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Volume 10 | April 11, 1957 | No. 29

THE NATURE OF SHIELD ABNORMALITIES IN THE TURTLE SHELL

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INTRODUCTION

Zoologists interested in the morphology and systematics of the turtles have long been impressed by an interesting phenomenon involving the epidermal shields of the turtle shell. A phylogenetic survey reveals an extraordinary uniformity of the pattern formed by these shields. In the central areas of both carapace and plastron the shield pattern appears to have been stabilized in the earliest (Late Triassic) members of the order, and has remained fixed in the vast majority of all turtles, fossil and recent.[1]

The pattern formed by the smaller, often inconspicuous scutes of the fringe areas of the shell displays a modest amount of variety, since it has undergone gradual reduction in the number of its elements in the course of turtle evolution. Among the shields of the fringe areas of the shell the anteriormost scales of the plastron and the inframarginal scutes show the least amount of phyletic stability and the marginal scutes of the carapace the most.[2]

In sharp contrast to the notable phyletic stability of this shield pattern is its rather great individual variability in all families of

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[1] Aside from the Trionychidae, Dermochelyidae and the sole Recent member of the Carettochelyidae, in which the epidermal shields have been reduced entirely, there are only five exceptions. They are: the plastron of *Macrochelys* (Chelydridae), the modern cheloniid genera *Caretta* and *Lepidochelys* (discussed in detail in Zangerl and Turnbull, 1955), and the emyid genera *Notochelys* and *Clemydopsis*, where certain abnormalities, found among other turtles, appear to have become the normal pattern of the species.

[2] The typical number of marginal scales is 12 on either side of the carapace. Only in the most primitive forms is this number greater and only in the family Kinosternidae is it smaller (11 on either side). In some of the more specialized members of the Testudinidae the twelfth pair of marginals is fused.

Recent turtles. A number of students have inquired into the character and nature of this variation and a good review of the literature was presented by Lynn and Ullrich (1950). Many of the suggested explanations are highly speculative. Gadow (1899) and Newman (1906) thought of the occurrence of supernumerary shields as atavistic phenomena, but later Newman (1923) retracted his earlier interpretation and regarded certain pattern irregularities "as the result of a minimal phase of twinning." Coker (1910) opposed the atavism theory and saw in the pattern variability evidence of developmental disturbances without phylogenetic significance. Other suggestions as to the causes of this variation in turtles are: arrested development (Wandolleck, 1904; Hildebrand, 1930); possible foreshadowing of future evolutionary events (Berry, 1935); pressure on the eggs due to crowding in the nests (Coker, 1910); and humidity factors at critical times during embryonic growth (Lynn and Ullrich, 1950). Only the last study is based upon experimental evidence.

Our own observations tend to indicate that the problem is a complex one and that different causative factors may be responsible for various kinds of pattern variations. In an attempt to gain a more comprehensive picture of the types of pattern variation in Recent turtles, a record (complete with diagrams) of a very large number of species and individuals has been compiled. The evaluation of this material is far from complete, but a few general aspects of pattern variation have been analysed and form the substance of the following report.

MATERIALS

A total of 2,220 individuals, representing 118 species and 7 families, were examined in the course of this study. These constituted the complete collection of turtles at Chicago Natural History Museum at the time (1954). Soft-shelled and marine species were not included in the study, the former because of their lack of scutes and the latter because of the small sample available to us.

In the sample, 951 (or about 43 per cent) exhibited one or more variations from the typical shield pattern of their particular species. The average number of abnormalities per abnormal individual was found to be 1.8. The abnormalities were of three general types (fig. 138): (1) heterotopic sulci or incomplete expression of normal sulci; (2) the addition or loss of scales; and (3) areal abnormalities.

