Paul L. Risley. In 1930 he published a study entitled "Anatomical Differences in the Sexes of the Musk Turtle, *Sternotherus odoratus* (Latreille)." This study utilized 30 adults of each sex, collected in the vicinity of Ann Arbor, Michigan. In the course of this work 14 measurements were made on each specimen. Using the length of the carapace as the basic or independent variable, twelve charts were prepared, showing the co-ordinates representing each specimen for all but one of the other characters (figs. 21-30). The regression lines were drawn for each sex; and, from the separation of the lines and the scatter of the individual points, Dr. Risley drew conclusions as to the value of each subsidiary or dependent character in distinguishing the sexes.

Dr. Risley has courteously sent me the schedules of the original measurements which were made in the preparation of his paper and has kindly permitted me to use them for the derivation of illustrative adult correlations. I have therefore computed the correlation coefficients, using both the length of the carapace and the length of the plastron as basic measurements. The results are set forth in Tables 41 and 42. They are of interest as showing the reduced correlation which exists in a population which does not include a full ontogenetic series, although it is to be remembered that these turtles are adult only in the sense of having reached sexual maturity; they have not entirely ceased to grow as do adult birds and mammals.

The following will serve to explain Dr. Risley's measurements and the character designations in Tables 41 and 42: The plastron length was measured from the anterior end to the anal notch. The width of the plastron, I, was taken across the posterior edge of the humeral shields; II was measured across the posterior edge of the gular shields. The connecting bridge is that joining the carapace and plastron, the measurement being made where the indentation is deepest. The width of the head was taken at the anterior edge of the tympanic membrane. Tail length, I, is from the end of the carapace to the tip of the tail; II from the anal notch of the plastron to the tail tip. The preanal tail length was also measured from the anal notch. The lateral width of the tail, I, was taken at the mid-point of the preanal section of the tail; II at the tail tip. The thickness of the tail is the dorso-ventral thickness at the mid-point of the preanal tail section.

As has been stated before, the coefficient of correlation does not, in itself, provide a particularly useful statement of concomitant variation where ontogeny is involved. In such cases regression equations and standard errors of estimate are more informative. For this reason I have included in the tables the mean value of each variable and the constants of the regression equations. I have assumed straight-line relationships throughout, this being usually sufficiently accurate in cases of limited ontogenetic range (in this case adults), as is further verified by Dr. Risley's diagrams. Thus the equations take the form $Y = a + bX$, Y being the dependent variable,

a the regression constant, b the regression coefficient, and X the independent variable, the carapace or plastron length in this study. For clarity, where the plastron is the basic measurement, a' and b' have been substituted for a and b. All measurements and values in the equations are in millimeters. The standard errors of estimate are the optimum estimates of population dispersions, rather than those of the samples.

Dr. Risley's measurements represent so unusual and complete a series that I shall turn aside from correlations for the moment and employ them in an evaluation of sexual dimorphism, using the methods suggested in a study of the tail lengths of snakes (Klauber, 1943a, pp. 40 and 46). This method of analysis involves the following steps in ascertaining sexual dimorphism in one character.

1. Determine the regression line for each sex, the length over-all, or length of body, being employed as the basic measurement, that is, the independent variable. As a part of the computation determine the standard error of estimate. In the present case the length of the carapace will be used as the basis of comparison, since it is obviously more valid as a measure of size than the length of the plastron.

2. Decide on a standard length (in terms of the independent variable) at which sexual dimorphism is to be determined. This is important since in most organisms the extent of sexual dimorphism, with respect to measurable characters, is subject to ontogenetic change. Adult differences are usually both highest in value and of the most interest. In the musk turtles the males and females do not differ conspicuously in size. As a carapace length of 100 mm. represents a large, but by no means exceptional individual of either sex, this will be selected as the standard length at which sexual dimorphism is to be ascertained. In problems where there is a considerable difference between the sizes reached by the sexes, the standard size is preferably taken near the ultimate attained by the smaller sex; it should not involve extrapolation into fictitious sizes never reached by the smaller sex.

3. From the equations of the regression lines, determine the value of the dependent variable for each sex at standard length. For purposes of exposition these may be called the standard values (one for each sex) of the dependent variable.

4. Determine the coefficient of sexual divergence, usually expressed as a percentage. This will be the difference between the standard values of the dependent variable, divided by half their sum (*loc. cit.* p. 6).

5. To determine the significance of this difference, take the standard error of estimate for each sex as being the value of the standard deviation of the dependent variable at its mean value. Multiply this by the ratio between the standard and mean values of the dependent variable, there being, of course, separate ratios for each sex. This will give an estimate of the standard deviation of the dependent variable that would be found if all the specimens in the sample were of standard length; that is, in our

present example, we would have the dispersion of the dependent variable that should be present if all our turtles had carapace lengths of 100 mm. This method is based on a number of investigations which have indicated that the coefficient of variation of a dependent variable about a regression line remains substantially constant during life (*loc. cit.*, pp. 37 and 40).

6. The standard value of the dependent variable being known for each sex, and the estimated standard deviation of each having been computed, it is now possible to determine the significance of the sexual divergence by any one of the formulas for the significance of the differences between means. Or, the significance of the coefficient of sexual divergence may be computed from the formula for its standard error (*loc. cit.* p. 9). In either case N for each sex is taken as the number of specimens comprising the sample of that sex.

I think it may be appropriate to follow through the derivation of one value of the coefficient of sexual divergence and its significance to illustrate the method I have outlined. As an example we shall take the width of the head.

Let C stand for carapace length in mm. and H for the corresponding head width. Our regression equations, using the appropriate values of b and a set forth in Table 41 are:

Males ..... $H = .2493C - 1.27$
Females ..... $H = .1990C + 1.95$

It will be remembered that we have fixed 100 mm. as the standard adult carapace length at which the coefficient of sexual divergence in head width is to be determined. Substituting this value for C in the above equations, we find our standard values of head width to be 23.66 mm. for the males and 21.85 mm. for the females. These are the estimated average head widths that the samples would have if their carapace lengths were all 100 mm. The coefficient of sexual divergence is the difference between these averages divided by half their sum, that is, 23.66 – 21.85, or 1.81, divided by 22.75, or 7.96 per cent. These are the only calculations required to determine the coefficient of sexual divergence; to find whether this coefficient is significant is somewhat more involved.

The next values to be determined are the dispersions of head width about the regression lines at $C = 100$. From Table 41 we find that the standard error of estimate of head width for the males, at a mean head width of 22.680 mm., was 0.90 mm. But the standard value of the head width (males) was determined above to be 23.65 mm. This involves an increase of 0.97 mm., or 4.28 per cent. This is the amount by which we must increase the standard error of estimate to represent the dispersion (standard deviation) of head length about the regression line at a standard carapace length of 100 mm. The required standard deviation is 0.94 mm. Similarly in the case of the females, the required standard deviation is 0.72 (21.85/20.663) = 0.76 mm.

TABLE 41

Morphological Correlation in *Sternotherus odoratus*, with Length of Carapace as the Independent Variable

Character	Mean Length		Standard Deviation		Correlation Coefficient, *r*		Regression Coefficient, *b*		Regression Constant, *a*		Standard Error of Estimate		Adult Coefficient of Sexual Divergence, Per Cent
	M	F	M	F	M	F	M	F	M	F	M	F	
Length of carapace	96.080	94.073	9.053	6.235									
Length of plastron	65.340	70.637	6.726	4.691	.954	.863	.7090	.6496	−2.78	9.53	2.09	2.45	−8.93
Width of carapace	63.113	63.847	5.671	3.996	.823	.842	.5153	.5396	13.60	13.08	3.34	2.23	−2.89
Width of plastron, I	32.760	33.813	2.755	2.382	.895	.789	.3043	.3016	3.52	5.44	1.27	1.51	−4.74
Width of plastron, II	21.153	20.093	1.941	1.928	.844	.550	.1809	.1699	3.77	4.11	1.08	1.67	3.55
Width of connecting bridge	11.817	14.000	1.665	1.624	.823	.706	.1515	.1840	−2.74	−3.31	0.98	1.19	−19.49
Width of head	22.680	20.663	2.420	1.422	.933	.872	.2493	.1990	−1.27	1.95	0.90	0.72	7.96
Tail length, I	24.370	10.800	2.795	2.598	.505	.242	.1559	.1009	9.39	1.30	2.50	2.61	74.67
Tail length, II	33.720	22.317	4.203	3.376	.695	.706	.3227	.3825	2.72	−13.66	3.13	2.48	34.93
Preanal tail length	16.920	10.733	2.952	1.907	.644	.553	.2102	.1690	−3.27	−5.16	2.34	1.64	40.77
Postanal tail length	16.860	11.650	2.213	1.908	.424	.707	.2445	.2164	−6.63	−8.71	2.08	1.40	31.78
Lateral width of tail, I	10.390	6.893	1.265	0.764	.584	.512	.1398	.0628	−3.04	0.99	1.06	0.68	40.35
Lateral width of tail, II	2.537	1.693	0.406	0.159	.668	.281	.0300	.0072	−0.34	1.02	0.31	0.16	41.82
Thickness of tail	12.273	12.720	1.579	1.210	.638	.291	.1745	.0566	−4.49	7.40	1.26	1.20	−0.0075

NOTES:—All measurements are in millimeters, and are based on 30 turtles of each sex. Negative values of the coefficient of divergence indicate that the female measurements are greater than the male. Values of *r* above .463 are significant at the one per cent level; between .463 and .361 at the five per cent level; below .361 not significant. All values of the coefficient of sexual divergence are significant except that of the thickness of the tail.

