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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 97

Variation and Relative Growth in the Plastral Scutes of the Turtle *Kinosternon integrum* Leconte

BY

JAMES E. MOSIMANN

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
November 7, 1956

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VARIATION AND RELATIVE GROWTH IN THE PLASTRAL SCUTES OF THE TURTLE *KINOSTERNON INTEGRUM* LECONTE*

INTRODUCTION

MANY of the characters used in the taxonomy of turtles express a relation between two measurable parts. If the parts are growing differentially with respect to each other, the taxonomic representation of the relation of the two necessarily includes variation due to ontogenetic change. Since characters expressing such relations may often be of significance in describing geographic variation, the problem of relative growth in turtles merits investigation, not only for its own sake, but also because an evaluation of these growth-affected characters is of taxonomic importance.

Information on proportional changes correlated with increase in size is scattered through papers of diverse purpose. Many works on chelonian growth, with measurements made in respect to age, age classes, or time, contain implicit information of this sort. Examples of papers wherein authors either have made explicit statements or have designed graphs to indicate the relation of two characters include: Seeliger (1945) *Clemmys marmorata;* Crenshaw and Hopkins (1955) *Trionyx ferox* and *Trionyx spinifer;* Lagler and Applegate (1943) *Chelydra serpentina;* Woodbury and Hardy (1948) *Gopherus agassizi;* Risley (1930) and Klauber (1945) *Sternotherus odoratus;* Liu and Hu (1940) *Geoclemmys reevesi;* Cagle (1946, 1948*a*) *Pseudemys scripta;* Cagle (1954) *Chrysemys picta.* Others have been concerned with the growth of plastral scutes either directly in analyzing their growth, or indirectly in determining the age of individuals or in estimating their previous sizes. Examples of these usages include: Cagle (1946, 1948*b*, 1950, 1952, 1954) *Pseudemys scripta, Chrysemys picta,* and *Malaclemys terrapin;* Risley (1933) *Sternotherus odoratus;* Liu and Hu (1940) *Geoclemmys reevesi;* Sergeev (1937) *Emys orbicularis.*

Ewing (1939) worked on the dermal shields of the carapace of *Terrapene carolina.* Since his results are concerned with scute growth, they are of interest here.

A bibliography of growth in turtles as a general topic was given by Cagle (1946). Works on relative growth are, of course, found in numerous fields. In Huxley (1932) and Thompson (1952) various taxonomic groups are considered. Bibliographies may be found also in Reeve (1940), Olson (1951), Snyder (1954), and McIntosh (1955).

Much of the work done in the field of relative growth has been concerned with the practice of ascribing particular biological theories of growth to the mathematical forms of descriptively valid equations. In the present paper such a discussion is not necessary since the mathematical regressions used seem justifiable on purely descriptive statistical grounds. (For an example of a discussion of theories based on the mathematical forms of descriptive equations, see Simpson and Roe, 1939.) Kavanagh and Richards

*Received for publication March 26, 1956.

(1942) present a useful critical mathematical and logical study of some difficulties involved in studying relative growth.

The purpose of this report is to place on record my observations on variation and relative growth in the plastral scutes of a large sample of the turtle *Kinosternon integrum* from a localized geographical area and to present an analysis of the possible sources of the variation observed. Since the turtles used in this study were collected from an extremely localized area, I regard the variations represented by this sample of *K. integrum* as an example of those which can accrue in turtles not separated from each other by spatial or temporal factors. There is no apparent reason to think that the locomotor abilities of a given individual are not sufficient to permit it to traverse the area of collection during its lifetime. Thus, it is assumed that there is at least the physical possibility that each of the adult animals collected could have encountered any other, and that this sample might, as a result, represent an interbreeding population. The use of the word "population" in field studies may connote more than is actually known regarding the groups of animals studied. In order to avoid possible confusion with an actual interbreeding population in the sense of Dobzhansky (1951:15), I am limiting the term, implying only a relation between locomotor ability and area of collection. The possibility that the definition of Dobzhansky may be applicable to this population of turtles so considered by me is obvious. The use of the term population in an abstract statistical sense, often requiring infinity as one of its characteristics, is avoided for the sake of clarity.

Acknowledgments

Gratefully, I wish to thank the following persons, all of the University of Michigan, who have materially aided in the progress of this study. Dr. C. C. Craig of the Statistical Research Laboratory and Dr. P. J. Clark of the Institute of Human Biology have furnished aid in the statistical treatment of the data. In this regard I wish particularly to acknowledge the aid of Dr. F. E. Smith of the Department of Zoology and of Dr. W. B. McIntosh of the Laboratory of Vertebrate Biology. All responsibility, however, for statistical uses and interpretations is my own.

I wish further to thank Mr. George B. Rabb and Dr. C. F. Walker of the Museum of Zoology for critical comments and suggestions during the course of this work. To Dr. Norman Hartweg of the Museum of Zoology I am particularly indebted. The photographs were taken by Dr. W. E. Duellman.

MATERIALS AND METHODS

Material

Available for this work was a series of *K. integrum* from an area of approximately one square mile at the edge of the town of Coalcoman, Michoacan, Mexico. Thirty-seven individuals (UMMZ[1] 103937-73) were taken by J. A. Peters on August 1, 1950, and 133 more (UMMZ 104826-33,

[1]UMMZ = University of Michigan Museum of Zoology.

104835-959) were collected by W. E. Duellman in late July and early August, 1951. Of these, 164 were suitable for measurement and are included in this report.

Measurements

Vernier calipers were used to measure plastron and carapace length. The latter is the straight-line distance, not the arc, from the most anterior to the most posterior part of the carapace. The plastron length was also

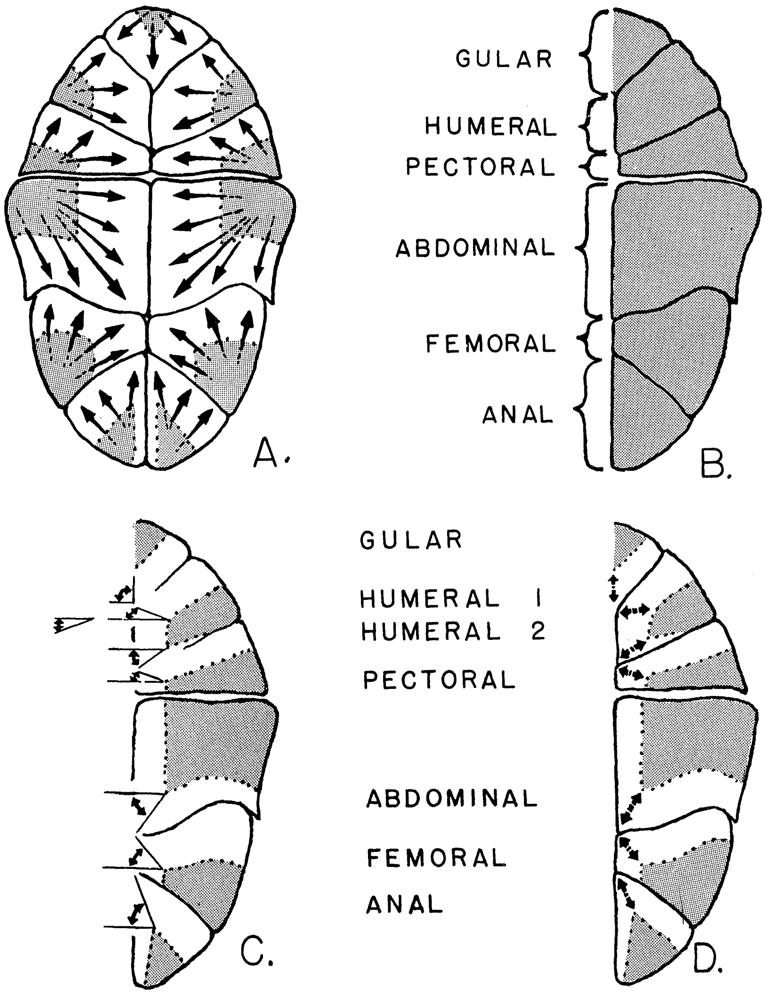

Fig. 1. Measurements and direction of growth in the plastron of *K. integrum:* A. Direction pattern of growth in plastral scutes; B. Mid-line measurements of each scute; C. Angular measurements to mid-line junctions with other scutes; D. Increment measurements of angular growth to mid-line from the point on a growth ring indicating the previous mid-line junction to the present mid-line junction of the scute with another.

taken in a single plane and was measured from the most anterior part of the plastron to the anal notch. In those turtles in which the anterior lobe was elevated, length was measured after the lobe had been forced into the same plane as the rest of the plastron. Throughout this study the anterior lobe is regarded as the part anterior to the hinge between the pectoral and abdominal scutes; the posterior lobe, the part posterior to that hinge.

Both the right and left plastral scutes were measured at mid-line (Fig. 1), but since there appeared to be little difference between the measurements, those of the left only were used for analysis. In some of the larger individuals it was difficult to determine scute borders because of lack of definitive margins (Pl. I, Fig. 1). Since error in measurements was probably relatively greater in scutes with lesser mid-line extent, measurements of the pectoral and femoral are presumably the least accurate and that of the abdominal the most accurate. I was not able to determine on the basis of external characters the sex of most individuals with plastra less than 110 mm., although all larger ones were easily determinable (Pl. I, Fig. 2).

TABLE I

Statistical Formulae and Tables Used and Referred to in the Text

Formulae	*References*
Regression equation	Hoel (1947:80)
Regression coefficients "a", "b"	Hoel (1947:85)
Significance of "a" (t_a)	Kenney and Keeping (1951:210)
Variance and standard deviation from regression ($S^2_{y.x}$, $S^2_{x.y}$, $S_{y.x}$, $S_{x.y}$)	Snedecor (1950:119, 122)
Variance and standard deviation (S^2, S)	Fisher (1950:46)
Correlation coefficient (r)	Hoel (1947:85)
Partial correlation coefficient ($r._L$)	Fisher (1950:188)
Normal curve fit	Kenney (1947:124-25)
X^2 test for goodness of fit	Hoel (1947:187)
Coefficient of variation	Snedecor (1950:40)
Line of organic correlation (reduced major axis)	Kermack and Haldane (1950:40 [1.2])
Tables	
Table of X^2	Snedecor (1950:190)
Table of Student t	Snedecor (1950:65)
Table of significance of r	Snedecor (1950:149)
Normal distribution ordinates	Kenney (1947:237-39)

Measurements were also made of angular scute increments; that is, the distance from the point on the last growth ring, indicating its previous mid-line juncture, to the present mid-line juncture, at the angle of the scute's growth toward mid-line (Fig. 1). These measurements of angular increments were obtained by means of an ocular micrometer at a magnification of 15 diameters. Most of the large turtles had no clear growth lines on their scutes and thus were not usable for this type of measurement. Data on angular increments were obtained from 57 turtles.

The mid-line dimensions of growth rings were measured for six turtles, and the sums of each series of scute growth lines were used to estimate previous plastron lengths. In this way the changes of mid-line measurements in the ontogenies of these individuals were approximated. Also, in two turtles the angle between a line perpendicular to mid-line and a line drawn from the point indicating the previous scute juncture on one growth ring to the similar point on the next added ring was measured through the succession of recognizable growth lines (Fig. 1). This was done to determine ontogenetic change in the angle of scute growth to mid-line.

Statistical Methods

Statistical formulae have been adapted and utilized from various texts, and references to the actual formulae and statistical tables used in this study are given in Table I.

RELATION OF MID-LINE SCUTE LENGTHS TO LENGTH OF PLASTRON

Scute Mid-line to Plastron Length Regressions

Scatter graphs were made of each plastral scute (left) mid-line dimension against plastron length (Figs. 2-7). The sex of individuals with plastra 110 mm. or longer was obvious. All were definitely adults, but no obvious gross sexual differences were indicated, although slight differences may possibly exist in the anal scute length relative to plastron length.[2]

Six sets of straight-line regression equations of the form $Y = bX + a$ and $X = b'Y + a'$ were computed as estimates of the average relation between each of the plastral scute mid-lines and plastron length. These lines were fitted to the data by the method of least squares; the sum of the squares of the deviations in Y was minimized for the first, and that of X for the second. The variances about the two regressions are not the same, reflecting the difference in the total or marginal variances between the scutes and plastron length (Table II).

Unfortunately, the regression statistics used here are strictly applicable on theoretical grounds only to those cases in which one of the variates is measured without error and hence is independent. This requirement is not satisfied in the present data, and thus it has been necessary to assume

[2]A graph of a sample of 72 *Kinosternon integrum* from the Rio de Colima, near Coquimatlan, Colima, in the University of Michigan Museum of Zoology shows clearly sexual dimorphism in the anal scute mid-line to plastron length relation. To judge visually, the variance about the regression line is higher than in the Coalcoman sample.

each variable in its turn as independent. This necessitates the use and interpretation of two regressions, the X on Y and the Y on X. With perfectly correlated data (r = 1) the two regressions are the same. With decrease in correlation from one, the X on Y line and the Y on X line diverge, until with no correlation (r = 0) they are perpendicular to each other; however, for purpose of the estimation of one value of a variate from a known value of the other, either the X on Y line or the Y on X line should be used.