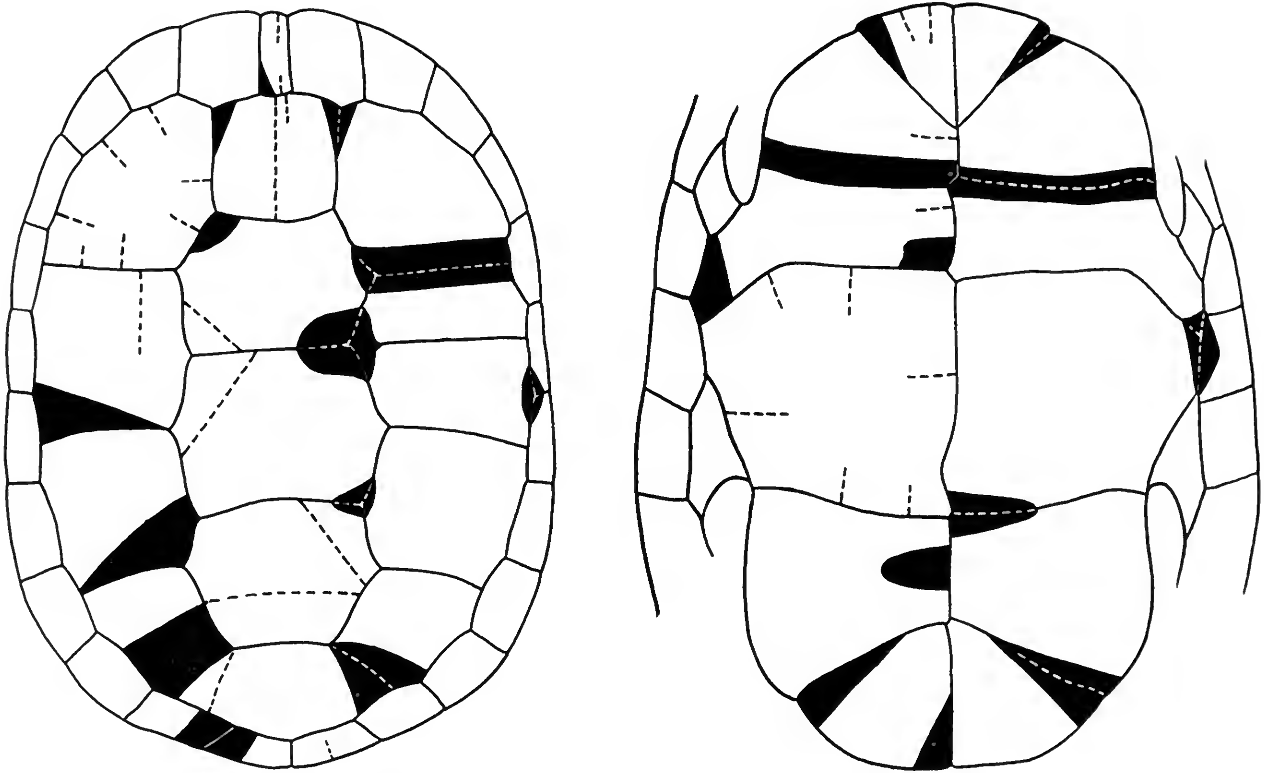

FIG. 138. The major kinds of abnormalities, illustrated on composite drawings of carapace and plastron. The various abnormalities are not restricted to the shields on which they are illustrated.

Variations involving heterotopic or abnormal sulci were the most common encountered. Rarely, heterotopic sulci were found to be paired and bilaterally symmetrical, but more often they appeared quite irregular in their distribution on the shields. The most common occurrence was that of an aberrant sulcus in contact with a normal one and extending a short distance upon a single scale. The addition or loss of scales was of two sorts. Frequently involved were the scales of the normal shield pattern, or scales that are normal for some other than the species at hand. Many of the abnormalities of this general type, however, were irregular, representing a new element with all new borders or more commonly utilizing pre-existing sulci for one or more of its borders. In many of the latter instances, the position of topographically normal sulci was altered by the introduction of the new element. Where this was not the case, elements utilizing pre-existing sulci for one or more borders could as well be classed with the heterotopic sulci. Areal abnormalities involving three or more scales in a continuous aberration were the rarest of the types. Most of these were profound alterations of the shield pattern with an abnormal distribution of shield area among normal elements.