We now have a simple problem involving the difference between two means. These means are 23.66 and 21.85 mm., and the respective standard deviations are 0.94 and 0.76 mm. In a case such as this, where the samples are of equal size ($N = 30$), the small-sample formula for the significance of the difference between means reduces to $t = (M_1 - M_2) / [(\sigma_1^2 + \sigma_2^2) / (N - 1)]^{1/2}$, the value of P being found in the t-table at $2N - 2$ degrees of freedom. In our particular problem we find $t = 8.15$, which gives a value of P far below 0.0001, thus showing that the sexual divergence in head width in *Sternotherus odoratus* is undoubtedly real and not the fortuitous result of the particular samples at hand.

This method has been applied to the data derived from Dr. Risley's measurements, with the results shown in the final column of Table 41. The question may be asked why I have not carried through, using the plastron length as a basis of comparison, after having set forth the regression-equation statistics, with the plastron as the independent variable, in Table 42. I considered this but thought it confusing; for the plastron itself is shown to be sexually dimorphic when the more fundamental carapace length is used as the basis of standardization or comparison. If one is interested in the relationship of two subsidiary characters, it will be best to determine their correlation by the method of partial correlation, thus eliminating the effect of variation in carapace length. I should also point out that one may compute the probable regression line (or lines if first one and then the other character be taken as the independent variable) representing the relationship between any two secondary characters that would exist if all individuals of the sample were converted to a standard carapace length.

We note, with respect to the correlations set forth in Tables 41 and 42, that nearly all are significant, although below the values usually found in full ontogenetic series. The lowest values are found in some of the female tail measurements.

With regard to sexual divergence, all characters are found to show highly significant differences ($P < 0.01$) except three: The width of the carapace is significantly different in the sexes but does not quite reach the one per cent level ($P = .017$); the width of the plastron, II, is almost exactly on the 5 per cent level ($P = .052$); and the thickness of the tail is quite without significance ($P = .983$). The sexual divergence in the width of the connecting bridge is rather surprisingly great. Of the main body-dimensions, the length of the plastron proves to have the highest coefficient of divergence. But it is in the tail length and width that the most significant and easily used criteria are found, especially the length of the tail when measured from the carapace to the tip. In this the adult regression lines are separated by five times the standard deviation of either sex about its own regression line. Thus the chance of overlapping specimens is very small, and a consistent and readily determinable criterion for distinguishing the sexes is available.

TABLE 42

Morphological Correlation in *Sternotherus odoratus*, with Length of Plastron as the Independent Variable

Character	Correlation Coefficient, r'		Regression Coefficient, b'		Regression Constant, a'		Standard Error of Estimate	
	M	F	M	F	M	F	M	F
Width of carapace	.830	.761	.7006	.6487	17.34	18.02	3.28	2.69
Width of plastron, I	.914	.940	.3746	.4776	8.28	0.08	1.16	0.84
Width of plastron, II	.824	.496	.2384	.2516	5.58	2.32	1.14	1.73
Width of connecting bridge	.887	.810	.2197	.2803	−2.54	−5.80	0.80	0.99
Width of head	.874	.770	.3146	.2355	2.13	4.03	1.22	0.93
Tail length, I	.488	.372	.2029	.2061	11.12	−3.76	2.53	2.50
Tail length, II	.742	.649	.4636	.4676	3.42	−10.71	2.92	2.66
Preanal tail length	.669	.452	.2937	.1837	−2.27	−2.24	2.27	1.76
Postanal tail length	.488	.710	.1604	.2887	6.38	−8.74	2.00	1.39
Lateral width of tail, I	.544	.413	.1024	.0672	3.70	2.14	1.10	7.20
Lateral width of tail, II	.661	.207	.0399	.0070	−0.07	1.20	0.32	0.16
Thickness of tail	.673	.339	.1579	.0876	1.96	6.53	1.21	1.18

NOTE:—Values of r' above .463 are significant at the one per cent level; between .463 and .361 at the five per cent level; below .361 not significant.

As an example of the use of the method of partial correlation in determining the relationship between two secondary or subsidiary characters, when the body length, as measured by the carapace, is held constant, I shall take the relationship of preanal and postanal tail lengths. The unadjusted correlations are as follows:

	Male	Female
Length of carapace to preanal tail length	.644	.553
Length of carapace to postanal tail length	.424	.707
Preanal to postanal tail length	.250	.587

Eliminating that part of the correlation between tail lengths due to variation in carapace length, we have the following net correlation remaining as being the true correlation between the two sections of the tail: Males, $r = -.032$; females, $r = .333$.

Neither of these correlations is significant at the usually accepted level of $P = 0.05$, although the female figure approaches significance ($P = 0.053$). Thus, in turtles of the same carapace size, virtually no correlation is to be expected between preanal and postanal tail lengths. Similar calculations may readily be made on any other pairs of subsidiary characters.

A somewhat similar situation is presented in connection with the correlations in toad dimensions presented in Table 38. If we eliminate body-length variability by the method of partial correlation, the residual correlation between the length and width of the parotoid glands in the specimens of *Bufo woodhousii* from Tulsa is reduced from 0.715 to 0.297.

Included in the correlations presented in Table 36 is that between body length and diameter in *Leptotyphlops*. The value of this relationship in taxonomic problems has previously been discussed.[26] A new, and unusually large and homogeneous series is now available in the collection of the California Academy of Sciences. This is a series of over 150 *L. humilis cahuilae* collected by Joseph R. Slevin and Wallace F. Wood on a small island in the Colorado River at Laguna Dam, Imperial County, California. Measurements were made on diameter and length with the help of Mr. Slevin. The regression equation of diameter on length is found to be $D = 0.115 + 0.0152\ L$. The standard error of estimate is 0.238 mm., or 8 per cent, as the mean diameter of 155 specimens is 2.980 mm. This per cent deviation from the regression line may be considered constant at all ages, and may be used in taxonomic difference problems in the manner suggested elsewhere for tail lengths.[27] It is evident that the thickness-to-length ratio in these little snakes may serve as an important key character, if adequate and well preserved series are available.

The correlations set forth in Tables 36 to 42 indicate the correlations between pairs of body characteristics such as length and weight, or between

[26] Trans. San Diego Soc. Nat. Hist., Vol. 9, No. 18, p. 98, 1940.

[27] Bull. Zool. Soc. San Diego, No. 18, p. 40, 1943.

pairs of body measurements such as body and head lengths. Somewhat similar are the relations between body lengths and body products. For example, there is a positive correlation within a subspecies between the sizes of mother snakes and the number of young produced, as shown by the following examples of series of *Crotalus viridis viridis*:

Series	Gravid specimens	Correlation between length of mother and number of young
Platteville	149	0.711
Pierre	107	0.704

Another correlation of somewhat the same type is the relationship between snake size and venom yield. Here we should naturally expect that venom volume would vary approximately with the third power of some head dimension—head length, for example. In any case the correlation coefficient is not particularly useful for the measurement of such a relationship, since the result will depend too much on the ontogenetic composition of the sample, in addition to which the relationship is probably not linear. Venom yield is a characteristic requiring fuller treatment than can be given here; I hope that the opportunity may later be available to present some statistics that have been accumulated on this subject. As an indication of the extent of correlation in an adult series, I computed the statistics of venom yield in 189 adult *C. lucasensis* ranging in length from 800 to 1240 mm. The correlation coefficient was found to be +0.552. The regression equation is: liquid venom yield in c.c. = −1.25 + 2.06 times the length of the snake in meters. Thus a snake one meter in length would yield about 0.81 c.c. of liquid venom, while one 1.5 meters in length (an unusually large snake for this species) should yield about 1.84 c.c. These figures apply to fresh specimens and manual milking. The dispersion is considerable (the standard error of estimate is 0.35 c.c.), as might be expected in a situation in which so many extraneous factors may affect individual venom yield, such as the condition of the glands and the extent to which they have been depleted by recent feeding, defense, ill health, or captivity. The season of the year (proximity to hibernation) may also cause a variation. In any case, venom yield should preferably be studied by ascertaining the nature of regression lines and the dispersion about such lines, rather than a mere calculation of the coefficient of correlation, as has been pointed out with respect to other morphological variables.