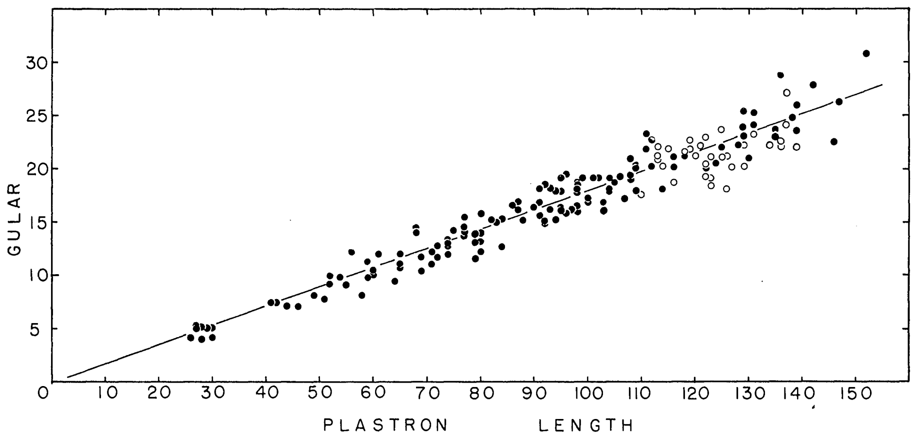

Fig. 2. Relationship between gular scute mid-line length and plastron length for 164 individuals of *K. integrum* from Coalcoman. For 110 mm. plastra and larger, black circles indicate males; hollow circles, females. Below 110 mm. plastra, black circles indicate either sex. Only the Y on X regression with plastron length as the independent variable is plotted.

For prediction of scute length from a known plastron length the Y on X regression, when plastron length is treated as the independent variable, should be utilized. For prediction of plastron length from a known scute length, when the scute measurement is regarded as the independent variable, the X on Y regression is the proper one to use. For the present data it would seem that plastron length is logically the better "independent" variable, since plastron length would seem to condition scute growth more than the latter would determine plastron growth.

Recently, Teissier (1948) has proposed the use of a single line in characterizing biological relations when neither variable is independent. Kermack and Haldane (1950), Kruskal (1953), and Teissier (1955) have further discussed the use of such a line termed the "line of organic correlation." The use of such a line is not a substitute for the use of the X on Y or Y on X regression. It does, however, give a single estimate of the trend of the scatter of points. Furthermore, the slope of this line is not directly related to the correlation coefficient. This line has been computed by techniques given in Kermack and Haldane (1950) for the reduced major axis of the correlation surface.

TABLE II

Statistical Data, Regressions, and Correlations Between Plastron Length and Mid-line Scute Lengths

All length measurements in millimeters.

	N	$\overline{Y}$ or $\overline{X}$	S	CV (Per Cent)	$CV_{y.x}$ (Per Cent)	r	y = b x + a	$S^2_{y.x.}$	$S^2_{x.y}$	x = b′ y + a′
Plastron (x). .	164	95.6	30.0	31.4	....	....	....	....	....	....
Gular	164	16.9	5.54	32.7	8.7	.964**	y = 0.18 x - 0.06	2.19	64.25	x = 5.22 y + 7.11
Humeral . . .	164	11.9	3.72	31.2	17.4	.826**	y = 0.10 x + 2.14	4.44	288.3	x = 6.65 y + 16.1
Pectoral . . .	164	4.7	2.06	43.9	33.4	.651**	y = 0.045 x + 0.42	2.46	522.1	x = 9.49 y + 51.1
Abdominal . .	164	29.2	10.2	34.9	4.7	.991**	y = 0.33 x - 2.42	1.87	16.22	x = 2.92 y + 10.3
Femoral . . .	164	8.0	3.19	39.8	26.1	.757**	y = 0.08 x + 0.32	4.37	387.3	x = 7.13 y + 38.5
Anal	164	24.7	7.89	32.0	9.0	.960**	y = 0.25 x + 0.54	4.89	70.84	x = 3.65 y + 5.50

$CV_{y.x} = \frac{100\, S_{y.x}}{\overline{Y}}$; for r, two asterisks (**) indicate significance from zero at the 1 per cent level.

Average Relations of Plastral Scutes to the Plastron

To determine whether regression is significantly present, a test was made of each correlation coefficient (r). Since all correlation coefficients were significantly different from zero at the 1 per cent level of significance, all regression slopes were also significantly different from zero.

The straight-line fits are thought to be accurately applicable in plastron lengths of about 30 to 150 mm., although relative to the estimates from

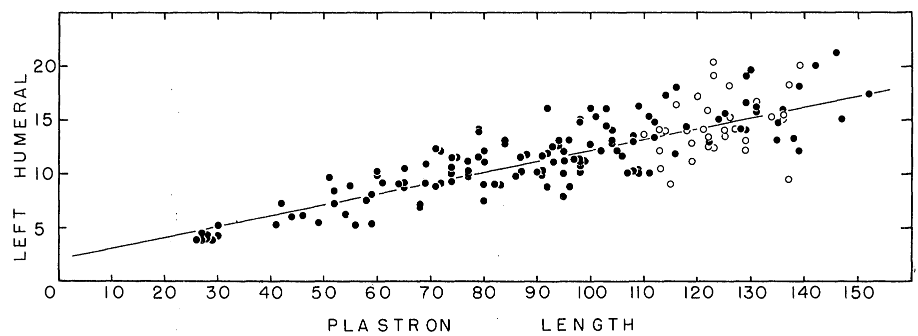

Fig. 3. Relationship between left humeral scute mid-line length and plastron length for 164 individuals of *K. integrum* from Coalcoman. See Fig. 2 for explanations.

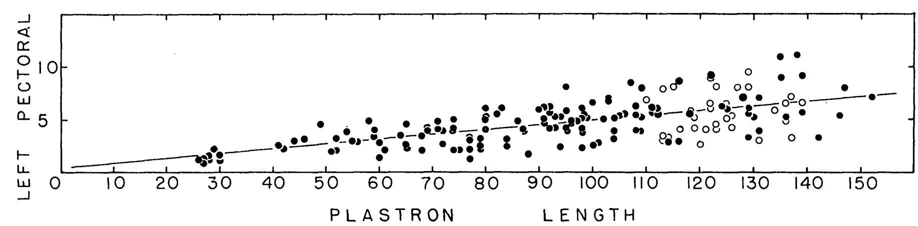

Fig. 4. Relationship between left pectoral scute mid-line length and plastron length for 164 individuals of *K. integrum* from Coalcoman. See Fig. 2 for explanations.

larger plastra the 30 mm. estimates are probably poor. The graph (Fig. 5) for the abdominal scute seems to indicate some curvilinearity, and it is obvious that errors could occur in the use of the straight-line fit. That these errors are slight, however, is indicated by the very high coefficient of correlation (r = .991).

Since the arithmetic mean is that value from which the sums of squares of deviations are a minimum, and since the regressions are fitted by minimizing the sums of squares of deviations from the regression, the regression equations themselves can be considered as means. The equations, therefore, represent estimates of average proportional change in plastral scutes.

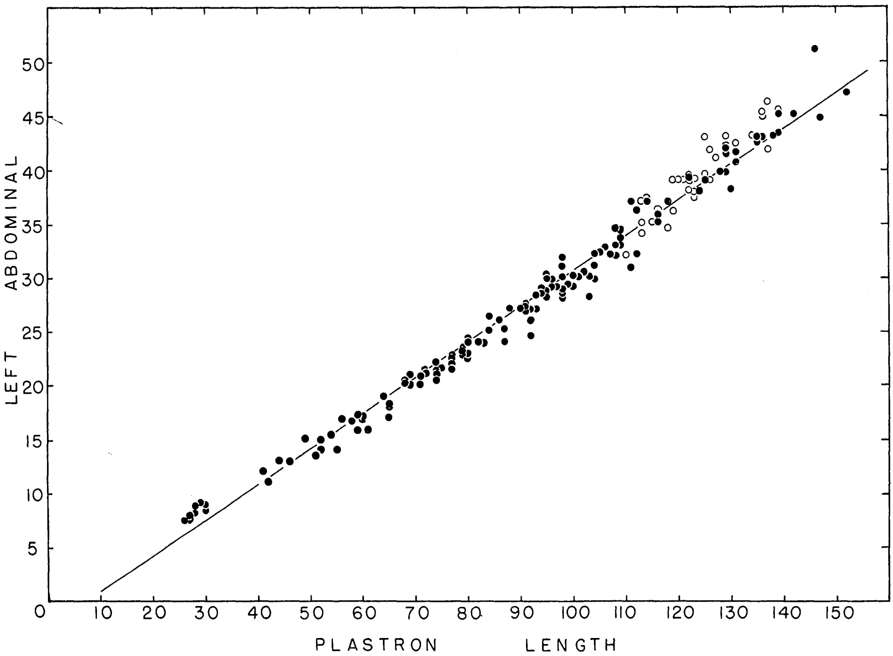

Fig. 5. Relationship between left abdominal scute mid-line length and plastron length for 164 individuals of *K. integrum* from Coalcoman. See Fig. 2 for explanations.

By noting the value for each of the scutes on plastron length (Y on X) regressions at plastron lengths of 30, 50, 60, 90, 120, and 150 mm., average plastra were constructed for these sizes (Table III). These averages, of course, do not necessarily represent the growth of any individual turtle, although the approximation may be very close. Some limitation should be placed on the interpretation of these plastra, since they represent separately

TABLE III

Average Plastra for Coalcoman *K. integrum* as Estimated from the Y on X Regressions

	Plastron Lengths (in mm.)					
Plastron	30	50	60	90	120	150
Gular	5.34	8.94	10.74	16.14	21.54	26.94
Humeral	5.14	7.14	8.14	11.14	14.14	17.14
Pectoral	1.77	2.67	3.12	4.47	5.82	7.17
Abdominal	7.48	14.08	17.38	27.28	37.18	47.08
Femoral	2.72	4.32	5.12	7.52	9.92	12.32
Anal	8.04	13.04	15.54	23.04	30.54	38.04
Total	30.49	50.19	60.04	89.59	119.14	148.69

TABLE IV

Growth Records of Individual Turtles as Obtained from Measurements of the Growth Lines of Plastral Scutes

Plastron lengths estimated by summation of growth-line lengths are enclosed in parentheses. Measurements (in mm.) are not necessarily those of all the visible growth lines on the plastron of the specimen concerned.

	Gular	Humeral	Pectoral	Abdominal	Femoral	Anal	Plastron Length
UMMZ 104890							
Present size	13.2	14.0	2.2	23.2	7.1	19.6	79
	10.5	10.8	1.8	18.8	6.7	15.2	(64)
	6.5	6.5	1.3	11.9	4.2	10.3	(41)
UMMZ 104899							
Present size	16.6	9.7	4.9	26.2	6.2	21.7	86
	15.6	9.6	4.2	24.5	6.2	21.4	(82)
	14.4	8.9	4.1	22.6	6.0	19.6	(76)
	13.4	8.8	4.0	21.0	5.9	18.9	(72)
	11.5	8.4	3.4	17.9	4.5	15.9	(62)
	8.6	5.7	2.9	13.6	3.4	12.5	(47)
UMMZ 104873							
Present size	22.0	15.6	5.9	39.0	13.0	27.7	125
male	18.2	14.8	5.3	33.1	10.2	24.2	(106)
	16.5	13.6	4.5	30.0	9.4	23.0	(97)
	14.1	12.3	4.2	24.8	8.5	18.4	(82)
UMMZ 104911							
Present size	21.0	19.6	5.2	38.2	13.6	29.6	130
male	16.7	18.8	3.7	32.7	11.5	26.7	(110)
	14.4	17.5	3.1	29.5	10.1	25.1	(100)
	12.6	15.0	3.1	25.4	8.6	21.5	(86)
UMMZ 104851							
Present size	27.9	20.1	3.2	45.2	12.1	34.8	142
male	21.0	17.2	2.5	36.0	10.3	27.7	(115)
	16.0	12.2	2.5	27.8	9.0	20.0	(87)
UMMZ 104894							
Present size	23.3	10.2	6.0	30.8	8.4	31.1	111
male	20.6	11.7	5.6	25.4	7.0	26.9	(97)
	11.3	7.7	4.5	16.5	5.4	15.6	(61)
	8.0	6.2	3.4	12.1	3.4	11.0	(44)

gained estimates of jointly varying biological entities. Also, mean estimates for the six scutes reflect varying degrees of accuracy due to different variances. The use of these averages in computing ratios between scutes is subject to limitation because of this and also because the mathematical ratio of two means and the mean of a ratio gathered from the same data need not be the same. Nevertheless, the plastra do provide the best independent mean estimates obtained from this study for the average Coalcoman turtle.