Representatives of the following genera have been examined:

- Dermatemyidae
    - *Dermatemys*
- Chelydridae
    - *Chelydra*
    - *Macrochelys*
- Kinosternidae
    - *Kinosternon*
    - *Sternotherus*
    - *Staurotypus*
- Testudinidae
    - *Homopus*
    - *Kinixys*
    - *Gopherus*
    - *Testudo*
    - *Malacochersus*
- Emyidae
    - *Graptemys*
    - *Pseudemys*
    - *Chrysemys*
    - *Malaclemys*
    - *Geoemyda*
    - *Emys*
    - *Cyclemys*
    - *Clemmys*
    - *Deirochelys*
    - *Geoclemys*
    - *Platysternon*
    - *Terrapene*
    - *Chinemys*
    - *Orlitia*
    - *Ocadia*
    - *Bellia*
    - *Mesoclemmys*
    - *Notochelys*
- Pelomedusidae
    - *Pelusios*
    - *Pelomedusa*
    - *Podocnemis*
- Chelyidae
    - *Chelys*
    - *Chelodina*
    - *Platemys*
    - *Hydromedusa*
    - *Phrynops*
    - *Batrachemys*
    - *Emydura*

METHODS

Most of the inferences made from these data were tested for significance by the standard chi-square test. Occasionally, when it was desirable to compare frequency distributions *in toto*, the Kolmogorov-Smirnov statistic was employed (described by Miller and Olson, 1955). These non-parametric tests are well suited for such materials, as they do not require the usual restrictive assumptions about the distribution being sampled.

For the purpose of analysis, several assumptions have been made regarding the sample. It has been assumed that the sample is a random accumulation of specimens with respect to normal and abnormal individuals. The sample is composed of all specimens of turtles in the collection of Chicago Natural History Museum at the time of study. It is deemed extremely unlikely that such a collection is biased with regard to such abnormalities as are studied here. Where the frequency of abnormal individuals has been studied in a particular species, it has been assumed that the species has been adequately sampled. This assumption seems warranted, since such detailed studies were made only in species where large samples were available (e.g., *Chrysemys picta*, 355). Where inferences have been made about all modern turtles (excepting marine and soft-shelled species), it has been assumed that the modern turtles are adequately represented in the sample. Since there are only about 250 modern species (other than soft-shelled and sea turtles) known and the sample contains representatives of 118, this assumption seems warranted.

DISTRIBUTION OF VARIATIONS UPON THE SHELL

The number of individuals showing each type of abnormality was counted. The number of variations for each shield or shield area was plotted on diagrams of the carapace and plastron (fig. 139).

In general, the plastron, with 1,092 instances of abnormality, is more subject to variation than the carapace, with 626 instances. Both the plastron and the carapace are slightly more variable in their posterior halves. The abdominal scale of the plastron was found to be the most variable single scale in the shell and the third pair of pleurals the least variable.

The posterior half of the carapace is roughly 10 per cent more variable than the anterior half. The greatest variation in the carapace involved the eleventh and twelfth marginals. The posterior half of the plastron was found to be about 6 per cent more variable than the anterior half. The axial scales are the most stable of the series.

In the sample as a whole, the average number of topographically discrete aberrations per abnormal individual was found to be 1.8. In Table 1 the frequency of multiple abnormalities was tabulated in four species for which large samples were available. The data