The rattles of the rattlesnake offer some interesting possibilities for correlation studies. There are three main variables involved—the snake length, the width of the proximal rattle, and the sequence number of the rattle in the string. The latter value will be known only if the string be complete. The relationship of rattle width to sequence number is definitely non-linear through the complete life range, but is substantially linear up to rattle number 6 in most species. The relationship between body length and the width of the proximal rattle is of the type involving body parts

and therefore is certain to show a high correlation, if the sample comprises specimens of all ages. The final pair of this trio comprises body length and rattle number (complete strings only). There is considerable sexual dimorphism in the adult range so that the sexes must be treated separately. All of these rattle relationships I hope to make the subject of a paper to appear later in another publication series; however, as suggestions of the degrees of correlation involved, the results of calculations on the males of the Platteville series of *C. v. viridis* are given in Table 43. It will be seen that the correlations are very high in all three cases.

There is another rattle correlation of which I should like to present an illustration at this time, namely, the correlation between the widths of successive pairs of rings in a series of rattles. This is designed to answer the following questions: Are rattlesnakes with small No. 1 rattles likely to have small succeeding rattles, or is each rattle independent of its predecessor? Although there is known to be a high correlation between the width of the proximal rattle and body size, it must be remembered that body size can affect rattle width only at the time a rattle is being hardened on the matrix. Even if we take a number of snakes having the same number of rattles (speaking, of course, only of complete strings) we should not expect absolute correlation between the size of body and the rattle width because different times will have elapsed in the several individuals since the hardening of the proximal rattle. In other words, assuming, for example, that we are dealing only with snakes having 5 rattles, some may have just exposed the fifth rattle, while others may have developed the fifth rattle several months before and may, therefore, be definitely larger than when that rattle was cast loose. But if we can show correlation between successive rattles of a string, thus indicating that a large No. 1 rattle is likely to be coupled with a larger-than-average No. 2, and so on, we have an indication that some snakes continually outstrip their fellows in size; or, what would have the same effect, tend to acquire their rattles later.

The results of such calculations, using the males of the Platteville series, are also shown in Table 43. It will be observed that this type of correlation is relatively high, particularly from No. 2 rattle on; the conclusion is inescapable that the several segments of a rattle string do tend to follow each other in deviations from the mean. The calculations were not carried beyond rattle No. 6, since not enough complete strings were available to afford authoritative data.

Another method of indicating the relationship between the dimensions of successive rattles of a string is by the method of rank correlation. Table 44 shows the gradual shifting of ranks in the rattle widths, in the strings of ten randomly selected males of *Crotalus ruber* from coastal San Diego County. The ten strings are arranged in an ascending order of magnitude, based on the width of the button or No. 1 segment. Where there is a tie for a position in the table, fractions have been used if two are tied, and

TABLE 43

Rattle Correlations: Males of Platteville Series of *Crotalus v. viridis*

Characters	*N*	*r*
Over-all length of body and width of proximal rattle	443	0.984*
Over-all length of body and number of rattles (complete strings only)	223	0.982
Rattle width and sequence number (carried to rattle No. 6 only)	658	0.968
Correlations between the widths of successive rattle segments:		
Numbers 1 and 2	132	0.637
Numbers 2 and 3	99	0.867
Numbers 3 and 4	97	0.821
Numbers 4 and 5	87	0.863
Numbers 5 and 6	21	0.844

NOTE:—All values of *P* are less than 0.0001.
* The corresponding value for 388 females is 0.996.

the middle position if three are tied. In the table, as set up, low numbers indicate smaller rattle dimensions.

It will be observed that some strings are quite consistent in their positions in the schedule, while others tend to skip about. For example, string number 4 is consistently low after the first rattle, while strings numbers 9 and 10 are consistently high throughout. String number 8 is first high, then low for four segments, then high for the remaining four.

TABLE 44

Rank Positions in 10 Rattles of *Crotalus ruber* Each Having 9 Segments

String Number	Segment Number 1	2	3	4	5	6	7	8	9
1	1	1	2	4½	7½	6	4	7	2½
2	2	5	5	4½	5	4	7	4½	5½
3	3	7	7½	7	7½	7	2½	4½	2½
4	5	2	3	2½	2½	1½	2½	1	1
5	5	8	5	2½	1	3	5½	6	7
6	5	6	7½	7	5	5	5½	3	4
7	7	3½	5	7	5	1½	1	2	5½
8	8	3½	1	1	2½	8	8	8½	9½
9	9	9	9	9½	10	9	9½	10	9½
10	10	10	10	9½	9	10	9½	8½	8

TABLE 45

Rank Correlation Coefficients
in Ten Sets of Rattles of *Crotalus ruber*

Segment Number	Segment Number 2	3	4	5	6	7	8	9
1	.57	.43	.36	.21	.45	.53	.43	.73
2	....	.87	.62	.41	.57	.59	.47	.56
3	....	....	.89	.65	.45	.38	.23	.38
4	....	....	....	.86	.47	.25	.24	.19
5	....	....	....	....	.68	.34	.48	.15
6	....	....	....	....	....	.75	.85	.55
7	....	....	....	....	....	....	.82	.78
8	....	....	....	....	....	....	....	.75

NOTE:—The figures in the body of the table show the rank correlations between any set of segments as numbered in the left hand column and any other set as numbered at the top. For example, the correlation between the third segments of all strings and the corresponding seventh segment is 0.38.

In Table 45 I have presented the rank correlation coefficients, as computed from Table 44. This correlation coefficient is not to be confused with the product-moment correlation coefficient, *r*, hitherto used throughout this discussion, the rank coefficient being a less accurate, and less-often used, indication of concomitant variation. It is useful when it is desired to secure approximate results and the number of items is relatively low (10 in the present case), for the calculations are much less laborious than in the derivation of the product-moment correlation coefficient.

In the present instance the coefficient is interesting in illustrating certain trends; for example, it will be observed that the adjacent segments are likely to be closely correlated, as might be expected, and as evidenced by the lowest diagonal row of figures. Some of the low correlations are the result of high irregularities in particular strings. The lowest figure of all, that between segments 5 and 9, results almost entirely from four strings: 1 and 3, which become relatively smaller in the larger rattle sizes, and 5 and 8 which occupy higher positions when segment 9 is attained than at segment 5. It is surprising, and probably accidental, that the most widely separated segments, that is, numbers 1 and 9, should show so high a correlation as 0.73. Thus an original string-order which has practically vanished at segments 4 and 5, is returned to at the end of the string.

In another test, this time on the rattles of male *C. lucasensis,* there being nine strings of at least 8 rattles each, the order was somewhat better maintained throughout. The rank correlation between the buttons (first rattles) and the fifth segments was 0.79, and between the buttons and the eighth segments was 0.55. Thus, there is a decreasing correlation as the distance between segments increases, rather than a dip as in the *ruber* sample.

In all three examples, *viridis, ruber,* and *lucasensis,* the correlation between the button and second rattle was lower than between succeeding pairs of segments, thus indicating a probably characteristic sequence variability.