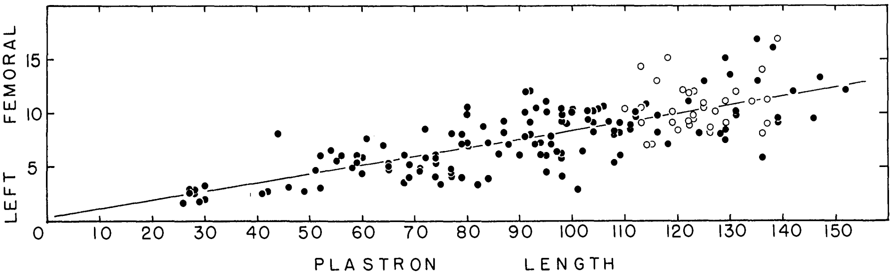

Fig. 6. Relationship between left femoral scute mid-line length and plastron length for 164 individuals of *K. integrum* from Coalcoman. See Fig. 2 for explanations.

Histories of growth in six turtles were obtained from measurements of growth lines by using these measurements as estimates of past scute sizes (Cagle, 1946). By comparing these measurements (Table IV) with the regression values for mid-line scutes against plastron length, it may be seen that the growth of an individual turtle can follow closely the average which

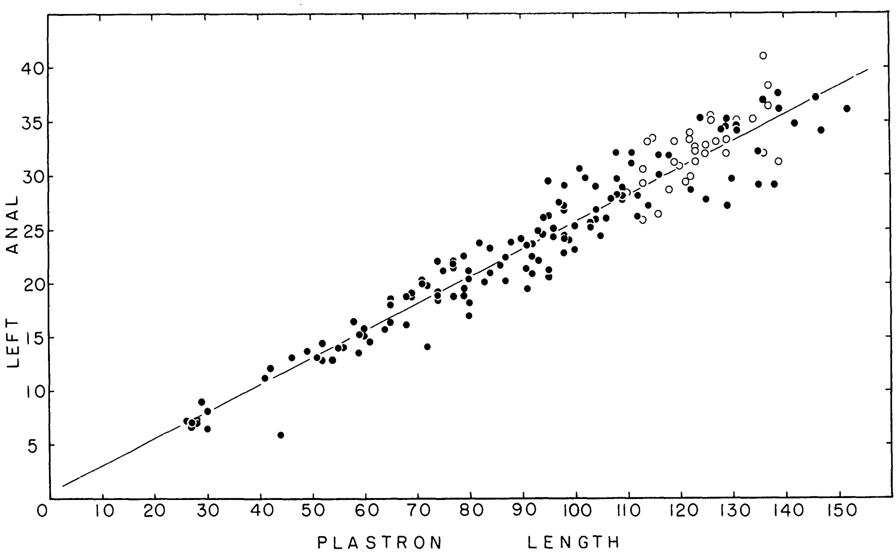

Fig. 7. Relationship between left anal scute mid-line length and plastron length for 164 individuals of *K. integrum* from Coalcoman. See Fig. 2 for explanations.

the regression represents for the Coalcoman population. The higher the correlation of the scute with plastron length, the closer the path of individual growth approximates the average of the population. The humeral scute of UMMZ 104894 showed an actual decrease in mid-line border with an increase of plastron length over one interval.

Proportional Changes in Scute Mid-line to Plastron Length

To test for proportional changes in the scute-plastron percentage, the regression lines were extended to the Y and the X axis, respectively. If "a," the intercept of the regression Y = bX + a, is zero, then Y = bX, the ratio Y/X = b, and thus this ratio is constant. This means that on the average there is no proportional change in such a ratio as plastron length increases. A test of the significance of observed deviation from scute over plastron percentage constancy can be made by testing whether or not "a" differs significantly from zero. If "a" is not zero, then over the interval for which the straight-line fit is applicable, changes in the ratio Y/X, or scute over plastron, are occurring.

TABLE V

Results of Tests of Significance of the Intercepts of the Regressions for Scutes and Plastron, and Carapace and Plastron

A positive intercept for a Y on X line (representing the intercept measured on the Y axis) equals a negative intercept for the corresponding X on Y line (representing the intercept measured on the X axis).

Measurements Related (Length)	Y on X Regression	X on Y Regression
Gular (y) vs. plastron (x) . . .	Y = 0.18 X - 0.06	X = 5.22 Y + 7.11*
Humeral (y) vs. plastron (x). .	Y = 0.10 X + 2.14**	X = 6.65 Y + 16.1**
Pectoral (y) vs. plastron (x). .	Y = 0.045 X + 0.42	X = 9.49 Y + 51.1**
Abdominal (y) vs. plastron (x).	Y = 0.33 X - 2.42**	X = 2.92 Y + 10.3**
Femoral (y) vs. plastron (x). .	Y = 0.08 X + 0.32	X = 7.13 Y + 38.5**
Anal (y) vs. Plastron (x) . . .	Y = 0.25 X + 0.54	X = 3.65 Y + 5.50*
†Carapace (y) vs. plastron (x).	Y = 0.9957 X + 8.10**	X = 0.9960 Y - 7.31**

*The intercept is significantly different from zero at the 5 per cent level of significance.

**The intercept is significantly different from zero at the 1 per cent level of significance.

†Measurements of turtles with plastra less than 110 mm. in length, and female turtles with plastra longer than 110 mm.

A drawback to this statistical method of testing for relative changes during growth is that it is indirect. Since the data here are bivariate and lack an independent variable, it has been necessary to use two regression lines and to interpret the intercepts of both. Moreover, there is no statistical reason why the tests of intercepts of the two lines fitted to the same data should give the same result, especially in cases of low correlation where the Y on X and the X on Y lines diverge considerably. In cases of high correlation, however, there should be little conflict in the results as interpreted from each regression.

The results of the intercept tests for regression lines are somewhat difficult to interpret because of the above-mentioned need for the use of the two regressions in interpreting the relation between each scute and plastron length (Table V). Of the six plastral scutes, only the abdominal shows clearly an average change in proportion to plastron length with the latter's increase. Both of the intercept tests and lines indicate a relative increase in the abdominal mid-line seam. For the remaining scutes there is no such clear-cut demonstration. The Y on X lines and the X on Y lines have diverged sufficiently because of less than perfect correlation so that significance tests of the two regression intercepts, and the lines themselves, give conflicting results. Since it is evident that the sum of plastral scute lengths is approximately equal to plastron length, it follows that there should be some average proportional reduction in the mid-line space of another plastral scute or scutes. The only scute with a change in this direction testing significantly different from zero by the intercept test is the humeral; however, the results of the X on Y intercept test and line and the Y on X intercept test and line for this scute differ. It would seem that the inconsistent results are due to the low correlation of this scute with plastron length. Very probably this scute shows an average decrease in plastral mid-line relative to plastron length increase. (This is supported somewhat by the ratio plot in Figure 11.)

The lines of organic correlation computed for the present data do not facilitate the interpretation of the differential growth relations in plastral scutes (Table VI). These lines, by definition, lie between the corresponding X on Y and Y on X regressions. The abdominal scute is thus indicated as having a positive proportional increase. No scute is shown as having a corresponding proportional decrease. The logical necessity for such a scute and the sole candidacy for this position of the humeral scute are unchanged. The fact is that it is difficult to demonstrate small proportional changes between two variables with a medium or low correlation.

A consistent presentation of the six plastral scute mid-line relations to plastron length is given by the six Y on X regressions. These six regressions are comparable in the sense that the same independent variable, plastron length, is assumed for all. They indicate for the abdominal a proportional increase to plastron length; for the humeral, a decrease; and for the remaining scutes no average proportional change with plastron length as the latter increases.

The proportional change shown for the abdominal scute is small, involving an increase of about 3 per cent of plastron length from a 50 mm. plastron to a 150 mm. one, and an increase of about 6 per cent from a 30 mm. plastron to a 150 mm. one. The probably real decrease shown by the Y on X line for the humeral scute is the same in percentage as the increase given above for the abdominal. Some of the four other scutes may have small proportional changes relative to plastron length increase, but it is not possible to detect them in the present data.

Reeve (1940) has criticized the use of the "a" test ("b" in Reeve's terminology) on the grounds that the standard error of "a" is a function of the mean ($\overline{X}$) of the independent variate. This results in an increase in the standard error of "a" with increase in the mean $\overline{X}$. Such increase reflects the graphically obvious fact that the farther the data are removed from the Y axis, the less accurate an estimate of "a," the Y intercept, becomes. Reeve thus shows the inefficiency of testing differences in position of two sample regression lines by means of testing the differences between their respective "a's."

TABLE VI

Y on X Regressions, Organic Lines of Correlation, and X on Y Regressions for Scute Length (Y) vs. Plastron Length Relations

The top line of each triplet is the Y on X; the middle, the organic line of correlation; the bottom, the X on Y (expressed as "y on x").

Gular (Y)	Y = .1777 X - 0.0558
	Y = .1846 X - 0.7139
	Y = .1913 X - 1.3606
Humeral (Y)	Y = .1025 X + 2.1422
	Y = .1240 X + 0.0886
	Y = .1503 X - 2.4228
Pectoral (Y)	Y = .0447 X + 0.4218
	Y = .0687 X - 1.8697
	Y = .1054 X - 5.3814
Abdominal (Y)	Y = .3312 X - 2.4170
	Y = .3400 X - 3.2583
	Y = .3428 X - 3.5241
Femoral (Y)	Y = .0804 X + 0.3206
	Y = .1063 X - 2.1518
	Y = .1403 X - 5.4037
Anal (Y)	Y = .2523 X + 0.5377
	Y = .2628 X - 0.4655
	Y = .2737 X - 1.5071

Reeve's objections do not seem to apply to the present usage. First, the "a's" are being tested from a hypothetical value, zero, not from another sample estimate of "a," and second, the values of $\overline{X}$, or the mean of plastron length, are the same at least for the six Y on X regressions, affording consistency in the estimates of the standard error of "a" for these six regressions.

PLASTRON LENGTH TO CARAPACE LENGTH RELATIONS

A scatter plot was made of carapace length on plastron length (Fig. 8). Here sexual dimorphism is clearly evident, and therefore the sexes were treated separately. Both X on Y and Y on X regressions were fitted to

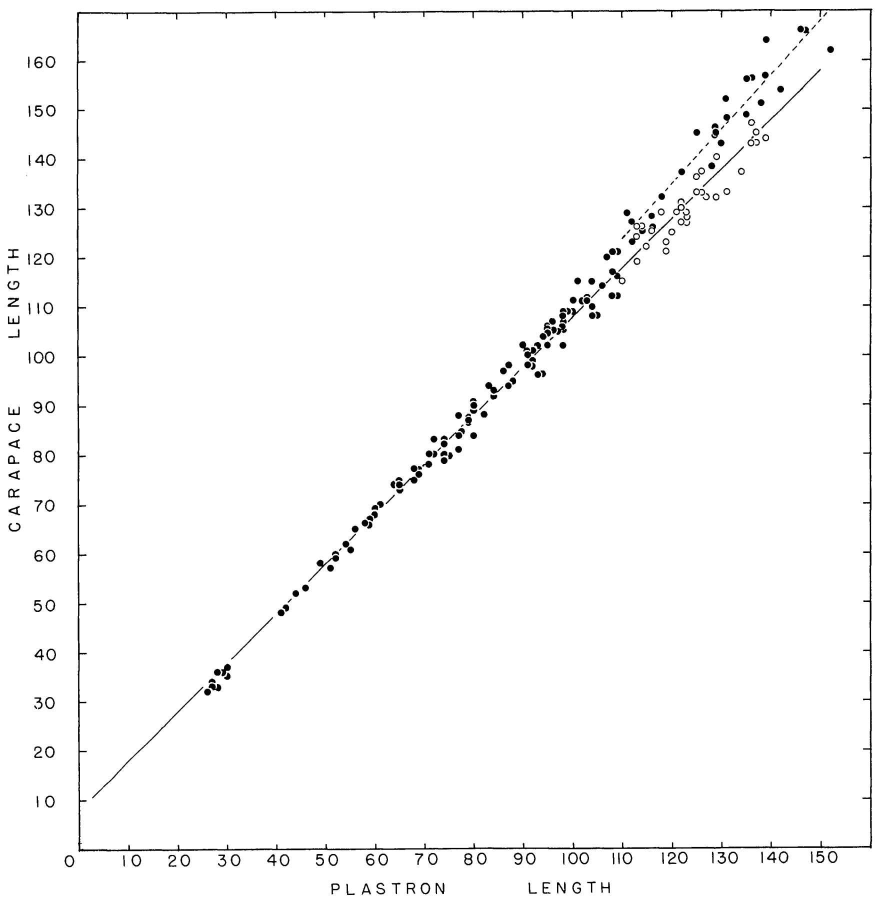

Fig. 8. Relationship between carapace length and plastron length for 162 individuals of *K. integrum* from Coalcoman. For 110 mm. plastra and larger, black circles indicate males, hollow circles indicate females. Below 110 mm. plastra, black circles indicate either sex. The solid line, the Y on X regression with plastron length as the independent variable, is shown fitted to undetermined individuals and females. The dotted line is shown fitted to the males alone.

turtles of undetermined sex (plastra below 110 mm.) plus females. There is a very high coefficient of correlation between plastron length and carapace length ($r = .996$). The high correlation coefficient seems to justify the use of the single line fitted to females and juveniles and indicates the same line or trend for both. Males, although deviating from the consistent linear trend exhibited by females and undetermined individuals, retain more juvenile proportions than do adult females (Fig. 8). Another line (carapace on plastron) was fitted to males alone. Taken together, males plus juveniles seem to show a somewhat curvilinear relation. The treatment here of fitting a line to the females plus juveniles and not to males plus juveniles is somewhat arbitrary. As was done for the regressions of mid-line scute dimensions against plastron length, a test was made of the intercepts to determine the significance of the observed proportional changes between plastron and carapace length. Tests were made only on the female plus juvenile pair of lines. The result (Table V) indicates a significant change in the plastron over carapace ratio with increase in size. The undetermined individuals and females showed an increase in plastron over carapace length ratio of 16 per cent with an increase in plastral size from 30 to 140 mm. Thus, in a ratio of plastral scute over carapace length, the chances for finding proportional change are considerably greater than in a ratio of plastral scute over plastron length.