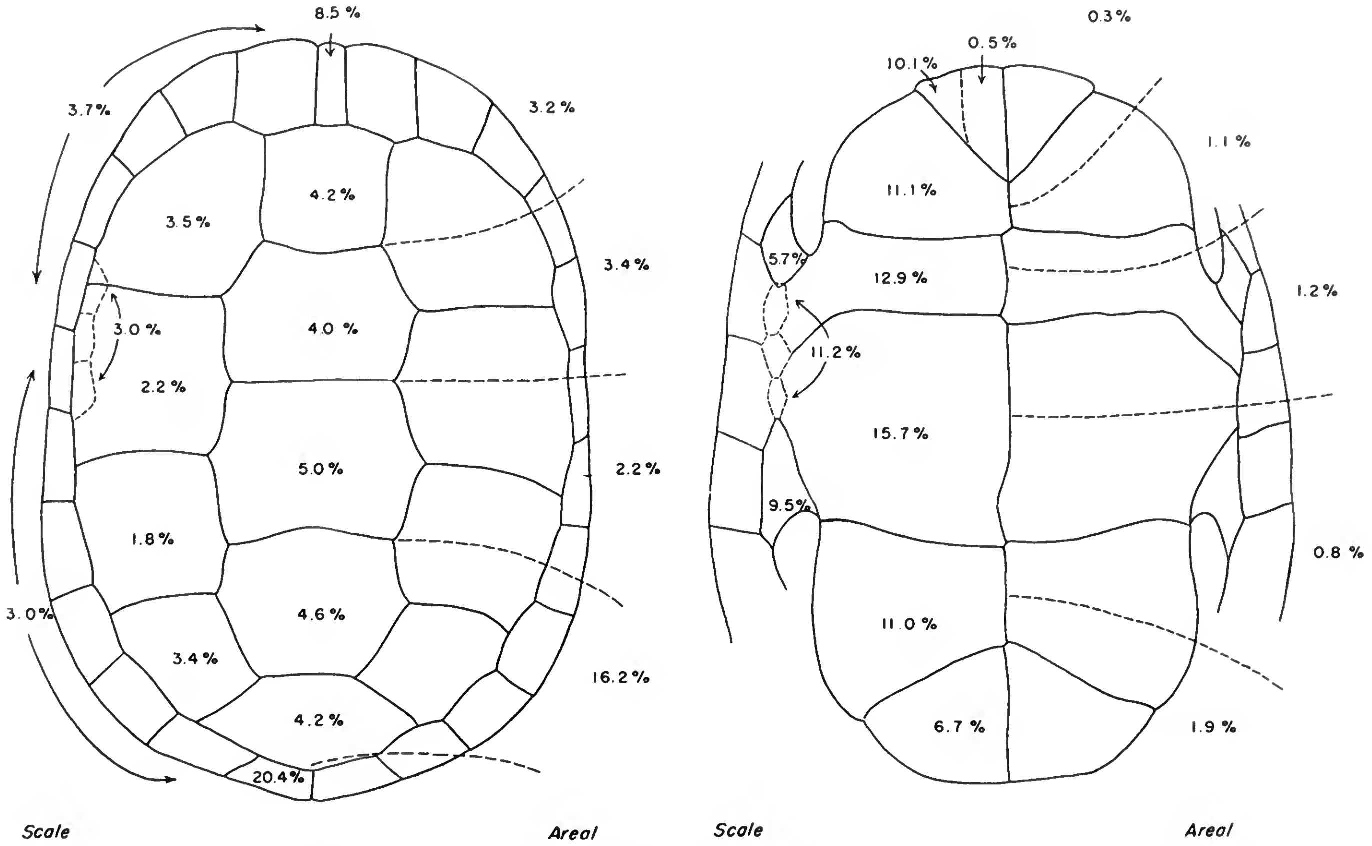

FIG. 139. The distribution of the shield abnormalities on the turtle shell. A, the carapace; B, the plastron.

indicate that an abnormal individual has approximately a 50–50 chance of having more than one abnormality.

The high frequency of multi-abnormal individuals presents an opportunity to study the relationship between the scales of the shell with respect to the occurrence of two or more discrete abnormalities. Scale inter-relationships were studied in detail in the sample of 109 multi-abnormal individuals of *Chrysemys picta* (Table 2). In general, it was found that multiple abnormalities were quite localized and occurred most frequently upon the same or immediately adjacent scales. Coincident occurrence of abnormalities on widely separated scales was commonly the result of profound disturbances affecting intermediate scales as well. The data reveal some tendency for coincident abnormalities to occur upon paired shields, but this tendency is less striking than the relationships between adjacent scales. These observations were confirmed in a similar study of *Terrapene carolina.* No attempt was made to test these conclusions by statistical means, since it is difficult to conceive of all scales as being discrete and equivalent units. Such tests would appear to be superfluous in view of the consistency of the relationships of each scale in each of the two species studied.