CORRELATION OF SUBCAUDALS AND TAIL PROPORTIONS

It might be expected that snakes with extra-long tails would have a higher than average number of subcaudals. This is not a particularly easy correlation to test, since the tail length changes with the growth of each snake, and we must either reduce each length of tail to the probable length at some standard body length,[28] or the comparison must be made using the tail-length proportion as one of the variables. But since the tail-length proportion itself involves sexual dimorphism and usually is not ontogenetically constant, if the proportion is to be used as one of the variables, it is necessary either to base the determination on specimens within a relatively narrow range with respect to age, or a correction for ontogeny must be made.[29] Specimens with incomplete tails must be omitted, and therefore a a species easy to sex and one in which the completeness of the tail may be readily ascertained, will comprise the best material for investigation. *Phyllorhynchus d. perkinsi* fulfills both of these requirements. The following correlations were found between the ratio of the tail length to length over-all, and the number of subcaudal scales, including in the study only adults of the Borego series exceeding 300 mm. in length:

	N	*r*
Males	139	0.503
Females	85	0.685

To see whether this correlation exists at birth, a test was made on the available broods of *Lampropeltis g. californiae* hatched in captivity at the San Diego Zoo. The correlations follow:

	N	*r*
Males	79	0.726
Females	70	0.750

In order to test a single brood, in which there could be no possibility of heterogeneity, I have used the counts and measurements of a brood of unborn young of *Natrix sipedon sipedon* from Windham, New Hampshire, recorded by J. A. Oliver and J. R. Bailey,[30] and find the following correla-

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[28] Occasional Papers San Diego Soc. Nat. Hist., No. 4, p. 22, 1938.

[29] Bull. San Diego Zool. Soc., No. 18, p. 40, 1943. The easiest method of making the correction for ontogeny, is to subtract a (or a') from each value of T before dividing by L (or B). It is assumed that the regression equation of T on L or B is known, otherwise one is compelled to restrict the investigation to snakes of about the same age.

[30] Biological Survey of the Connecticut Watershed, Report No. 4, p. 208, 1939.

tions between subcaudal counts and the ratio of tail length to body length (exclusive of tail):

	N	*r*
Males	18	0.765
Females	16	0.814

To try the alternate method of using a series of ontogenetically heterogeneous specimens, but correcting for ontogeny by using the constants of the regression equation, I have taken the Laguna Island series of *Sonora miniata linearis*. The results follow:

	N	*r*
Males	40	0.711
Females	58	0.394

Upon the rattlesnakes I have made two tests: the first on the San Patricio series of *C. cinereous*, all of which are young of the year, and the second on 200 adult *C. v. viridis* of the Platteville series, with these results:

	C. cinereous		*C. v. viridis*	
	N	*r*	*N*	*r*
Males	77	0.530	100	0.476
Females	61	0.368	100	0.429

Thus, correlation is present even in these short-tailed snakes. All of the correlations given above are highly significant ($P < 0.01$).

It will be noted that the juvenile correlations are higher than the adult. This suggests at once that the result may be caused by some special effect in the embryonic stage—that is, the longer the tail, the more scales are required to sheathe it properly. If this be the case we should find a correlation independent of tail proportionality, provided we can avoid the confusion produced by ontogeny and racial heterogeneity. This we can do by utilizing broods alone, treating each brood separately (for broods of the same subspecies often differ significantly in mean length at birth) and taking only those which have been preserved before birth, or soon enough afterward to avoid differential post-natal growth. With these restrictions we can compare directly tail length in millimeters and subcaudal scale counts, instead of tail proportionality and subcaudals as previously investigated. Material of this kind is not plentiful since the number of young of each sex should approximate 10 or more, and many species of snakes do not have such large broods.

In Table 46 the results of several such calculations are given. It will be seen that rather high correlations are the rule. Of course, the low values of *N*, imposed by the restriction to broods, prevents all but the highest values of *r* from being significant. However, if we combine the results

by the use of Fisher's z-transformation, we attain the following values, both of which are highly significant ($P = 0.0001-$): males, $r = 0.609$; females, $r = 0.615$.

TABLE 46

Correlation between Tail Lengths and Subcaudal Scale Counts in Snake Broods

Species	Locality	Males		Females	
		N	r	N	r
Elaphe laeta	Texas	7	0.854*	9	0.788*
Natrix s. sipedon†	Windham, N. H.	18	0.837**	16	0.865**
Thamnophis s. sirtalis†	Warren, N. H.	12	0.411	8	0.590
Thamnophis hammondii	San Diego County	14	0.465	14	0.287
Thamnophis hammondii	San Diego County	9	0.497	10	0.578
Thamnophis hammondii	San Diego County	12	0.256	20	0.398
Crotalus basiliscus	Sinaloa	10	0.592	14	0.640**
Crotalus basiliscus	Colima	14	0.617*	Too few	

* Significant; ** highly significant.

† Measurements from Oliver and Bailey.

I think there need be no hesitancy in concluding, both from the proportionality studies and those of absolute tail lengths in broods, that individuals with proportionately longer tails do have a higher than average number of subcaudals. One may speculate as to which is cause, and which effect, in this pair of characters. There is some evidence, in certain generic correlations, of there being an optimum size in various scales, so if there be a greater area to cover there will tend to be more scales to cover it. If such be the case, then proportionate tail length is the independent variable, and the number of subcaudal scales dependent. Possibly both variables are related to the number of caudal vertebrae; if this be true, both are dependent. The fact that these tail-ratio to subcaudal correlations tend to reduce with age indicates that the relationship is adversely affected by the exigencies of growth. It had occurred to me that the male-to-female ratio in tail lengths might be the same as the ratio in subcaudals; however, this would be impossible since the first ratio changes (in most species) with ontogeny, while the latter remains constant throughout life.

This tail-subcaudal correlation is another in which the homogeneity of the sample is of major importance; in a heterogeneous sample, a correlation would be anticipated and proofs based on such material would be quite irrelevant.

Although correlation has been shown to exist, in *P. d. perkinsi,* between subcaudals and tail spots, and likewise between subcaudals and tail-length

ratio, there is apparently only a slight correlation between tail spots and tail-length ratio, the results being as follows:

	N	*r*	*P*
Males	141	0.111	0.19
Females	85	0.221	0.04

A study of the same character made on the ringed phase of the broods of *Lampropeltis g. californiae* gave the following results, which show low and non-significant correlations:

	N	*r*	*P*
Males	28	0.108	0.58
Females	26	0.235	0.25

CORRELATION BETWEEN VENTRAL SCALES AND BODY LENGTH

The correlation between ventral scales and body length is somewhat analagous to that between subcaudals and length of tail, but is more difficult to test. For in the latter pair, which we have already discussed, we could fall back on the ratio of tail length to body size as a basis of comparison between specimens, thus avoiding the direct effect of age on tail length, and permitting the use of specimens not known to be of uniform age. In the present case we have available no such datum, and we are therefore compelled to find other means of eliminating the variability of body size because of age. In other words, we cannot prove that a certain snake has more ventrals than its fellows because of its larger size (or vice versa) without first assuring ourselves that the larger size does not merely result from greater age.

Here again we are handicapped by the slow, but continued, growth of adult snakes, as compared with the static situation in adult birds and mammals. It would be easy to determine whether there is any correlation between the sizes of the sparrows in a certain area and the numbers of some particular series of their feathers because we could eliminate the growth factor as affecting size by adhering entirely to adults. This we cannot do in snakes; if we take a group of snakes which we know to be adults because of their relationship with the sizes of juveniles and adolescents, and we compare the largest with the remainder, in some characteristics such as ventral scales, we are certain to be diluting the effect because the group comprising the remainder will contain individuals on their way up to becoming exceptionally large. Therefore, we must either accept, as proof of this correlation, lower figures than the true correlation because of this dilution, or, we must use some expedient to avoid the differential effects of age. The size variation, even in homogeneous series collected at a single season (at a hibernation den, for example), is sufficiently great so that, at best, only the young of the year and the first year class of adolescents can be segre-

gated from the rest of the population. Often even the one-year-old adolescents cannot be segregated, owing to overlapping with the lagging young adults.[31] And in the adult stage the individual variation in size, compared to the average annual growth, is so great as to obliterate completely any differences between the several yearly groups comprising the total adult population.[32]

The investigation which I have in mind is not to be confused with that which is concerned with the question of the elimination of defective juveniles or aberrants from a population—that is, whether there is a difference between the means (or standard deviations) of juvenile and adult populations through differential selection. That is a separate problem which has lately received attention from several authors.[33] The present study contemplates only the question whether the largest snakes in a single age-class have higher or lower ventral scale counts than others in the same class.

I have repeatedly stressed, to the point of boredom, the necessity of avoiding geographical or ecological heterogeneity in studies such as this, yet I cannot but mention it again in the present situation. Generic, specific, and racial correlations between size and ventral scales are already too well known to require any further proof, although the equations of these relationships may merit further study. But in the present problem we are interested only in the question of the existence of such a concomitant variation within a homogeneous population, and I cannot but caution once more against using a sample so diverse in origin as to involve the beginning of racial differentiation.