SCUTE MID-LINE TO SCUTE MID-LINE RELATIONS

Scute Mid-line to Scute Mid-line Correlations

A study was made of the interrelation of the plastral scutes at mid-line, that is, the relation of the scute dimensions to each other. The length of all scutes is strongly correlated with plastron length (Table II), and the simple correlations between the scutes strongly reflect this relationship, rather than actual relations of the scutes to each other. The positions of adjacent scutes in the plastron suggest that as a scute has a larger mid-line dimension, its neighbor has a relatively smaller one and thus that the two are negatively correlated. The correlation coefficients, however, do not indicate this, since all simple scute-scute correlations are positive (Fig. 9). This reflects, as noted previously, the common correlation of both with plastron length.

Interscute relations were analyzed separately for the anterior plastral lobe (gular, humeral, and pectoral scutes) and the posterior plastral lobe (abdominal, femoral, and anal scutes). Partial correlations were used to estimate the relation of one scute with another, independent of the correlation of either with plastron length. Thus, the partial correlations are used as a measure of the effect of one scute on another at mid-line, with the joint effect of plastron length on both eliminated. The results (Fig. 9) show significant negative partial correlations only between adjacent scutes. The gular and humeral, the humeral and pectoral, but not the gular and pectoral show a negative relationship at mid-line. Similarly, in the posterior lobe

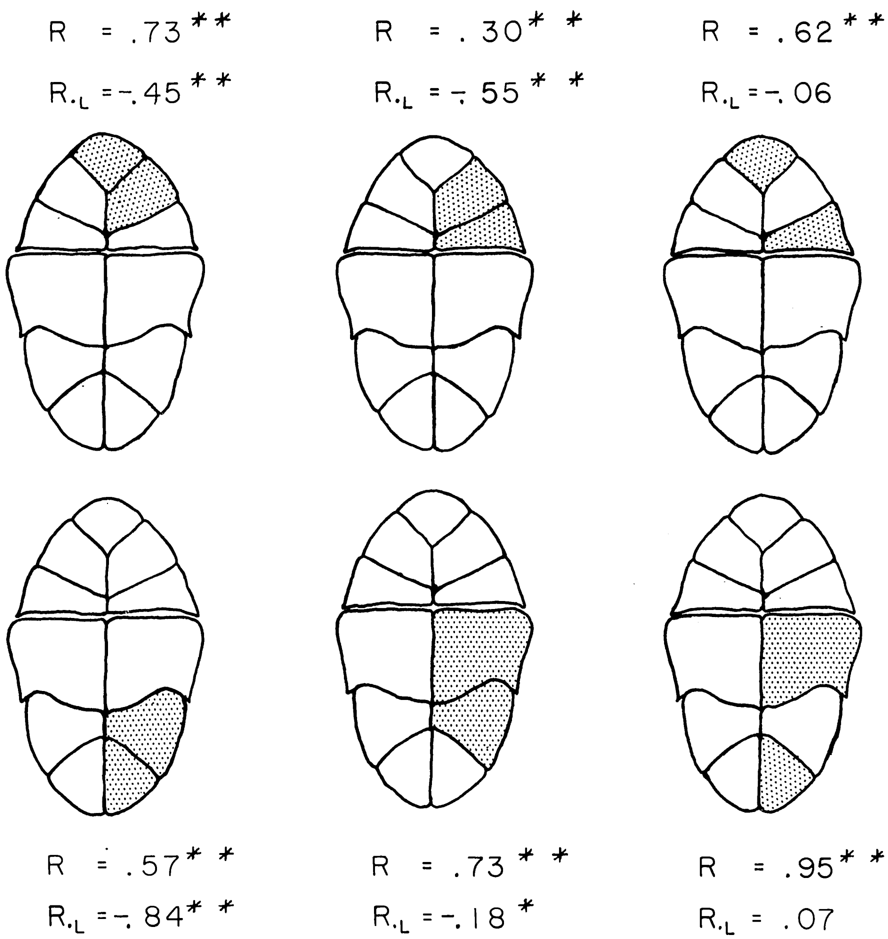

Fig. 9. Relationship between sets of plastral scute mid-line lengths as indicated by the correlation coefficient, R, and the partial correlation coefficient, $R._L$, with plastron length eliminated. The figures above and below each plastron apply to the two scutes shaded in the adjacent figure. Two asterisks indicate significance from zero at the 1 per cent level; one, significance at the 5 per cent level; no asterisk, lack of significance from zero.

the anal and femoral, the abdominal and femoral, but not the anal and abdominal show significant negative relations. There may be some biological connection between these negative relations of adjacent scutes and the angle of the junction of the two scutes so related. The negative correlation between the abdominal and femoral scutes is so small that it is of no predictive value. These two scutes meet at approximately right angles. The other three pairs of adjacent scutes meet at acute angles and have fairly high negative partial correlations.

The effect of a strong negative correlation on a ratio between two such related scutes might be to increase the variability of the ratio. If, as one scute increased, the other showed a corresponding decrease, the values of the ratio of the two would tend to become extreme. A small change in a scute could therefore produce a large change in a ratio.

Mid-line Relations and Part-Whole Relations

The sum of the mid-line dimensions for the six plastral scutes is approximately equal to the plastron length, and consequently as linear dimensions the scute lengths can be considered as parts of a whole. In such a part-whole situation, when the whole is held constant, there is mathematically a strong tendency for the parts to be negatively correlated. This can be appreciated most readily from the limiting case of two linear divisions of a single line. Let A and B represent the parts and T the whole; therefore, $A + B = T$. If T is held constant, which is approximately what is done in the partialling out of T in the partial correlation approach, then $A = -B + C$, and the two are negatively related with a negative partial correlation of one. Although this expresses the fact that for lines of length C, when A is larger, B is correspondingly smaller, the negative relation might not be a useful evaluation of the biological relation of A to B. For example, A could be increasing independently of B, and hence be really uncorrelated with B. In such a case the total, T, would be completely determined by A and B and have no real independent significance. The partialling out of T, producing the negative correlation between A and B, would give a numerically correct, but biologically meaningless estimate of the relation of A and B. As the number of parts increases, there is less and less rigidity to the mathematical model described above, and the automaticity of negative partial correlations between any two parts when the whole is partialled out is by no means assured.

There seem to be several indications that the partial correlations obtained in the present application are meaningful. Biologically, plastron length is a measure of bone tissue, whereas scute lengths are measures of epidermal material. Thus, plastron length is not an arbitrary sum of scute mid-line lengths and hence has a distinct meaning. Also, plastron length and each scute length were independently measured. Furthermore, there is reason to believe that plastron length is a more immediate result of causes affecting growth processes of the whole animal than are epidermal scute lengths. Plastron length represents growth of the bone complex which is probably more important in conditioning scute growth than the latter is in conditioning bone growth. In addition, six parts (scutes) constitute the total, and this allows freedom from the rigid mathematical model described above. The two partial correlations computed involving the abdominal scute, whose variance constitutes the greatest proportion of the variance of plastron length, are both small (Fig. 9). In the case of the partial correlation between the anal and abdominal scutes, which have the two largest parts of the total variance and are the two longest at mid-line on the plastron, the limiting case of two parts totaling to the whole is approached most closely. The partial correlation between these two scutes, however, is not significantly different from zero. This seems to indicate that mathematically rigid part-whole relations are not alone applicable in explaining the results obtained. It should be stressed that the occurrence of negative partial correlations between the mid-line scute measurements is not surprising in view of the part-whole relations exhibited. That negative partial correlations occur between some scutes and not between others is of interest.

Some properties of part-whole relations as outlined in connection with a biological problem (total length, tail length, body length in snakes) may be found in Klauber (1943). Snedecor (1950:162-64) discussed the problem, and Yule and Kendall (1945:297) presented a brief analysis of the standard deviation of the sum of two variables, which is important in its consideration.

SCUTE OVER SCUTE RATIO VARIABILITY

Mid-line Scute Ratio Variability Relative to Plastron Length

The ratios for all combinations of scutes in the anterior lobe and for all in the posterior lobe were computed. In each instance the smaller scute was expressed as a percentage of the larger. Scatter graphs of these ratios against plastron length generally indicate poor correlation with plastron length (Fig. 10-15).

The two plots of ratios involving the humeral scute, which probably decreases relative to plastron length increase, although showing high variability, apparently indicate the expected proportional changes. The humeral over gular ratio shows some decrease with increase of the plastron, and the pectoral over humeral seems to show some average increase. However, in the latter ratio especially, the average changes are almost valueless for predictive purposes because of the high variability exhibited in the scatter graphs. The pectoral over gular ratio, in which neither of the scutes independently showed a proportional change with increase in plastron length, shows no correlation with plastron length. In the posterior lobe ratios, the femoral over anal, in which neither scute changes proportionally to plastron length with increase of the latter, shows no correlation with plastron length. The anal over abdominal ratio shows an expected decrease in accord with the relative increase of the abdominal scute. The femoral over abdominal ratio, however, apparently shows no, or virtually no, correlation with plastron length.

By expressing the relative variability of each scute as 100 times the standard deviation of its regression on plastron length divided by its mean scute length, a modified coefficient of variability ($CV_{y.x}$), an expression of variation of the scute relative to plastron length, can be obtained. In the femoral over abdominal ratio, a small scute with a relatively large variability ($CV_{y.x}$ = 39.8 per cent) is placed over a large scute with relatively small variability ($CV_{y.x}$ = 4.7 per cent). In this ratio it may be that the

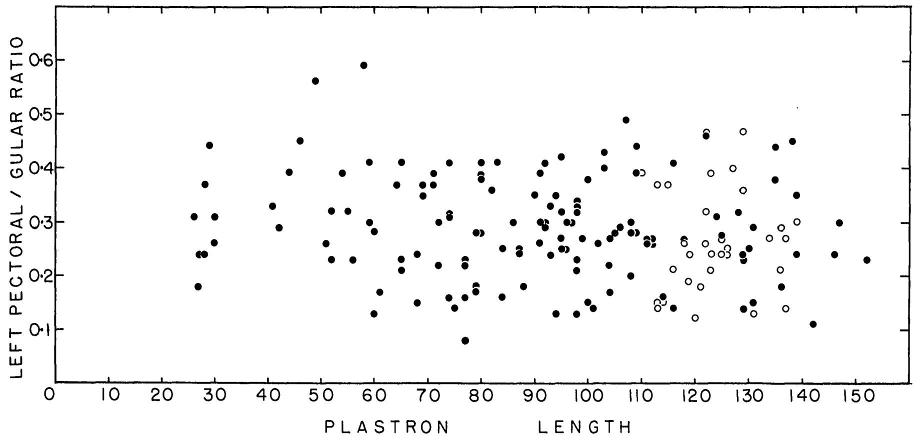

Fig. 10. Relationship between the ratio of left pectoral scute mid-line over gular scute mid-line and plastron length for 164 individuals of *K. integrum* from Coalcoman. For 110 mm. plastra and larger, black circles indicate males, hollow circles indicate females. Below 110 mm. plastra, black circles indicate either sex.