TABLE 1.—Frequencies of multi-abnormal individuals in four species.

SAMPLE	Sample size	Single/ individual	Multiple/ individual	Multiple/ Single
Chrysemys picta	355	56	83	1.48
Terrapene carolina	187	32	41	1.28
Kinosternon subrubrum	84	16	13	0.81
Pseudemys scripta	193	35	35	1.00
			Average =	1.14

Tests for the independence of the right and left sides of each shield of *Chrysemys picta* and *Terrapene carolina* were made (Table 3). It was found that in each shield the condition of one side with respect to normality or abnormality is not independent of the condition of the other side. This conclusion is consistent with the observations that there is some tendency for paired abnormalities and a strong tendency for multiple abnormalities to occur upon adjacent shields.

TABLE 2.—The number of individuals of *Chrysemys picta* showing coincidence of abnormality in carapace.

	C	V_1	V_2	V_3	V_4	V_5	P_1-R	P_1-L	P_2-R	P_2-L	P_3-R	P_3-L	P_4-R	P_4-L	M_1-R	M_1-L	M_2-R	M_2-L	M_3-R	M_3-L	M_6-R	M_6-L	M_7-R	M_7-L	M_8-R	M_{11}-R	M_{12}-R	M_{12}-L
Cervical		1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
Vertebral 1			4	1	2	3	3	3	3	3	2	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Vertebral 2				5	5	4	5	3	6	4	5	2	4	1	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Vertebral 3					7	3	3	1	4	3	5	2	4	3	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Vertebral 4						17	4	1	5	2	7	3	14	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vertebral 5							4	2	4	2	5	2	13	8	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Pleural 1—Right								1	5	2	4	1	4	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Pleural 1—Left									2	3	1	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Pleural 2—R										3	5	2	4	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Pleural 2—L											2	3	1	2	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Pleural 3—R												3	6	2	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Pleural 3—L													2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleural 4—R														4	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Pleural 4—L															0	0	0	0	0	0	0	0	0	0	0	0	1	1
Marginal 1—R																1	0	0	0	0	0	0	0	0	0	0	0	0
Marginal 1—L																	1	1	1	1	0	0	0	0	0	0	0	0
Marginal 2—R																		1	1	1	0	0	0	0	0	0	0	0
Marginal 2—L																			1	1	0	0	0	0	0	0	0	0
Marginal 3—R																				1	0	0	0	0	0	0	0	0
Marginal 3—L																					0	0	0	0	0	0	0	0
Marginal 6—R																						1	1	1	0	0	0	0
Marginal 6—L																							1	1	0	0	0	0
Marginal 7—R																								1	1	0	0	0
Marginal 7—L																									0	0	0	0
Marginal 8—R																										0	0	0
Marginal 11—R																											1	0
Marginal 11—L																											1	0
Marginal 12—R																												15

TABLE 2.—The number of individuals of *Chrysemys picta* showing coincidence of abnormality in plastron.

	G-R	G-L	H-R	H-L	PE-R	PE-L	A-R	A-L	IN-R	IN-L	F-R	F-L	AN-R	AN-L	X-R
Gular–R		3	2	2	3	1	2	1	4	4	0	0	0	0	0
Gular–L			2	3	2	1	1	0	2	2	0	0	0	0	0
Humeral–R				6	4	2	3	2	2	2	2	1	0	0	1
Humeral–L					3	5	2	3	2	1	2	1	0	0	0
Pectoral–R						6	7	3	3	3	2	3	0	1	0
Pectoral–L							4	5	1	0	2	2	2	1	0
Abdominal–R								6	5	6	2	2	0	2	0
Abdominal–L									3	3	1	1	1	1	0
Infra–Marginals–R										28	2	1	1	3	0
Infra–Marginals–L											2	1	1	3	0
Femoral–R												3	2	0	1
Femoral–L													0	1	0
Anal–R														1	0
Anal–L															0
Axial–R															

TABLE 3.—Test for the independence of the right and left sides in *Chrysemys picta*.