In fact, the present study has disclosed several instances wherein marked variations exist in the average and maximum sizes of snakes from localities quite closely contiguous. For example, *Diadophis amabilis similis* was found to reach a larger size in the foothill and mountain areas in San Diego County than around San Diego Bay. Greater rainfall and the denser inland vegetation evidently are more favorable conditions for this subspecies. This is rather to be expected since the species, in its general range along the Pacific Coast, prefers moist areas and is not found in the desert. This

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[31] See fig. 4, p. 20, Occ. Papers San Diego Soc. Nat. Hist., No. 3, 1937. Mr. Arnold Grobman, who suggested the existence of this type of correlation in correspondence in 1941, informs me that the segregation of one-year adolescents was found possible in a winter-den series of *Opheodrys vernalis*.

[32] *Op. cit.* p. 31.

[33] Klauber, L. M., Trans. San Diego Soc. Nat. Hist., Vol. 8, No. 20, p. 197, 1936; Bull. Zool. Soc. San Diego, No. 15, p. 18; Stuart, L. C., Misc. Pubs. Univ. Mich., No. 49, p. 18, 1941; Dunn, E. R., Am. Nat., Vol. 76, No 762, p. 104, 1942; Inger, Robert, Am. Nat. Vol. 76, p. 527, 1942; Vol. 77, p. 87, 1943.

correlation between size and rainfall is not universal in the genus, however, since the largest species, *Diadophis regalis laetus,* is found in a relatively arid area.

Similarly, in San Diego County, *Phyllorhynchus decurtatus perkinsi* reaches a maximum size in the vicinity of Benson's Dry Lake, and other areas at about the same distance from the foot of the mountains, decreasing both westward toward the mountains, or eastward out into the desert. But *Sonora occipitalis annulata* finds its optimum condition (if size be considered the criterion) somewhat further out in the desert, the largest specimens occurring in the unmodified desert areas surrounding the Imperial Valley. These observations prove again the necessity of reducing samples to rather narrow territorial limits, if true homogeneity is to be attained.

Another difficulty in this problem is that of obtaining fully representative samples of wild populations. This generally restricts the investigation to the smaller species, since the biggest specimens of the larger species are often not preserved because of their bulk, and thus the available specimens do not comprise a complete and unbiased sample of the population.

There is one kind of series which satisfies all conditions of homogeneity with respect to both age and locality—namely, broods. The same broods in which the tail length to subcaudal scale counts correlations were tested, were checked for the correlation between body length and ventrals, with the results set forth in Table 45. All correlations are found to be below the level of significance. The combined correlations are likewise without significance: males, $r = 0.173$, $P = 0.152$; females, $r = 0.044$, $P = 0.72$. Therefore it appears that snakes, at least as represented by these broods, start life without any evidence in their body characteristics of the kind of size to scale-count correlation found in the tails.

There is one other way in which these pairs of characters differ: subcaudals and tail lengths have somewhat the same coefficients of variation, but body lengths in broods are more variable than ventral scale counts, the latter being among the most consistent of herpetological characters. Example data are given in Table 48. It will be noted that the average variability in the body length is two or three times that of the ventrals, while tail length variability is less than 40 per cent above that of the subcaudals.

The same table indicates that the variability in the scale counts in broods is usually lower than in other series. In most series of snakes, even when territorially homogeneous, the coefficient of variation of the ventrals averages about 2 per cent, and the subcaudals usually run 5 per cent or more.

TABLE 47

Correlation between Body Lengths and Ventral Scale Counts in Snake Broods

Species	Locality	Males N	Males r	Females N	Females r
Elaphe laeta	Texas	7	−0.098	9	0.577
*Natrix s. sipedon**	Windham, N. H.	18	0.113	16	−0.205
*Thamnophis s. sirtalis**	Warren, N. H.	10	0.150	8	0.256
Thamnophis hammondii	San Diego County	14	0.352	13	0.048
Thamnophis hammondii	San Diego County	9	0.084	10	0.067
Thamnophis hammondii	San Diego County	12	0.050	20	−0.123
Crotalus basiliscus	Sinaloa	10	0.174	14	0.148
Crotalus basiliscus	Colima	14	0.324	Too few	

No correlations are significant.

* Measurements from Oliver and Bailey.

It is known, both from studies of captive broods and of series of young of the year collected at the time of hibernation, that variability of growth is considerable during the first months of life. Specimens which are successful in securing food grow rapidly, while others remain virtually static. Therefore, it is possible, even assuming no correlation between body length and ventrals at birth, that such a correlation might exist in young of the year sometime after birth. Two series were tested: The San Patricio series of *C. cinereous,* and a series of Platteville juvenile *C. v. viridis* collected in the autumn of 1931. The results, which are quite conflicting, follow:

	Males N	Males r	Males P	Females N	Females r	Females P
San Patricio *cinereous*	76	0.392	0.0005	63	0.296	0.019
Platteville *viridis*	66	−0.297	0.016	58	−0.076	0.57

It will be observed that there is positive correlation in *cinereous* and negative in *viridis,* although in the females of the latter it is not significant.

Series of snakes of approximately uniform ages may be secured at hibernating time in areas subject to such climatic conditions that the snakes resort to dens for the winter, provided it is possible to segregate the several age-classes. In the case of the rattlers this can be done with moderate accuracy by restricting the selection to snakes with some particular number of rattles, and excluding those with incomplete strings. For example, in eastern Colorado, in the autumn when the snakes are gathering at the dens, snakes with 5 rattles exceed those with 6 or 4, thus indicating that 5 is the mode for the group of snakes aged about 14 months, which are entering their second winter. Certainly none of these is two months old, and it is very doubtful if any is 26 months.

TABLE 48

Coefficients of Variation in Broods
(Expressed in Per Cent)

Species	Locality	Males				Females			
		Ventrals	Body Length	Subcaudals	Tail Length	Ventrals	Body Length	Subcaudals	Tail Length
Elaphe laeta	Texas	1.16	4.86	4.65	7.33	2.45	4.65	3.49	4.62
Natrix s. sipedon	Windham, N. H.	1.14	1.79	2.78	6.49	1.18	4.30	3.78	6.28
Thamnophis s. sirtalis	Warren, N. H.	2.03	1.61	3.31	1.74	1.81	1.00	2.92	2.91
Thamnophis hammondii	San Diego County	1.18	3.71	2.40	3.21	2.20	3.00	3.18	3.82
Thamnophis hammondii	San Diego County	0.90	3.03	3.58	4.58	1.77	4.13	3.24	5.35
Thamnophis hammondii	San Diego County	1.44	6.32	1.88	6.65	0.92	3.25	2.22	4.14
Crotalus basiliscus	Sinaloa	1.24	1.60	5.67	5.56	1.35	1.80	6.46	5.49
Crotalus basiliscus	Colima	1.29	5.79	4.34	4.48	Too few		Too few	
Unweighted mean		1.30	3.59	3.58	5.01	1.67	3.16	3.61	4.92

NOTE:—Calculations of standard deviations have been corrected to optimum population estimates.

I have therefore surveyed the rattlers of the Platteville series which were collected around the dens in autumn, taking only those with complete strings of 5 rattles, and have calculated the correlations between body length and ventral scutes, with the following results:

Males			Females		
N	*r*	*P*	*N*	*r*	*P*
44	−0.011	0.94	51	0.157	0.28

No significant correlation is indicated and we may assume that, if any really exists, it is masked by individual variations at this time of the life cycle, which represents a period of rapid growth.

One obvious method of testing whether the largest snakes in any series have higher than average ventral counts is to compare the means of the larger specimens with the general means, although the general means will, as I have stated, be somewhat affected by snakes on their way up to becoming unusually large specimens. I have applied this method to the Platteville and Pierre series of *C. v. viridis* with the following results:

	Platteville		Pierre	
	Males	Females	Males	Females
Lower limit of large specimens, mm.	860	790	940	860
Number of large specimens	26	26	34	50
Total specimens	441	392	342	333
Mean ventrals, large specimens	179.885	185.769	177.706	183.840
Mean ventrals, all specimens	178.868	185.806	176.775	184.045
Difference between means	1.017	−0.037	0.931	−0.205
Significance of difference, *P*	0.097	0.954	0.091	0.675

These differences prove to be below the usually accepted level of significance, although the males approach that level. It is therefore indicated that the large males may have a slightly higher average number of ventrals than the rest of the population, while no such correlation with age is evident among the females.