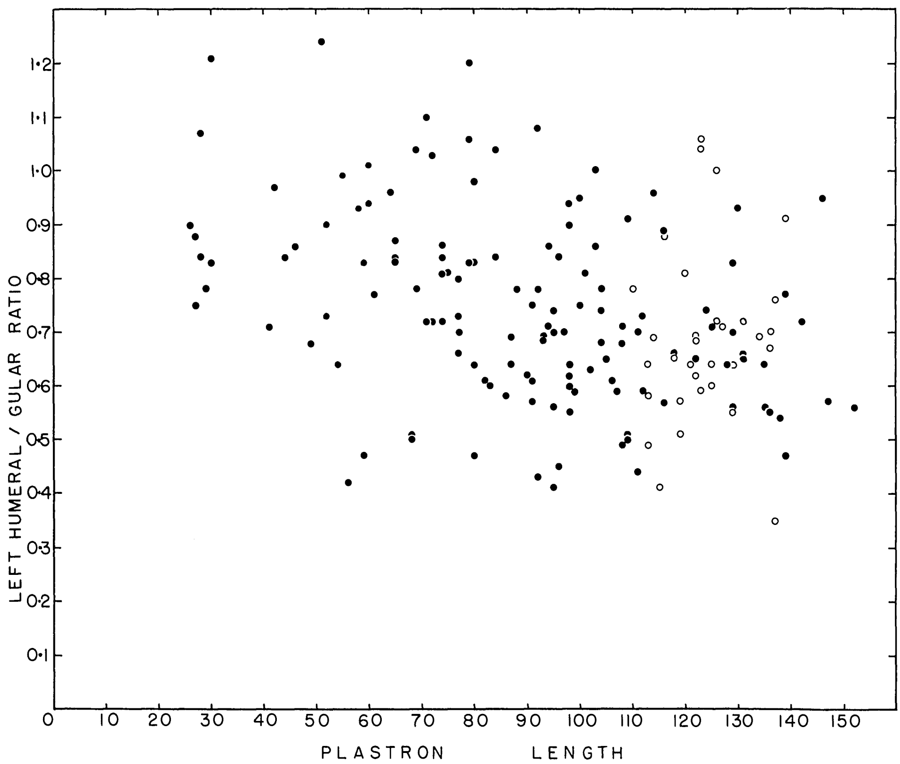

Fig. 11. Relationship between the ratio of left humeral scute mid-line over gular scute mid-line and plastron length for 164 individuals of *K. integrum* from Coalcoman. See Fig. 10 for explanations.

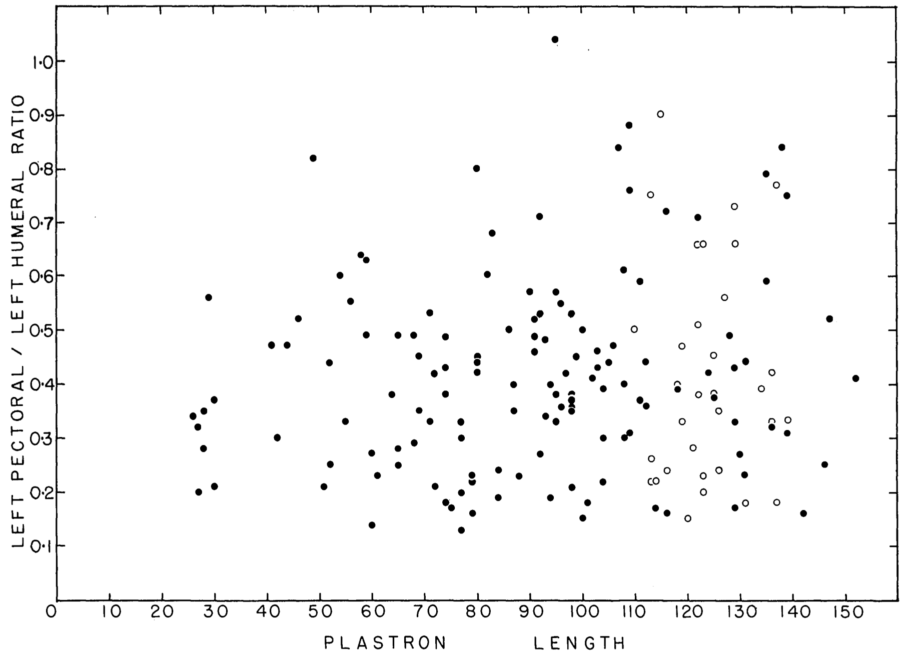

Fig. 12. Relationship between the ratio of left pectoral scute mid-line length over left humeral scute mid-line and plastron length for 164 individuals of *K. integrum* from Coalcoman. See Fig. 10 for explanations.

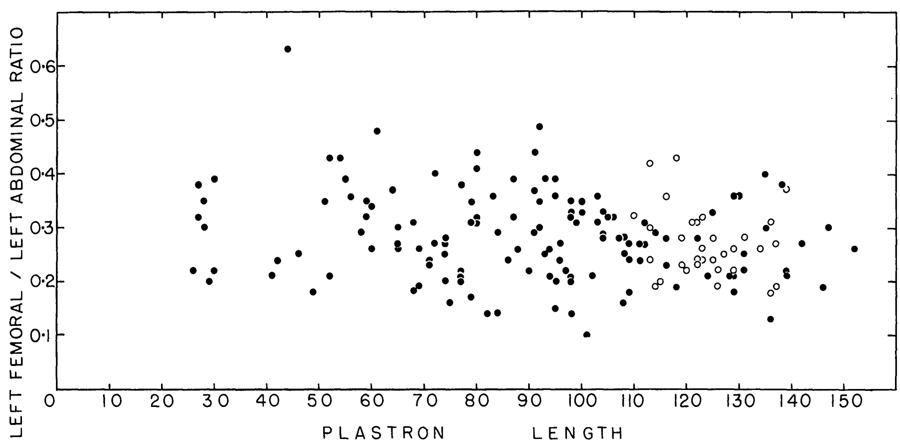

Fig. 13. Relationship between the ratio of left femoral scute mid-line over left abdominal scute mid-line and plastron length for 164 individuals of *K. integrum* from Coalcoman. See Fig. 10 for explanations.

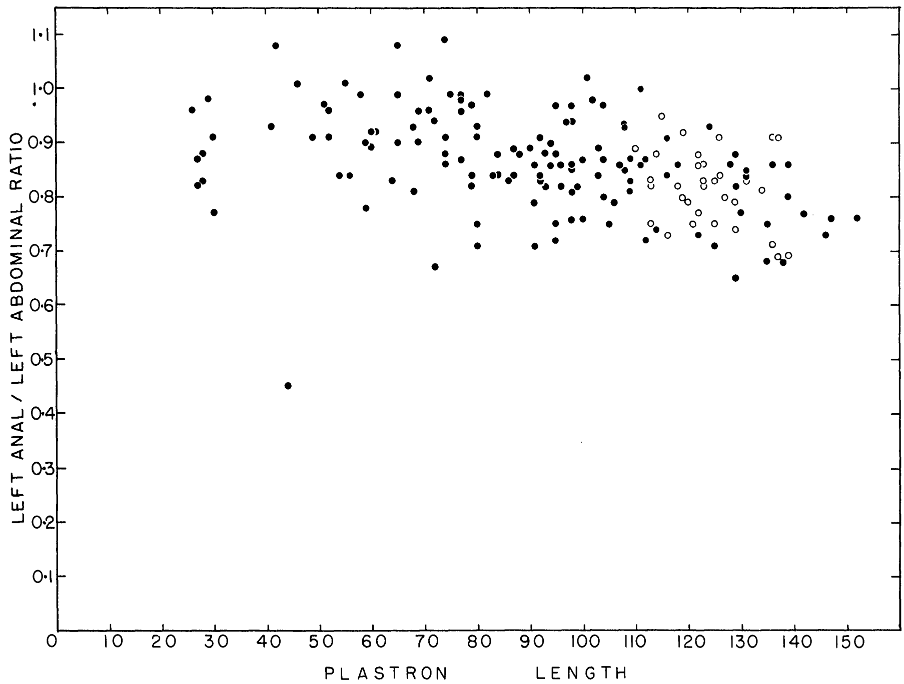

Fig. 14. Relationship between the ratio of left anal scute mid-line over left abdominal scute mid-line and plastron length for 164 individuals of *K. integrum* from Coalcoman. See Fig. 10 for explanations.

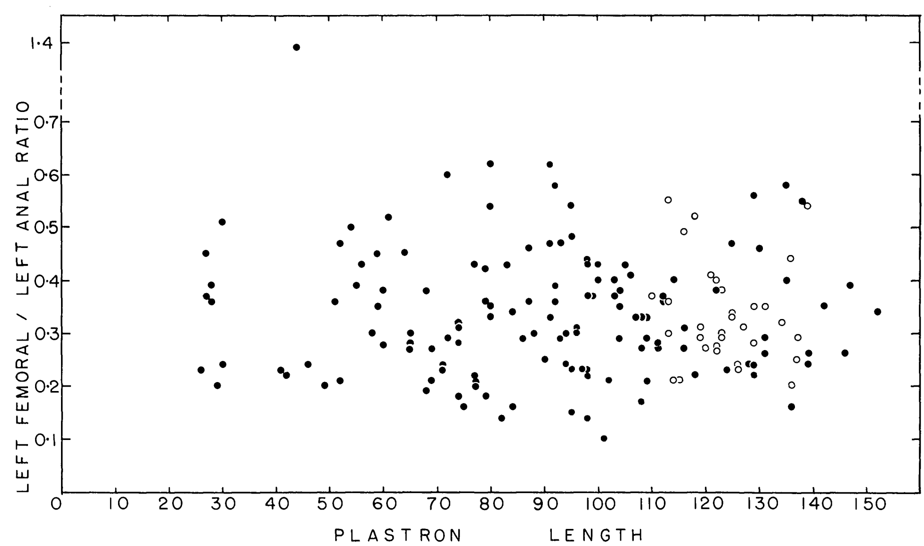

Fig. 15. Relationship between the ratio of left femoral scute mid-line over left anal scute mid-line and plastron length for 164 individuals of *K. integrum* from Coalcoman. See Fig. 10 for explanations.

main expression is that of the variability of the femoral scute. Possibly reflecting the disproportionate effects of the variabilities, the small mean change of the abdominal scute relative to plastron increase is obscured in the ratio. Detailed information on the variability of the actual ratios and the scutes involved in them is presented in Table VII.

TABLE VII

Statistical Data Pertaining to Plastral Scute Ratios and to Scutes Composing the Ratios for Coalcoman *K. integrum*

All length measurements in millimeters.

Ratio	$\overline{X}$	s	$\overline{Y} / \overline{Y}$	s / s	$S_{y.x}/S_{y.x.}$	$r._L$
Humeral† / Gular	0.73	0.177	11.95 / 16.93	3.72 / 5.54	2.08 / 1.47	- .455**
Pectoral / Humeral†	0.41	0.185	4.69 / 11.95	2.06 / 3.72	1.57 / 2.08	- .556**
Pectoral / Gular	0.28	0.098	4.69 / 16.93	2.06 / 5.54	1.57 / 1.47	- .057
Anal / Abdominal†	0.86	0.087	24.66 / 29.25	7.89 / 10.22	2.21 / 1.37	.070
Femoral / Abdominal†	0.28	0.081	8.01 / 29.25	3.19 / 10.22	2.09 / 1.37	- .185*
Femoral / Anal	0.33	0.110	8.01 / 24.66	3.19 / 7.89	2.09 / 2.21	- .840**

†Scute changing or probably changing proportionately to plastron length increase. $r._L$ is the partial correlation coefficient between the two scutes with plastron length as the eliminated variable. Estimates of $S_{y.x}$ are from Table II.

*Significance from zero at the 5 per cent level.

**Significance at the 1 per cent level.

Ratio Frequency Distributions

The frequencies of the ratios discussed above were grouped and graphed as histograms (Figs. 16-21). In this process any borderline values were alternately placed in higher and lower categories in an attempt to avoid consistent bias in a single direction.

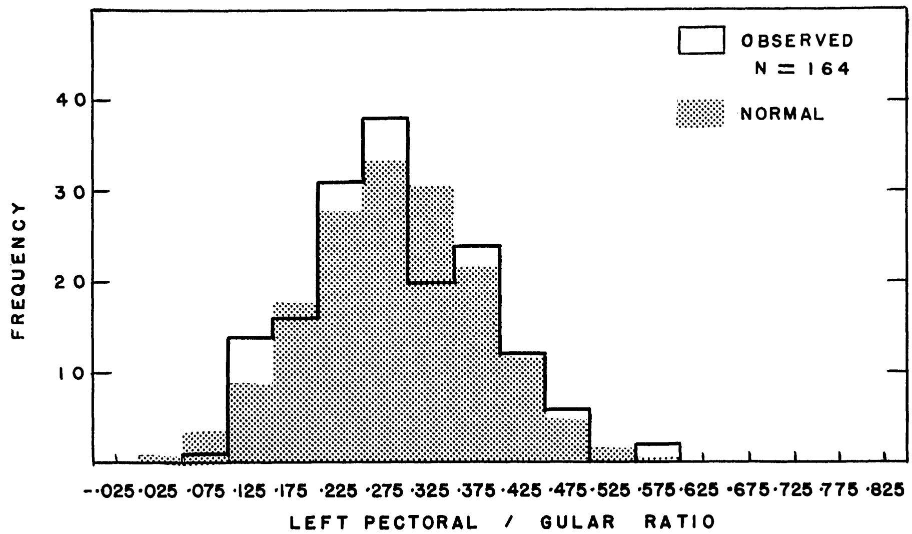

Fig. 16. Frequency distribution of the ratio left pectoral scute mid-line over gular scute mid-line compared with the normal distribution for the same mean and standard deviation.

Because of the mathematical properties of ratios which range only from zero to plus infinity, there is some inherent bias to positive skewing in their frequency distributions. The question remains, however, how far in actual practice frequency distributions of ratios may deviate from a normal, or at least a symmetrical, distribution.