A. CARAPACE

	Right side abnormal	Right side normal	Totals
Left side abnormal	44(8.66)	14(49.34)	58
Left side normal	9(44.34)	288(252.66)	297
Totals	53	302	355
	$\Pr(X^2_{(1)} \geq 73.06) < 0.001$		

B. PLASTRON

	Right side abnormal	Right side normal	Totals
Left side abnormal	54(15.6)	24(62.4)	78
Left side normal	17(55.4)	260(221.6)	277
Totals	71	284	355
	$\Pr(X^2_{(1)} \geq 151.88) < 0.001$		

A similar chi-square test was run on the independence of the plastron and carapace with respect to multiple abnormalities. In the two species studied, *Chrysemys picta* and *Terrapene carolina*, the shields were found to be independent in this respect.

$$(Pr\{X^2_{(1)} \geq 2.26\} > 0.10 < 0.20,\ Pr\{X^2_{(1)} \geq 1.68\} > 0.10 < 0.20).$$

This condition is analogous to that of the relationship between the dermal shields. Studies of fossil turtles indicate that the ventral and dorsal dermal shield patterns have evolved independently of one another. Apparently after the over-all adaptive relationships of the plastron and carapace are satisfied, the detailed patterns within the dorsal and ventral shields act as independent morphological units.

SPECIMEN SIZE AND THE FREQUENCY OF ABNORMALITY

The relationship between the frequency of abnormal individuals and size, as expressed by the total length of the shell, was investigated. It was found that in *Chrysemys picta*, individuals of various sizes were not equally subject to abnormality. The size distribution of abnormal individuals was found to be different from that of normal individuals at the 0.01 level of significance in this species (fig. 140).

The difference between the size distribution of abnormal and normal individuals in *Chrysemys picta* is due to the high frequency of abnormals in the larger size classes. As can be seen in the X^2 test (Table 4), there are more abnormal individuals above the median size in this species than could be expected if the condition of abnormality were uniformly distributed with respect to size.

Chi-square tests of the hypothesis that there are equal numbers of abnormal individuals above and below median size, were made for ten other species (Table 5). Three species, *Pseudemys scripta, Graptemys pseudogeographica* and *Chelydra serpentina* (and *Chry-*