Possibly in this test I have taken too large a proportion of the population in the category of "large" specimens. Some herpetologists with whom I have discussed this problem have expressed the opinion that the correlation with size would be evident only in a few unusually large individuals —specimens of outstanding size which seem to occur in every large series. For such a study I shall take the largest territorially homogeneous series available to me, although restricting the investigation to the smaller species of snakes in which the field collector would be likely to retain every available specimen, thus affording an unbiased sample of the population. For such purposes I have selected the five largest individuals of each sex in each series, and have determined how many of these possess more ventrals

than the mean of the series. I think this a better test than to compare the mean of the five with the mean of the series, as by this method each individual is given separate recognition. We can then determine whether the disposition of the extra-large specimens, above and below the species means,[34] deviates from a haphazard arrangement.

The results of this study, which included seven species, are presented in Table 49. It will be observed that in every instance more than half of the large specimens have more ventral scutes than the mean of their series; in five cases, three out of five individuals are above the mean; in seven series, four are above; and in two series every one of the specimens is higher than the group mean. Altogether, 53 out of 70 specimens are above the means of their respective series. The possibility of such a high proportion having resulted from chance is less than one in ten thousand. I am particularly impressed with the evidence deduced from the series of *A. q. sargii, G. nasalis,* and *S. m. linearis,* all of which were collected in such restricted localities that there is no possibility of the correlations having resulted from ecological clines. The first two were secured in cafetal debris within a few hundred square feet; the latter on an island covering but a few acres. I therefore conclude that in these little snakes the largest adults do tend to have higher than an average number of ventral scutes.

From these several types of tests it may be concluded that, in homogeneous series of snakes of approximately the same age, correlation is not generally evident between size and the number of ventral scales, but the largest individuals do tend to have an above-average number of ventrals.

CHANGES OF SCUTELLATION WITH AGE

The question whether unusually large snakes have more ventral scales than their fellows is in some degree related to the problem of possible changes in either the means or dispersion of scale characters with age. Robert F. Inger (1942, 1943) has lately reported some studies of this nature, particularly with respect to abnormalities in juveniles and their absence from older groups.

Deformed and freakish juveniles in broods born in captivity and in clutches of eggs hatched in the laboratory are quite common, but whether exceeding the proportion of aberrants occurring under natural conditions, I cannot say. We know, at least, that the growth curves of snakes under the artificial conditions of captivity are considerably distorted. This can be easily deduced from measurements, either of the snakes themselves, or of the rattle strings of rattlesnakes. At any rate, aberrant individuals in broods are frequently encountered. Some are so deformed that they obviously would not survive, as for example, snakes without eyes, with malformed heads, or twisted bodies. Often low records for ventral or sub-

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[34] It would be more accurate to use the median, but, as the ventral distributions are substantially normal, we will not err appreciably if the mean be taken as the datum.

TABLE 49

Comparison of Ventrals of Five Largest Specimens with Mean Ventral Counts

Species	*Adelphicos q. sargii*		*Geophis nasalis*		*Diadophis a. similis*		*Phyllorhynchus d. perkinsi*		*Toluca l. varians*		*Sonora m. linearis*		*Sonora o. annulata*	
Series	Volcan Zunil		Volcan Zunil		Vic. San Diego City		Borego		Acultzingo		Laguna Island		Borego	
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Number of specimens	74	63	124	91	108	102	209	143	72	70	41	55	141	67
Body lengths, 5 largest, mm.**	224	294	242	241	311	362	420	442	268	281	259	263	289	319
	223	283	239	237	304	338	416	434	254	262	259	255	271	295
	221	279	238	233	291	328	414	423	247	256	257	251	270	293
	218	273	231	233	290	326	413	419	245	254	245	250	270	293
	214	267	231	229	287	325	408	416	233	253	242	248	270	281
Ventrals, 5 largest	127	136	124*	130*	188	201*	174	190*	125*	136*	159*	167*	151	172*
	128*	141*	124*	125*	196*	212*	176*	184	123	132	154	165	159*	167*
	129*	134	124*	123	192*	211*	176*	185	128*	136*	161*	172*	158*	168*
	127	139*	122*	123	192*	204*	176*	191*	129*	129	158*	170*	159*	168*
	134*	142*	122*	126*	192*	196	176*	192*	128*	133*	158*	169*	156*	163*
Mean ventrals, entire series	127.12	137.70	120.48	123.56	190.22	200.70	174.09	187.80	124.11	132.57	155.61	166.46	152.73	162.25

* Individuals with more ventrals than the group mean.

** It should be emphasized that these are body lengths only, not lengths over-all.

caudal scale counts within a subspecies are established by these juveniles. Some quite freakish individuals have survived in captivity; for example, at the San Diego Zoo there is a pair of adult *Pituophis c. annectens* with heads so disproportionately small as to be ludicrous. But most of these extreme deformities must be lethal, and this comparatively early in life. Therefore, whether average differences between juveniles and adults are found will depend somewhat on the age at which the young are preserved. If the young are preserved at birth, unquestioned differences will be evident, as discussed by Dunn and others, and as Inger has proved. Also, if broods comprise a large part of the juvenile comparative material, they may in themselves introduce group divergences inherited from their parents.

With the thought that it would be worth-while to investigate possible differences in scalation in different age groups, after the lethally deformed have been eliminated, I have taken my two largest homogeneous series of rattlers, the Platteville and Pierre series of *C. v. viridis*, both of which were collected at dens in the fall or spring, and have arbitrarily divided them into three groups by size: juveniles, immatures (adolescents), and adults. The group dimensional limitations were decided upon after examining the distribution histograms for low points in frequency, which would indicate year-class boundaries; probably few individuals have been placed in an incorrect category. Complete rattle strings also aided in reaching decisions. The limits of the categories, and the number of specimens available, are as follows:

	Platteville			Pierre		
	Limits	M	F	Limits	M	F
Juveniles	up to 399 mm.	125	104	up to 419 mm.	80	72
Immatures	400-649 mm.	114	124	420-699 mm.	99	83
Adults	650 mm. and up	202	164	700 mm. and up	163	176
Totals		441	392		342	331

Ontogenetic differences in scale counts might be attributed either to differential selection or to actual changes in the scales themselves. I think it is usually assumed that no such changes occur in the scales, as would be judged by the relationship of each shed skin with its successor, although I know of no published statistical proof of this continuity. Differential selection might affect either the mean count of a series of scales, or the dispersion about that mean.

Tables 50 and 51 show the means, standard deviations, and coefficients of variation for each age group of the two series of rattlesnakes. I should call attention to the fact that in these tables the figures after the decimal points are not carried out as far as they were in the computations; to do so tends to make a visual study of the results more difficult. This procedure explains possible discrepancies which might appear in cross-checking. Also, it is to be remembered that there were slight variations in N (as compared to the figures given above) because of an occasional specimen in which,

TABLE 50

Variations in the Statistics of Characters with Age
Platteville Series of *Crotalus v. viridis*

Character	Mean			Standard Deviation			Coefficient of Variation, per cent		
	J	I	A	J	I	A	J	I	A
Scale rows	26.41	26.59	26.43	0.959	0.948	0.954	3.63	3.57	3.62
Ventrals, male	178.92	178.86	178.84	3.326	2.795	3.016	1.86	1.72	1.69
Ventrals, female	185.77	186.12	185.59	3.419	2.784	3.336	1.84	1.50	1.80
Subcaudals, male	25.71	26.49	26.01	1.424	1.448	1.485	5.54	5.47	5.71
Subcaudals, female	20.37	20.41	20.24	1.239	1.510	1.745	6.08	7.39	8.62
Supralabials	14.73	14.79	14.75	0.803	0.860	0.858	5.44	5.82	5.81
Infralabials	15.77	15.99	15.84	0.992	0.928	0.970	6.29	5.82	6.13
Body blotches, male	42.88	41.96	42.02	3.585	3.059	3.558	8.34	7.29	8.47
Body blotches, female	43.74	43.03	42.40	3.479	2.798	3.422	7.95	6.50	8.07
Tail rings, male	9.82	9.53	9.59	1.186	1.010	1.269	12.08	10.60	13.24
Tail rings, female	7.59	7.32	7.30	0.924	0.938	0.930	12.10	12.82	12.74

J—juvenile; I—immature; A—adult.