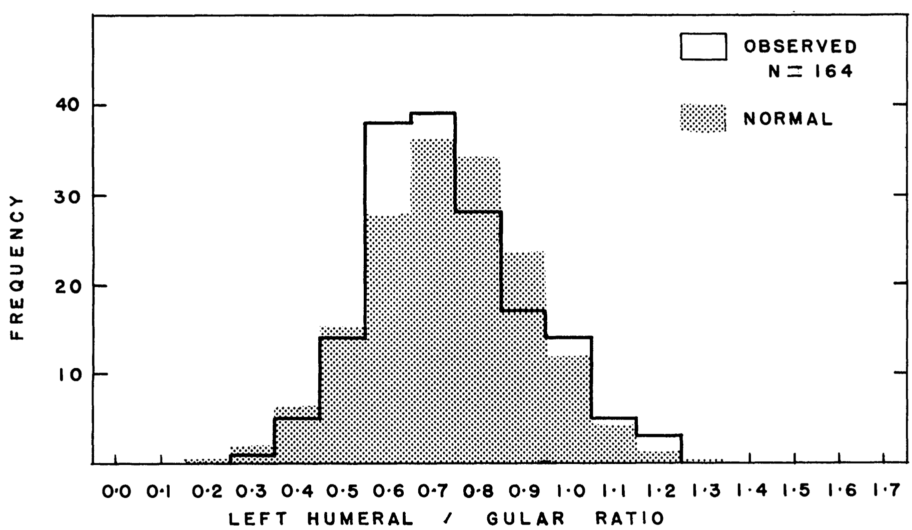

Fig. 17. Frequency distribution of the ratio left humeral scute mid-line over gular scute mid-line compared with the normal distribution for the same mean and standard deviation.

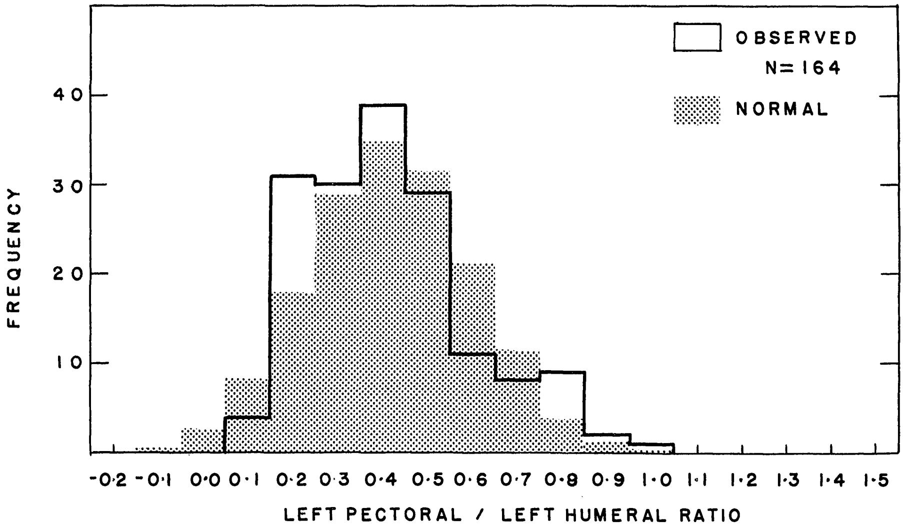

Fig. 18. Frequency distribution of the ratio left pectoral scute mid-line over left humeral scute mid-line compared with the normal distribution for the same mean and standard deviation.

Normal curves were fitted to the ratio frequency distributions and X^2 tests made to determine the goodness of fit. These X^2 tests were used with K-3 degrees of freedom where K is the number of categories used in grouping the data: one degree of freedom lost for the fit mean, one for the fit sigma, and one in the application of the test (Hoel, 1947:194).

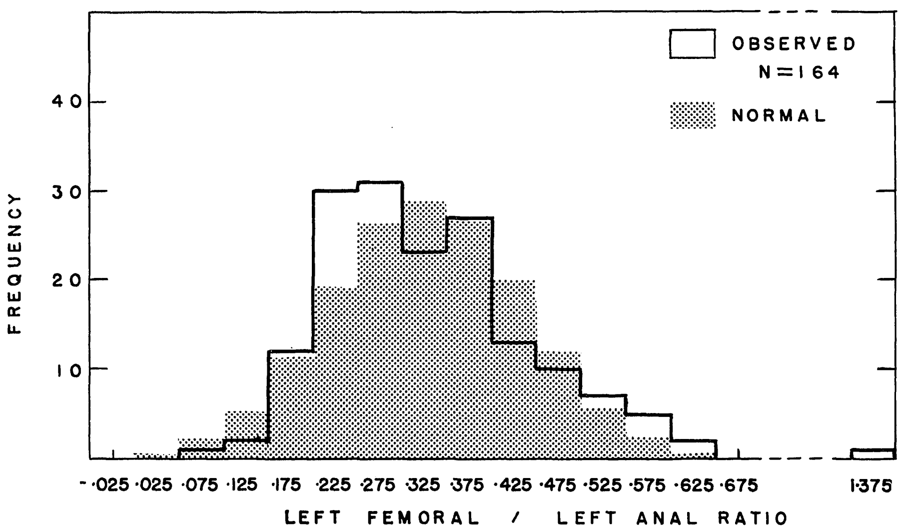

Fig. 19. Frequency distribution of the ratio left femoral scute mid-line over left anal scute mid-line compared with the normal distribution for the same mean and standard deviation.

The results (Table VIII) indicate that four of the empirical distributions are not significantly different from normal by X^2 at the 5 per cent level. These are the ratios of humeral/gular, pectoral/gular, anal/abdominal, and femoral/abdominal. Two distributions, however, are significantly different from normal at the 1 per cent level, the femoral/anal, and the pectoral/humeral. All six frequency distributions are visually not very conspicuously different from the normal distribution, but all appear somewhat positively skewed. Moment tests might detect this skewness better than the X^2, since in the latter low frequency categories (usually at the tails of histograms and curves) must be grouped until an expected frequency

TABLE VIII

Plastral Scute Ratio Frequency Distribution Statistics

Ratio Distribution	Number of Categories	Lowest Expected Frequency	Degrees of Freedom	X^2	P
Anal/Abdominal	8	4.99	5	2.46	$.70 < P < .80$
Pectoral/Gular	9	4.62	6	11.29	$.05 < P < .10$
Humeral/Gular	8	5.72	5	9.14	$.10 < P < .20$
Femoral/Anal	9	8.62	6	17.26**	$P < .01$
Pectoral/Humeral	8	5.32	5	31.23**	$P < .01$
Femoral/Abdominal	7	8.11	4	6.00	$P \cong .20$

*For X^2 significant departure at the 5 per cent level.
**Significant departure at the 1 per cent level.
No asterisk indicates no significant departure of observed from "normal" frequencies.

of about five or greater is obtained for the category with the lowest expected value.

It is possible that frequency distributions of ratios whose means are close to zero might be affected by this lower limit to a greater extent than those of ratios whose means are relatively large. If so, there would tend

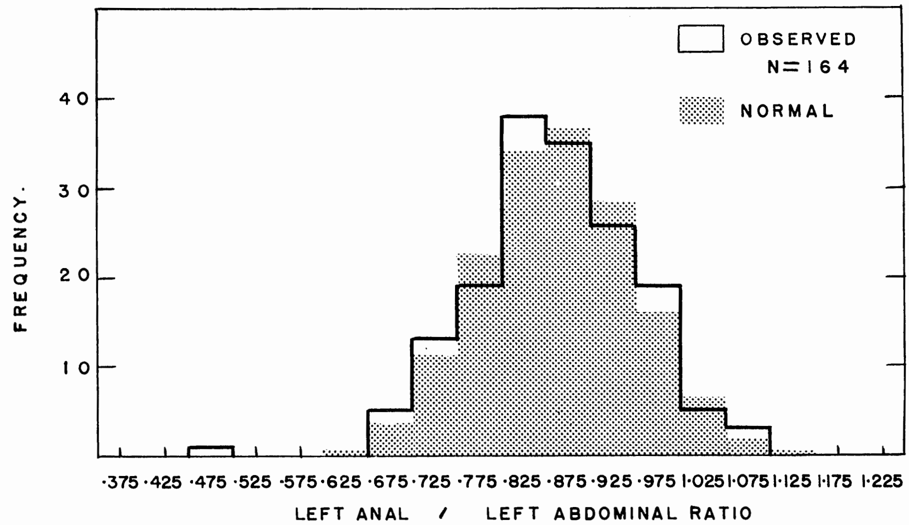

Fig. 20. Frequency distribution of the ratio left anal scute mid-line over left abdominal scute mid-line compared with the normal distribution for the same mean and standard deviation.

to be more positive skewing in distributions with the low mean values. In the present six examples, however, of four distributions not significantly different from normal, two had small mean values and two had relatively large ones. Of the two distributions significantly different from normal, one had a small mean value and the other a relatively large one.

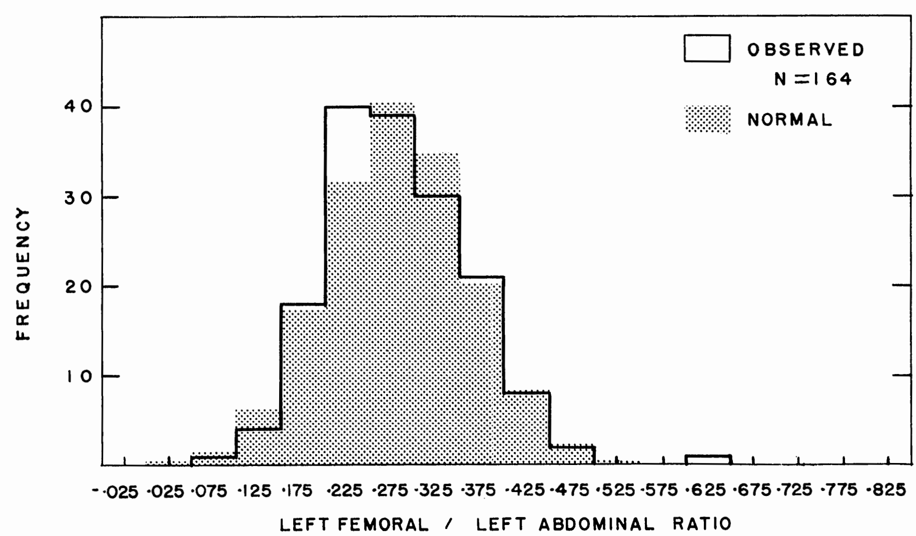

Fig. 21. Frequency distribution of the ratio left femoral scute mid-line over left abdominal scute mid-line compared with the normal distribution for the same mean and standard deviation.

It was noted in the section on scute mid-line to scute mid-line relations that a ratio of two negatively correlated scutes might show extreme values due to the negative correlation. The two frequency distributions different from normal were each made of two scutes negatively correlated with each other; however, a third distribution, that of the gular/humeral, with a fairly high negative partial correlation between its constituents, did not test differently from the normal.

Three of the four ratio distributions not demonstrably different from normal involved either the humeral or the abdominal scute. The former probably exhibits, and the latter does exhibit, small mean differential growth relative to the plastron. The scatter graphs of the ratios against plastron length (Figs. 10-15) afford a means of checking the unequally represented sizes of turtles whose ratios form the histograms. With larger numbers of small animals, the forms of the four distributions involving these scutes might change somewhat. From the present data, which have a fairly even size distribution, there is certainly little effect of the small differential scute-length changes in producing skewing, and consequently nonnormality.

Thus, from the data at hand, no conclusive statements can be made as to the cause of the greater skewing in two of the distributions as opposed to the remaining four.

SCUTE INCREMENT RELATIONS AND SCUTE ANGULAR RELATIONS

Scute Increment to Scute Increment Regressions

The relations of scute increments (See Fig. 1 and Measurements) to each other were studied to ascertain the amount each scute actually added in the direction of mid-line relative to the others. Since a measurement for each scute increment was taken between the last growth line and the mid-line of the plastron, time and environmental conditions are represented in approximately the same manner in each set of increment measurements. Detailed statistical information for these increments is given in Table IX. A comparison of mean scute increments to mid-line length means shows that there is no necessary connection between the size of a scute at mid-line and the actual amount of its addition toward mid-line.

The relation of each increment to the gular increment was studied. The gular was chosen as the base scute because of its high correlation with plastron length, its lack of differential growth with respect to plastron length, and its angular position or directioning toward mid-line. The correlation coefficients for all increments with the gular increment are of about the same value ($r = ca.\ .93$) with the exception of the anterior increment of the humeral (humeral 1), which is lower ($r = .88$). This is probably due to the difficulty of finding the correct angle on this growth ring from which to measure to mid-line.

In the six graphs (Figs. 22, 23) the joint relation of each scute incre-

TABLE IX

Statistical Data, Regressions, and Correlations Between the Gular Increment and the Remaining Scute Increments

All length measurements in millimeters.