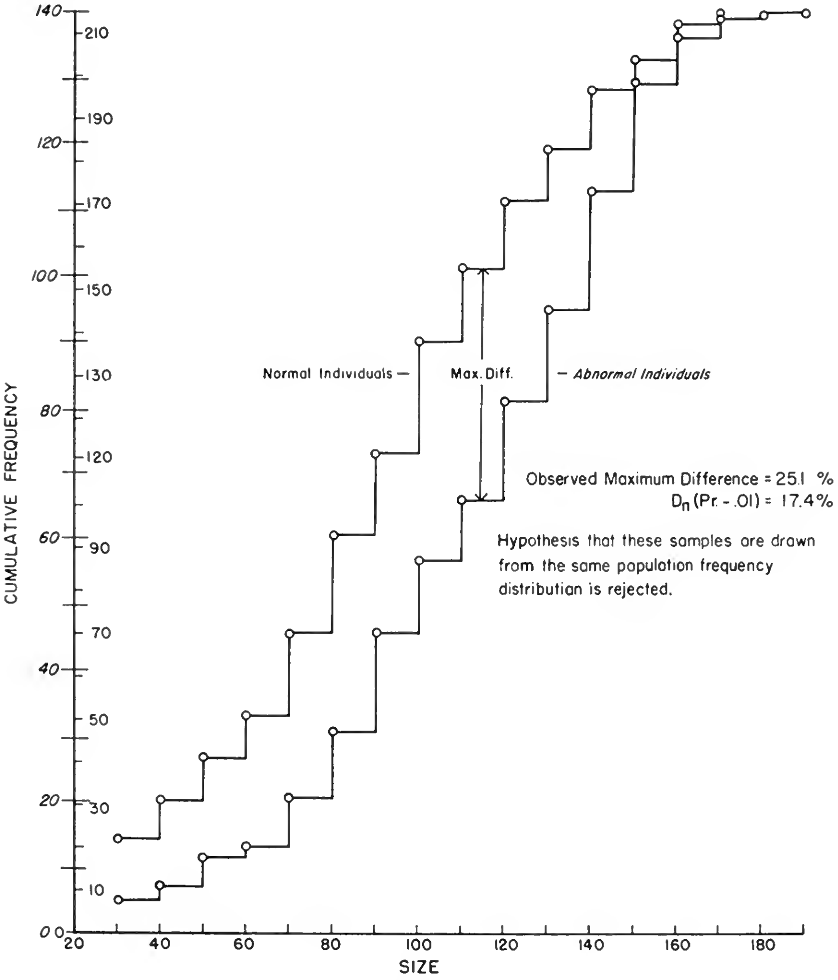

FIG. 140. Size and abnormality in *Chrysemys picta:* Kolmogorov-Smirnov test.

TABLE 4.—Size and abnormality. X^2 test of sample of *Chrysemys picta.*

	Above Median Size	Below Median Size	Totals
Observed	88	52	140
Theoretical	70	70	140
	$\Pr(X^2_{(1)} \geq 9.26) < 0.005$		

TABLE 5.—The results of the X^2 tests of the hypothesis that there are as many abnormal individuals above the median size of a given species as below.

Species	Mode of life	Abnormals		X^2
		Above Median	Below Median	
Pseudemys scripta	Aquatic	49	22	10.27
Graptemys pseudogeographica	"	25	9	7.53
Chelydra serpentina	"	31	11	9.52
Sternotherus odoratus	"	30	17	3.63
Kinosternon subrubrum	"	14	15	0.03
Terrapene carolina	Terrestrial	50	40	1.11
Geoclemys reevesii	"	7	3	1.60
Gopherus agassizi	"	7	4	0.82
Gopherus berlandieri	"	9	11	0.05
Testudo denticulata	"	5	8	0.69

semys picta), were found to have significantly higher frequencies of abnormals above the median size. With regard to the remaining species, there is insufficient evidence to reject the hypothesis, as they have insignificantly higher frequencies of abnormal individuals above median size or about equal numbers above and below.

With the exceptions of *Sternotherus odoratus* and *Kinosternon subrubrum,* the species that did not exhibit a higher frequency of abnormalities among the larger size classes are terrestrial forms. The possibility that such a distribution of abnormality is related to mode of life prompted a more rigorous examination of the two exceptions. Employing the Kolmogorov-Smirnov test, we found that the size distributions of abnormal and normal individuals were different at the 0.01 level of significance in *Sternotherus odoratus* but not so in *Kinosternon subrubrum.*

As will be shown later, there is reason to believe that terrestrial and semi-aquatic turtles are more subject to abnormality than aquatic turtles. If this is so, then the higher frequency of abnormalities and the greater chance of sampling bias in the very small samples of terrestrial turtles available to us may mask any tendency towards the kind of distribution seen in *Chrysemys picta.* In view of this possibility, another approach was attempted in the case of these forms.

The size distributions of individuals having a single abnormality and of multi-abnormal individuals were plotted for several species. The resulting figures (for *Terrapene* see fig. 141) indicate that with increase in size, multi-abnormal individuals become increasingly more common. Among the multi-abnormal individuals in the samples of *Chrysemys picta, Terrapene carolina,* and *Kinosternon subrubrum,* individuals exhibiting five or more discrete abnormalities are found only in the larger size classes.

Thus in seven out of the eleven species studied from this aspect, there is a definite relationship between abnormality and size. In at least five of these species there is sufficient evidence to believe that the frequency of abnormal individuals is higher among the larger size classes. Two of the exceptions to this condition show an increase in the number of multi-abnormal individuals with increase in size. The four remaining species are so poorly represented in the sample that no attempt was made to study the size distribution of multi-abnormal individuals in these forms.