TABLE 51

Variations in the Statistics of Characters with Age
Pierre Series of *Crotalus v. viridis*

Character	Mean			Standard Deviation			Coefficient of Variation, per cent		
	J	I	A	J	I	A	J	I	A
Scale rows	26.51	26.58	26.50	0.936	0.968	1.012	3.53	3.64	3.82
Ventrals, male	176.20	176.65	177.12	3.303	3.121	3.000	1.87	1.77	1.69
Ventrals, female	183.94	184.45	183.85	3.242	3.378	3.294	1.76	1.83	1.79
Subcaudals, male	26.11	26.03	26.22	1.411	1.274	1.357	5.40	4.89	5.17
Subcaudals, female	20.20	19.75	20.19	1.497	1.383	1.432	7.42	7.00	7.09
Supralabials	14.92	14.89	14.95	0.795	0.847	0.899	5.33	5.69	6.06
Infralabials	15.92	15.80	15.77	0.955	0.987	0.938	6.00	6.26	5.96
Body blotches, male	44.43	43.64	43.50	3.569	2.929	3.075	8.01	6.71	7.07
Body blotches, female	44.09	43.53	43.70	3.215	2.883	3.385	7.29	6.64	7.74
Tail rings, male	9.68	10.16	10.24	1.134	1.360	1.247	11.73	13.39	12.18
Tail rings, female	7.40	7.43	7.53	1.030	1.061	1.166	13.93	14.28	13.51

J—juvenile; I—immature; A—adult.

through injury, some character may be indeterminate. It is impossible to tabulate all these details without expanding the tables beyond all reason.

All differences were tested in pairs for significance. With respect to the means, 17 out of 66 were found to be significant at the usually accepted 5 per cent level, and, of these, 9 reach high significance ($P < 0.01$). However, I do not consider such statistics of particular moment, since, with these relatively large samples, small and unimportant differences may prove statistically significant. It is more important to consider the differences quantitatively and with respect to consistency in trend. As far as the latter is concerned, there is no character in which a uniform trend is observable in both sexes and in both series. By this I mean a consistent directional trend from the juveniles, through the immatures, to the adults, or in the reverse direction. Thus, in the Platteville series, the means of three characters increase slightly but consistently from the adult to the juvenile stage; these are: male ventrals, female body blotches, and female tail rings. Yet not one of these trends is validated by the Pierre series, and in two instances they are reversed. The consistent trends in the latter series are toward higher means from juveniles to adults in male ventrals, and male and female tail rings; and in the opposite direction in infralabials.

From the standpoint of significance, the greatest differences are those between the subcaudals of the males of the Platteville series (juveniles to immatures) and the infralabials of the same pair.

Quantitatively the differences are best measured and compared by the coefficients of divergence. While differences up to 4 per cent in the pattern criteria are not unusual and in one case reach 5.67 per cent (juveniles to adults in the male tail rings of the Pierre series), these are not of great importance, since the pattern characters are quite variable and cannot be counted with particular accuracy. On the other hand, few scale characters exceed one per cent between any pair; in fact, except for the subcaudals, the only pair having a divergence exceeding one per cent is the infralabials in the Platteville series (juveniles to immatures) which is 1.39 per cent. The subcaudal differences reach 3.70 per cent in the Platteville series (male juveniles to immatures) and 2.25 per cent in the Pierres (female juveniles to immatures). But even here there is no consistency, for in one case the juveniles are higher, while in the other the contrary is true. I therefore conclude that, as far as these two series are concerned, there is no material ontogenetic change in mean scale counts, either because of differential selection, or an actual change in the scales themselves, were any proof of the latter considered necessary.

As to the coefficients of variation, the important point is to determine whether there is a reduction in variability from juveniles to adults by reason of the elimination of defective or aberrant juveniles. In these two series of rattlers, if there were any considerable number of freak youngsters at birth, they must have been eliminated before the snakes gathered at the dens. For in the Platteville series, only four characters out of eleven

show a decrease in variability from juveniles to adults, while in the Pierre group six out of eleven show this decrease. And these juvenile-to-adult differences only reach a significant level in two out of 22 cases; these are female subcaudals of the Plattevilles, and supralabials in the Pierres. Furthermore, in both of these cases the adults are more variable than the juveniles. I think we may conclude, without question, that in these two series of rattlesnakes, we have no evidence of a consistent decrease in variability with age, in these characters of scalation and pattern. I re-emphasize the fact that these conclusions are based on populations from which the extreme defectives at birth have already been eliminated.

ACKNOWLEDGMENTS

In a paper such as this, which attempts to illustrate a variety of types of correlation, I have drawn freely for basic material—that is, both measurements and scale counts—on the published and unpublished records of others. While my own collection contains some thousands of specimens of snakes from the southwest, including several homogeneous series of the type upon which these studies are based, many kinds of paired variables could not be secured therefrom. For data of this kind I have had recourse to certain papers of Boulenger, Cochran, Deraniyagala, Dunn, Oliver and Bailey, Van Denburgh and Slevin, and Wall, which are listed in the bibliography. For unpublished series of scale counts on snakes, I am greatly indebted to the following: Dr. Howard K. Gloyd, Chicago Academy of Sciences; Mr. Arthur Loveridge, Museum of Comparative Zoology; Dr. James A. Oliver, American Museum of Natural History; Mr. Karl P. Schmidt, Chicago Natural History Museum; Dr. Hobart M. Smith, University of Rochester; and Dr. Edward H. Taylor, University of Kansas. An exceedingly complete series of turtle measurements were supplied by Dr. P. L. Risley of the State University of Iowa. Valuable and extensive original series of measurements on amphibians were generously contributed by Mr. M. Graham Netting, Carnegie Museum; Mr. Coleman J. Goin, University of Florida; and Dr. Albert P. Blair, New York Zoological Society. Dr. Henry S. Fitch kindly placed at my disposal all of the scale counts and measurements which were made in the course of preparation of his fine monograph on the garter snakes of the *ordinoides* group. To Mr. Joseph R. Slevin, of the California Academy of Sciences, I am not only indebted for many valuable series of scale counts, but also for laboratory assistance in making large numbers of measurements. I have had the advantage of discussing some of the problems treated herein with Mr. Charles M. Bogert, Dr. Raymond B. Cowles, Mr. Arnold Grobman, Dr. Ernst Mayr, and Mr. Thomas Rodgers. Scale counts in my own laboratory have been made by Lawrence H. Cook, James F. Deuel, Robert S. Hoard, Philip M. Klauber, Harvey Wylie, Robert Menzies, and especially Charles E. Shaw. I was much aided in the making of tabulations and statistical computations by Mrs. Elizabeth Leslie, Harry Omar, Charles E. Shaw, Doris Heyneman, and my daughter, Alice K. Miller. As usual, I have had the advantage of the valuable criticisms and suggestions of Mr.

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SUMMARY AND CONCLUSIONS

1. Some uses of correlation studies are outlined. The present investigation adheres to homogeneous series.

2. Methods of making correlation tests, and of interpreting results are discussed.

3. The necessity for standardizing character definitions and methods of measurement to insure comparable statistics is pointed out.

4. Examples are given of the use of the correlation coefficient as a measure of bilateral symmetry in characters which exist separately on the two sides of the body. Cases wherein a variable can take only one of two values are cited in terms of the tetrachoric correlation coefficient.

5. A number of characters entailing rather wide dispersions are investigated with respect to bilateral symmetry. Most correlations of this character are high. The use of correlation tables as illustrations of concomitant variation are shown to be preferable to the usual tabular summaries. Such correlation tables often increase accuracy by suggesting a recheck of aberrant specimens; they also aid in devising more accurately restrictive keys.

6. Incomplete lateral scale rows of snakes have a bilateral symmetry which increases with an increase in the total proportion of the snake's body that they occupy.

7. By the method of partial correlation, studies are made of the horizontal, vertical, and diagonal linkage between labial scales. In two series of rattlesnakes, the horizontal correlations are found to be significantly higher than the vertical or diagonal, between which there is in turn no significant difference. In several colubrids these conclusions are confirmed, except that the vertical correlation is higher than the diagonal.

8. Some of the same characters investigated for bilateral symmetry were also tested for net bilateral unbalance. Some unbalances are found, amounting in one case to a divergence of over 6 per cent.

9. A number of correlations between different series of scales are computed both in rattlers and other snakes. Where sexual dimorphism is evident in a character, it is essential to treat the sexes separately.

10. There is no indication of correlation between scale rows and ventrals in rattlesnakes. Correlation is occasionally present between ventrals and subcaudals, especially in the males. Significant correlations are

often found between different series of head scales, particularly in contiguous pairs. Correlation is evident between dorsal scale rows and labials, but not between ventrals and labials.

11. Colubrids offer less fruitful fields than rattlesnakes for testing correlations, as they have fewer variable scale series.

12. There is usually no correlation between ventrals and subcaudals in most colubrids and other non-rattlers. This applies to homogeneous series; examples are presented showing how a fictitious correlation results in a series which is heterogeneous with respect to sex, locality, or species (through misidentification).