Increment	N	$\overline{Y}$ or $\overline{X}$	S	CV (Per Cent)	r	y = b x + a	$S^2_{y.x}$	$S^2_{x.y}$	x = b′ y + a′
Gular (x)	57	2.03	1.05	51.7	....	....	....	....	....
Humeral 1 . . .	57	2.15	1.33	61.9	.887**	y = 1.12 x - 0.13	0.383	0.239	x = 0.70 y + 0.52**
Humeral 2 . . .	57	2.31	1.35	58.6	.943**	y = 1.21 x - 0.15	0.206	0.124	x = 0.73 y + 0.34**
Pectoral . . .	57	2.32	1.43	61.8	.941**	y = 1.28 x - 0.29*	0.238	0.128	x = 0.69 y + 0.43**
Abdominal . . .	57	4.01	2.15	53.5	.933**	y = 1.91 x + 0.14	0.605	0.145	x = 0.46 y + 0.20
Femoral	57	3.39	1.82	53.5	.934**	y = 1.61 x + 0.12	0.427	0.143	x = 0.54 y + 0.20
Anal	57	2.81	1.46	52.1	.920**	y = 1.28 x + 0.21	0.333	0.172	x = 0.66 y + 0.17

*For r, a, and a′, significance from zero at the 5 per cent level.
**For r, a, and a′, significance from zero at the 1 per cent level.
No asterisk indicates a or a′ not significantly different from zero.

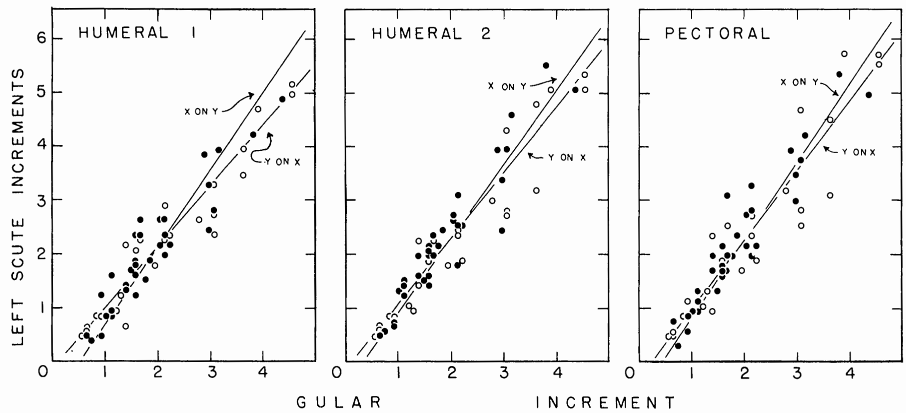

Fig. 22. Relationship between scute increments of the anterior lobe of the plastron and the gular scute increment for 57 individuals of *K. integrum* from Coalcoman. Hollow circles indicate turtles with plastra over 90 mm. in length; black circles, those with plastra less than 90 mm. in length. Measurements (in mm.) were originally made with an ocular micrometer. Both X on Y and Y on X regressions are indicated.

ment with the gular increment to plastron length is indicated in an approximate fashion. Increments of turtles with plastra over 90 mm. long are indicated differently from those with plastra of lesser length. Although this is by no means a sensitive test, visually there does not seem to be much difference in the relation of the scute increments to each other for the two size groupings of plastron length.

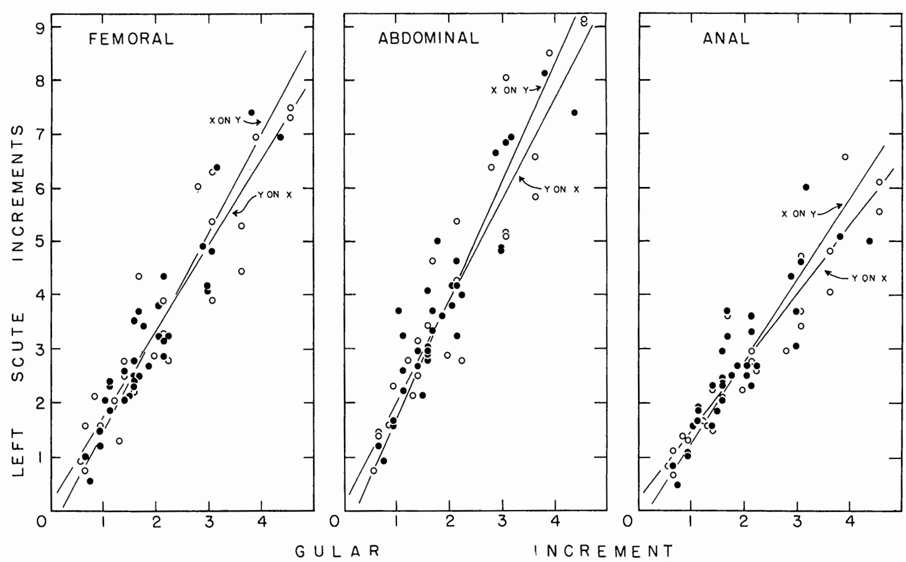

Fig. 23. Relationship between scute increments of the posterior lobe of the plastron and the gular scute increment for 57 individuals of *K. integrum* from Coalcoman. See Fig. 22 for explanations.

The problems in the use of regression statistics for these data are the same as those described previously for the mid-line dimensions since there is no truly independent variable. For prediction, the Y on X line gives the best estimate of a scute increment from a known gular increment, and the X on Y line gives the best estimate of a gular increment from a known scute increment. Lines of organic correlation were not computed.

Proportional Differences Between Large and Small Increments

Again an interpretation may be made from the intercepts of the regression lines. If, in $Y = b X + a$, "a" is zero, then the gular increment is the same proportion of the other increment with increase in size of the latter. If "a" is not zero then the scute increment/gular increment is a function of increase in size of the gular increment and changes correspondingly. This would indicate different growth rates between the gular and the other scute. Hence, tests of "a" may be used in this analysis in a fashion similar to the usage employed before.

In the tests of "a" both Y on X and X on Y regressions were tested. For the Y on X lines, only the intercept of the pectoral increment relation was different from zero. This was at the 5 per cent level. For the X on Y lines, three X intercepts were significantly different from zero at the 1 per cent level of significance. These were the intercepts of the two humeral increments and of the pectoral increment.

To judge from the X on Y increment regressions, the humeral is increasing faster relative to the gular. Actually, the humeral mid-line probably decreases relative to plastron length, whereas the gular mid-line does not. Also, the pectoral increment increases relative to the gular increment, but the pectoral mid-line measurement shows no demonstrable average change relative to plastron length nor does the gular mid-line. The evidence from the Y on X regressions indicates that none of the scutes with the exception of the pectoral shows differential growth addition at mid-line with respect to the gular scute. Neither of the two regression lines indicates a significant proportional change in growth rate for the increment of the abdominal scute which increases at mid-line relatively faster than plastron length. Therefore, neither the X on Y line nor the Y on X line (the line of organic correlation lies somewhere between these) indicates any relation in actual differential growth rates of the scutes towards mid-line with actual mid-line proportional changes.

Despite this lack of agreement of growth rates with mid-line proportional changes, it is possible that the differences between increments noted may produce the changes observed at mid-line for the abdominal and humeral scutes. Constant proportionality between the increments of two scutes is not sufficient basis for the conclusion that there is no differential growth between them. If a part 1 mm. long increases 1 mm. and another part 2 mm. long increases 1 mm., the former doubles its size, and the latter increases only by half. Before the increment addition, the first part is half of the second; after the addition, it is two-thirds of the second. Obviously, the proportional changes of incremental addition with respect to the original size as well as relative changes in the rate of incremental addition are important in understanding relative growth in plastral scutes.

Although the abdominal shows no proportional change in its rate of incremental addition with respect to the gular, the difference in size of the two scutes in small turtles makes it possible that these rates of addition could produce differential increase at mid-line.

To estimate mid-line sizes of the two scutes from the 50 mm. average plastron, the gular is about 63 per cent of the abdominal. By use of the slope of the gular increment on abdominal increment regression, it is seen that the gular increases incrementally 46 per cent of, or about half as fast as, the abdominal. Since the abdominal angular increase does not all contribute to the mid-line dimension, and the increase of the gular does, some correction must be made for the percentage of the abdominal angular increment which enters mid-line. This percentage can change during ontogeny. In a very rough estimate of this as about 80 per cent (Table X), the ratio of

TABLE X

Angular Changes in Growth of Plastral Scutes to Mid-line as Measured from Growth Lines of Two Turtles

The percentage of growth effective at mid-line (sine of the angle) is given in parentheses after the angle. A negative angle indicates that scute growth is not contributing to mid-line.

UMMZ 104894 - Male Angle and Per Cent	Initial Abdominal Scute Growth Line Length (mm.)		
	12.1	16.5	25.4
Gular	90° (100)	90° (100)	90° (100)
Humeral 1	4° (7)	0° (0)	-25° (-42)
Humeral 2	35° (57)	44° (69)	60° (87)
Pectoral	7° (12)	3° (5)	0° (0)
Abdominal	45° (71)	60° (87)	65° (91)
Femoral	60° (87)	56° (83)	40° (64)
Anal	79° (98)	79° (98)	79° (98)
UMMZ 104857 - Female Angle and Per Cent	**Initial Abdominal Scute Growth Line Length (mm.)**		
	13.0	23.0	28.0
Gular	90° (100)	90° (100)	90° (100)
Humeral 1	-6° (-10)	-7° (-12)	-9° (-16)
Humeral 2	31° (51)	31° (51)	31° (51)
Pectoral	7° (12)	7° (12)	7° (12)
Abdominal	53° (80)	60° (87)	64° (90)
Femoral	41° (66)	37° (60)	35° (57)
Anal	80° (98)	75° (97)	72° (95)

the average gular mid-line increase over abdominal increase is about 57 per cent. Since this is less than the 63 per cent proportion between the two at small size, the increase of the gular does not seem to keep pace with the increase of the abdominal, and the latter might be expected to increase relatively faster at mid-line. The gular increase is highly correlated with plastron length and shows no proportional change with respect to it; therefore, the difference in growth explained above could account for the changing proportion between the length of the abdominal and that of the plastron.

In analyzing the growth of the humeral scute in this manner, more complications are met than in analyzing that of the abdominal. The humeral rate of angular incremental increase is proportionately faster than that of the gular. Also, humeral mid-line changes must be analyzed in terms of two angular increments and two angles made with mid-line. Both of these angles can change during ontogeny. The significance of these angles is discussed in the following section, but it is sufficient to say here that, regardless of its rate of growth, the humeral scute seems so directed to mid-line that it does not increase, but actually loses mid-line space at the anterior end and gains it at the other end. Because of these complications little accuracy would be obtained from a detailed treatment such as that given the abdominal scute. As a result of the interaction of these factors, the relative decrease in humeral mid-line with plastron length increase could be caused in a fashion similar to that shown as possible for the abdominal scute. Thus, in both the abdominal and humeral scutes differences in relative growth rates alone might cause proportional mid-line changes. However, ontogenetic changes in the angles which the scutes make with mid-line further complicate the situation.

Angular Relations of Scutes to Mid-line

Measurements were made of the angles which successive growth rings indicate that the scute formerly made with mid-line (Table X). These measurements are included for the purpose of showing that the angle which a scute makes with mid-line can change during ontogeny.

To obtain an estimate of the growth efficiency of a scute in adding to its mid-line, one can measure the angle which the scute makes with a line perpendicular to mid-line and find the sine of the angle (Fig. 24). For example, the gular scute makes a 90° angle with such a line, the sine of 90°

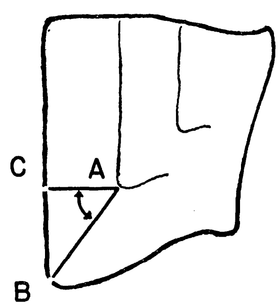

Fig. 24. Angle which the scute makes from its point of previous mid-line junction (as indicated by its growth ring) with its existing mid-line junction. BC is the mid-line increase effected by the growth increment AB. BC/AB is percentage of angular growth effective in adding to mid-line dimension. Since BC/AB is also the sine of the angle BAC, changes in the angle which the scute makes with mid-line affect its growth at mid-line. Note the angular change.

is one, and the scute has 100 per cent efficiency in growth toward mid-line. This is simply to say that all of its angular incremental growth adds to its mid-line dimension. The humeral scute in the anterior lobe and the similarly located femoral scute in the posterior lobe both need two angular measurements to express mid-line angular efficiency; however, only a single measurement was taken for the femoral scute.

The changing angular efficiencies in the individual ontogenies presented (Table X) show that these may be important factors in mid-line proportional changes. Although these have been shown in individuals only, and these changes may or may not produce average changes in the population, they may be of importance in producing mid-line proportional changes, and may possibly explain plastral scute proportional changes at mid-line, as well as the previously discussed incremental growth.

DISCUSSION AND CONCLUSIONS

The preceding analyses reveal a number of interrelated features of the plastron and plastral scutes of *K. integrum*.

Small proportional change with respect to plastron length has been demonstrated in the abdominal scute mid-line and is also probably indicated in the humeral scute mid-line dimension. The remaining four scutes show no demonstrable changes. In general, plastral scute mid-lines show little change in growth relative to plastron length.

The carapace length has been shown to exhibit differential growth with respect to plastron length. As a result, use for taxonomic purposes of a plastral scute mid-line over carapace length ratio, although expressing a valid morphological relation, is complicated. The use of a ratio of a plastral scute mid-line over carapace length, rather than plastron length, greatly increases the possibility of discovering ontogenetic change. Further, in a variational study the source of the variability becomes important, and the limitation of the ratio to the description of causal relations is desirable. In this particular situation it appears obvious that the fundamental differential growth relation between plastron length and carapace length is merely reflected by the use of a plastral scute over carapace length ratio.

From this example it can be seen that it is desirable, for understanding or for attempting to understand what the variability of a ratio expresses, to compare parts which can be biologically closely connected; for example, a plastral scute with plastron length. All manner of combinations of measurement in ratio form can be valid for the purpose of taxonomically delimiting forms and for expressing real morphological relations. However, in terms of understanding these delimitations and expressions, in the interpretation of the variability of their ratios, and particularly in the assignment of biological significance to their variability, it is best to use ratios expressing a "sensed" biological connection. Combinations of more than one ratio to produce a single index number can obscure hopelessly the meaningfulness of the index, and it seems that such a practice is usually unnecessary.

The cause of the small differential growth effects observed in the abdominal scute mid-line and probably in the humeral mid-line relative to plastron length is uncertain. The work on growth increments shows that these may possibly account for the changes. The demonstration of changes in the angles of scutes during ontogeny for two individuals points to another possible cause of mid-line proportional change. From the present data no conclusive statement can be made. It does seem of interest that a change in the angle which a scute makes with mid-line might result in a change in mid-line proportions with no change in relative growth rate.

Negative relations between adjacent scute mid-line seams were shown to exist in the anterior lobe and to be present in similarly situated scutes in the posterior lobe. They indicate that as one scute has more mid-line space, its adjacent neighbor has relatively less. These negative relations could be produced by causes operating during the development of the embryo, in the individual's posthatching ontogeny, or throughout pre- and posthatching growth. The assignment of a direct causal connection between scutes so related is not justified. No matter what causal sequences are operating, the growth pattern of one scute appears to be related somewhat to that of its neighbor whether due indirectly to causes common to both, or more directly to the effect of one scute on the other.

Complications in the assignment of causes to mid-line growth relations can be seen to accrue from several sources. Mid-line relative growth is a compound effect of the actual growth rate of the scute addition, the percentage this forms of the previous scute size, and the amount of this growth effective in adding to the mid-line dimension. This last is determined largely by the angle at which the scute is forming toward mid-line. Therefore, the growth expression of a scute at mid-line could be high because of a slow, medium, or fast incremental growth rate combined with a high angular or percentage efficiency, or it could be high because of a low angular efficiency combined with a fast incremental growth rate. Changes in either the angle or growth rate can further complicate the situation. A change in actual growth rate may be compensated for by a change in angle and therefore may not produce any change in the scute's relative growth at mid-line. In addition to the joint effects of growth rates and angles, there are the possible effects of adjacent scutes on each other, which may be indicated by the negative relations demonstrated between them. Thus, by examining only morphologically determinable variation, it can be seen that mid-line growth is the result of a complex of causes.

The frequency distributions of plastral scute ratios show the variation of plastral scutes. Four of the ratio distributions are not very different from the normal distribution, and two others are significantly different. The latter do not appear visually to be extremely far from a normal or at least a symmetrical distribution. This fact justifies the use of normal statistics in the analysis of these ratios beyond a possible more general justification based on the distribution of the means of samples (Fisher, 1950:114). In any event, the frequency distribution of ratios of plastral scutes can be close to the normal distribution.

The great variability of the mid-line scute ratios makes the small average proportional growth changes in scute mid-lines relative to plastron length more or less inconsequential from the point of view of the taxonomic interpretation of small samples. Thus, small samples are much more likely to produce misleading mean differences because of the large variability coupled with nonrandom sampling rather than because of any average mean proportional change due to differential growth. As has been pointed out, comparison of the plastral scute with plastron length is less apt to reflect differential growth effects than is comparison of a plastral scute with carapace length.

This great variability in plastral scute ratios is not encouraging from the point of view of their use in taxonomic work. The range of variation is very high, and may well be due to causes other than genetic. A possible mode of ecological effect on plastral scute variation may be mentioned, although it is admittedly speculative. If the angles which a scute makes with mid-line were changed depending on fast or slow growth of the turtle during early periods of development, it is obvious that different scutes, placed differently with respect to mid-line, would be differentially affected by these angular changes. This differential effect would then cause some scutes to change relatively their mid-line dimensions. Thus, depending on conditions favoring or not favoring rapid growth at hatching, different year-classes in the population might exhibit differences in plastral scute proportions. At present there is little evidence to support this; however, as shown in this paper, the angles can change. One should be aware of the possibility of such a phenotypical effect in taxonomic analysis.

The use, as by Sergeev (1937) and Cagle (1946, 1950), of a ratio formula:

$$\frac{\text{present scute length}}{\text{present plastron length}} = \frac{\text{scute growth line length}}{\text{former plastron length}}$$

to estimate past plastral sizes implies lack of differential growth between the scute length concerned and plastron length, as these authors were well aware. A proportion of this type is a substitute for regression analysis when the scute length is used as an independent variable, and plastron length is estimated from a known scute length as inferred from its growth line. In the sample at my disposal the most efficient estimation of past plastral sizes can be made from the abdominal scute length. Small differential growth changes in this dimension would produce some error if the simple ratio proportion were used; however, estimation of past plastral sizes can be made with a high degree of accuracy from the X on Y, that is, plastron length on abdominal scute length, regression.

This study has dealt in large part with segments (scute mid-line lengths) of a linear whole (plastron length). There is no necessary biological equality between the sum of mid-line epidermal scute lengths and plastron length, which is essentially a measurement of bone tissue. Also, since all measurements were made independently, exact mathematical properties of a part-whole relation need not occur. However, the sum of scute mid-lines is approximately the same as plastron length, and certain of the data reflect this close approximation. For example, the slopes of all the Y on X regressions of scute length on plastron length are less than one, a necessary result when relating a part as dependent variate to a whole as independent variate. It may also be noted that the scutes longer at mid-line, which form a greater proportion of plastron length than do shorter ones, have higher correlations with plastron length than do shorter ones. Negative partial correlations would be expected to occur when the effect of the total, plastron length, is partialled out, and this has been previously discussed. Properties such as these, when indicated by the empirical data, reflect the biological situation exhibited in the mid-line measurements of plastral scutes which, in terms of linear dimensions along a single line, form parts totaling approximately to a whole, plastron length.

SUMMARY

Plastral scute mid-line variation was studied in a sample of 164 specimens of *Kinosternon integrum* from the vicinity of Coalcoman, Michoacan, Mexico. Regressions of each scute mid-line against plastron length were computed. From these, proportional change or the lack of proportional change was shown in scute mid-lines with plastron length increase. The abdominal scute was shown to increase, and humeral scute was shown to probably decrease relatively. Both changes were small. The other scute mid-lines showed no demonstrable change. The use of the regressions in this work was discussed.

Average plastra were estimated from the separate regression lines. Several individual growth histories were obtained for comparison with the regressions indicating average changes for the population.

The carapace length was shown to change proportionately to plastron length with increase in size. Sexual dimorphism was clearly evident in this relation.

Scute mid-line interrelationships were analyzed by the method of partial correlations. The use of partial correlations in a part-whole scheme was briefly discussed. Significant relations were found only between adjacent scutes in the anterior lobe and in similarly located scutes in the posterior lobe.

The variability of six ratios between various plastral scutes was studied with reference to plastron length, and also with reference to the frequency distribution of each ratio. The ratios were so highly variable that the small mean changes in plastral scute length relative to plastron length were of little predictive importance. Difficulties in taxonomic analysis may well result from this high variability. Four of the six ratio frequency distributions were so close to the normal distribution that they did not significantly differ from normal when tested by X^2 for goodness of fit.

Angular scute increments were measured by means of an ocular micrometer for 57 turtles. The gular increment was used as a basis for comparison, and other scute increments were compared with it. Increment regressions were used in an attempt to analyze the relative rate of increment addition toward mid-line of the various scutes. The significance of these in producing mid-line proportional changes was discussed.

The angles which the scutes form with mid-line were analyzed in two turtles by measurements taken from growth lines. The angles of some scutes were shown to change during the development of these individuals. Their possible significance to mid-line relative growth was noted.

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PLATE I

Fig. 1. Two old individuals of *Kinosternon integrum* showing marginal "breakdown" of plastral scute seams which causes difficulty in measuring.

Fig. 2. Female (left) and male (right) individuals of *Kinosternon integrum* showing secondary sexual characteristics of the degree of marking of the lower jaw, and size of tail.

PLATE I

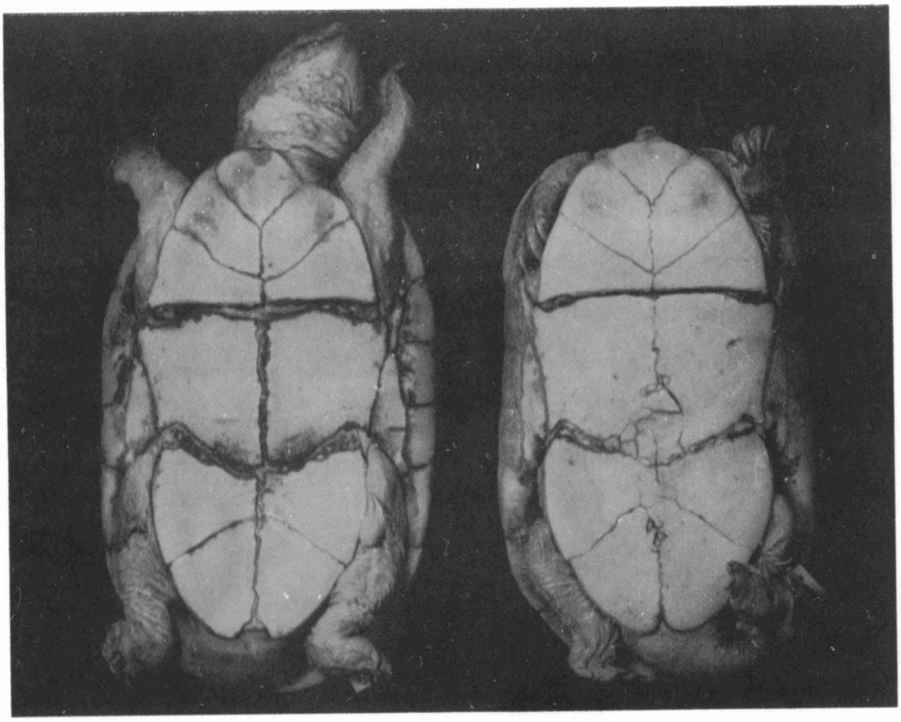

Fig. 1

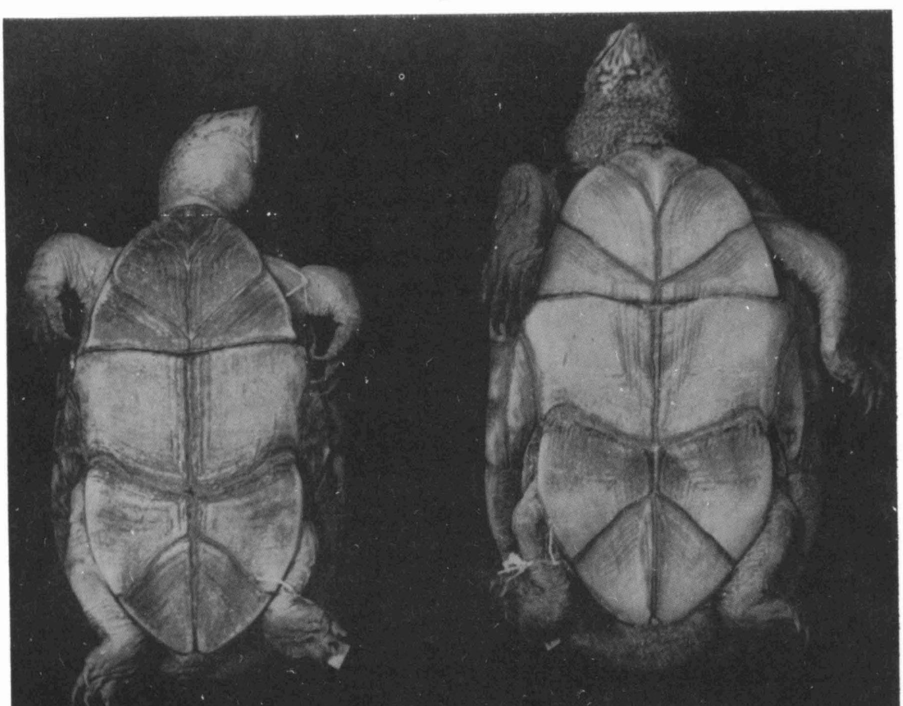

Fig. 2

(CONTINUED FROM INSIDE FRONT COVER)

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