13. One boid and two colubrid species are selected, because of character variability, for study of paired scale series. A correlation between scale rows and labials is again in evidence. Some other correlations are disclosed, particularly between pairs of head scales.

14. The number of dorsal scale rows at different parts of the body are correlated in *Pituophis*.

15. A few example lizard scale correlations are derived.

16. Studies of pattern correlations in snakes are made. There is a fairly high correlation between body blotches and tail spots. Correlation between ventral scales and body blotches is rare, but between subcaudal scales and tail spots or rings is frequent.

17. It is pointed out that the correlation coefficient is not a particularly good criterion for the study of morphological correlations, which are sure to be high because of the mutual effects of growth. However, a number of examples are given for both reptiles and amphibians. Such relationships are better studied by determining the character of the regression line and the dispersion about that line. An example study of sexual dimorphism is given.

18. The method of partial correlation may be employed to ascertain the true net correlation between a pair of characters if both are subsidiary to a third. A set of examples, based on head dimensions in a series of garter snakes, is given.

19. A few correlations in body products (young and venom) are cited.

20. A variety of correlations involving the rattles of rattlesnakes are worked out.

21. A moderate correlation is the rule between proportionate tail length and the number of subcaudal scales of snakes.

22. Correlation between body length and ventral scales can only be determined for groups of uniform age. Such a correlation seems absent in broods. However, in homogeneous series of snakes the largest individuals are likely to have more than an average number of ventrals.

23. Two large series of rattlesnakes, collected at hibernating dens, are divided into three age classes: juveniles, immatures, and adults. Studies of group means and coefficients of variation indicate no definite trends in either scale characters or blotches. Thus, aberrant juveniles, which might be expected to cause high dispersions, have already been eliminated at the time of entering hibernation.

REFERENCES

Arkin, H. and Colton, R. P.
1940. Statistical Methods, Fourth Edition. New York.

Baten, W. D.
1938. Elementary Mathematical Statistics. New York.

Boulenger, G. A.
1920. Monograph of the Lacertidae, Vol. 1. London.

Chesire, L.; Saffir, M. and Thurstone, L. L.
1933. Computing Diagrams for the Tetrachoric Correlation Coefficient. University of Chicago.

Clark, F. H.
1941. Correlation and Body Proportions in Mature Mice of the Genus *Peromyscus*. Genetics, Vol. 26, pp. 283-300.

Clark, P. J. and Inger, R. F.
1942a. Scale Reduction in Snakes. Copeia, pp. 163-170.
1942b. Scale Reduction Studies in Certain Non-Colubrid Snakes. Copeia, pp. 230-232.

Cochran, Doris M.
1941. The Herpetology of Hispaniola. Bull. U. S. Nat. Mus., No. 177, pp. VII + 398.

Croxton, F. E. and Cowden, D. J.
1939. Applied General Statistics. New York.

Deraniyagala, P. E. P.
1939. The Tetrapod Reptiles of Ceylon. Vol. I, Testudinates and Crocodilians. Colombo.

Dunn, E. R.
1915. The Variations of a Brood of Water Snakes. Proc. Biol. Soc. Washington, Vol. 28, pp. 61-68.
1923. The Salamanders of the Family Hynobiidae. Proc. Amer. Acad. Arts and Sciences, Vol. 58, No. 13, pp. 445-523.
1942. Survival Value of Varietal Characters in Snakes. Am. Nat., Vol. 76, No. 762, pp. 104-109.

Ezekial, M.
1941. Methods of Correlation Analysis, Second Edition. New York.

Fisher, R. A.
1941. Statistical Methods for Research Workers, Eighth Edition. Edinburgh and London.

Fitch, H. S.
1940. A Biogeographical Study of the *Ordinoides* Artenkreis of Garter Snakes (Genus *Thamnophis*). Univ. Calif. Pubs. in Zool., Vol. 44, No. 1, pp. 1-150.

Hagood, Margaret J.
1941. Statistics for Sociologists. New York.

Hubbs, C. L.; Hubbs, L. C. and Johnson, R. E.
1943. Hybridization in Nature between Species of Catostomid Fishes. Cont. Lab. Vert. Zool., Univ. Mich., No. 22, pp. 1-76.

Hubbs, C. L. and Whitlock, S. C.
1929. Diverse Types of Form Development in a Single Species of Fish, the Gizzard Shad. Papers Mich. Acad. Sci., Arts, and Letters, Vol. 10, pp. 461-482.

Inger, R. F.
1942. Differential Selection of Variant Juvenile Snakes. Am. Nat., Vol. 76, No. 766, pp. 527-528.
1943. Further Notes on Differential Selection of Variant Juvenile Snakes. Am. Nat., Vol. 77, No. 768, pp. 87-90.

Kenney, J. F.
1939. Mathematics of Statistics, 2 Vols. New York.

Klauber, L. M.
1931. A Statistical Survey of the Snakes of the Southern Border of California. Bull. Zool. Soc. San Diego, No. 8, pp. 1-93.
1936a. A Statistical Study of the Rattlesnakes: I Introduction; II Sex Ratio in Rattlesnake Populations; III Birth Rate. Occ. Papers San Diego Soc. Nat. Hist., No. 1, pp. 1-24.
1936b. A Key to the Rattlesnakes with Summary of Characteristics. Trans. San Diego Soc. Nat. Hist., Vol. 8, No. 20, pp. 185-276.
1937. A Statistical Study of the Rattlesnakes: IV The Growth of the Rattlesnake. Occ. Papers San Diego Soc. Nat. Hist., No. 3, pp. 1-56.
1938. A Statistical Study of the Rattlesnakes: V Head Dimensions. Occ. Papers San Diego Soc. Nat. Hist., No. 4, pp. 1-53.
1939a. A Statistical Study of the Rattlesnakes: VI Fangs. Occ. Papers San Diego Soc. Nat. Hist., No. 5, pp. 1-61.
1939b. A Further Study of Pattern Dimorphism in the California King Snake. Bull. Zool. Soc. San Diego, No. 15, pp. 1-23.
1940a. A Statistical Study of the Rattlesnakes: VII The Rattle. Occ. Papers San Diego Soc. Nat. Hist., No. 6, pp. 1-62.
1940b. The Worm Snakes of the Genus *Leptotyphlops* in the United States and Northern Mexico. Trans. San Diego Soc. Nat. Hist., Vol. 9, No. 18, pp. 87-162.
1941. The Frequency Distributions of Certain Herpetological Variables. Bull. Zool. Soc. San Diego, No. 17, pp. 5-31.
1943a. Tail-length Differences in Snakes with Notes on Sexual Dimorphism and the Coefficient of Divergence. Bull. Zool. Soc. San Diego, No. 18, pp. 1-60.
1943b. A Graphic Method of Showing Relationships. Bull. Zool. Soc. San Diego, No. 18, pp. 61-76.

Oliver, J. A. and Bailey, J. R.
1939. Amphibians and Reptiles of New Hampshire. Biol. Surv. Conn. Watershed, Survey Report No. 4, pp. 195-217.

Peters, C. C. and Van Voorhis, W. R.
1940. Statistical Procedures and Their Mathematical Bases, New York.

Risley, P. L.
1930. Anatomical Differences in the Sexes of the Musk Turtle, *Sternotherus odoratus* (Latreille). Papers Mich. Acad. Sci. Arts and Letters, Vol. II, pp. 445-464.

Simpson, G. G. and Roe, Anne
1939. Quantitative Zoology. New York.

Stuart, L. C.
1941. A Revision of the Genus *Dryadophis* Stuart. Misc. Pubs., Mus. of Zool., Univ. Mich., No. 49, pp. 1-106.

Tippett, L. H. C.
1937. The Methods of Statistics, Second Edition. London.

Treloar, A. E.
1939. Elements of Statistical Reasoning. New York.

Van Denburgh, J.
1920. A Further Study of Variation in the Gopher-Snakes of Western North America. Proc. Cal. Acad. Sci., Ser. 4, Vol. 10, No. 1, pp. 1-28.

Van Denburgh, J. and Slevin, J. R.
1913. The Galapagoan Lizards of the Genus *Tropidurus*. Proc. Calif. Acad. Sci., Fourth Ser., Vol. 2, pp. 133-202.

Wall, F.
1923. Notes on Snakes Collected on Annasigalla Estate from August, 1920, to December, 1921. Spolia Zeylanica, Vol. 12, Part 46, pp. 252-270.

Yule, G. U. and Kendall, M. G.
1937. An Introduction to the Theory of Statistics, Eleventh Edition. London.