So far we have treated these abnormalities as if they were of the same morphological significance. As the suite includes many quite different variations, it is not likely that all reflect the operation of the same set of factors. The peculiarities of the size distribution of these abnormalities offer a means of investigating the differences between the kinds of variation.

The classification of the abnormalities mentioned earlier was expanded to recognize the following categories:

I. Individuals with one or more heterotopic sulci.
II. Individuals with one or more instances of incomplete expression of normal sulci.
III. Individuals with one or more instances of the loss of typical scales.
IV. Individuals with one or more instances of the addition of scales to the typical pattern.
V. Individuals in which a single disturbance affects the shape and area of one or more scales.

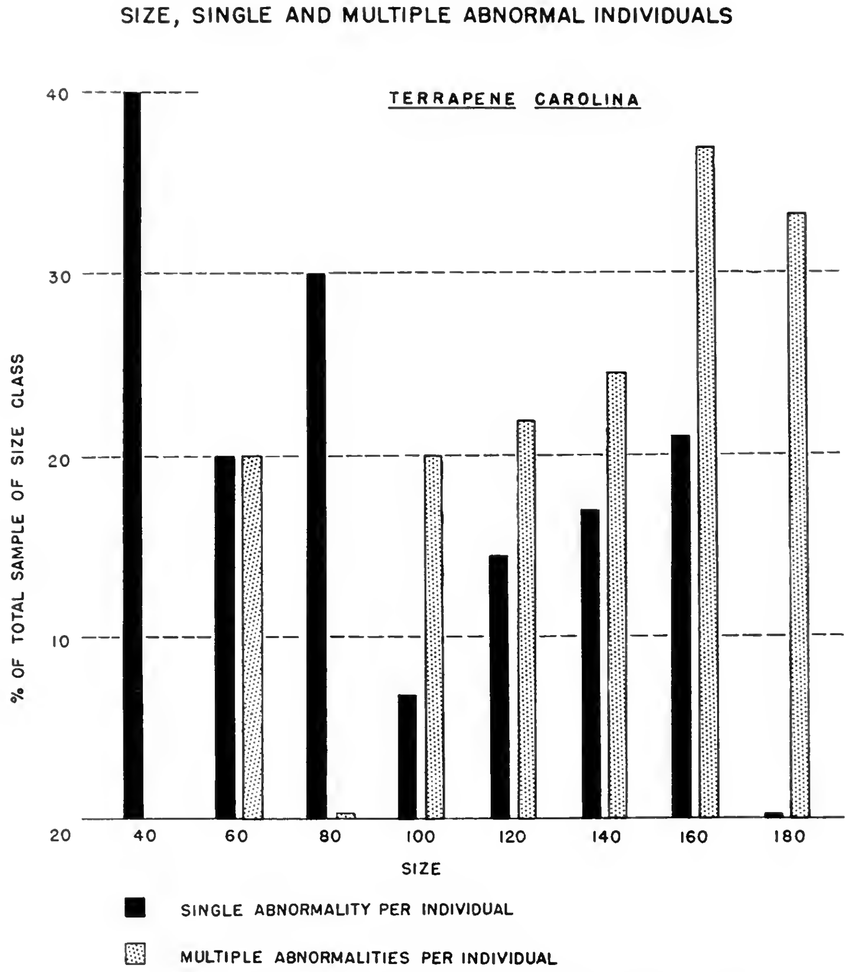

FIG. 141. The size distribution of multi-abnormal individuals in the sample of *Terrapene carolina*.

In *Chrysemys picta* and *Terrapene carolina*, classes I and IV accounted for most of the abnormalities encountered.

In *Chrysemys* there were sufficient numbers in classes I and IV for statistical analysis. Since some multi-abnormal individuals fall into both classes, it was not possible to compare these categories directly. Therefore, the size distribution of class I individuals was compared to the size distribution of all individuals other than those belonging to class I. A similar comparison was made, using the class IV sample. In both instances the hypothesis that the samples were drawn from the same population size distribution was rejected by the Kolmogorov-Smirnov test at the 0.05 level of significance. The interesting aspect of this analysis is that while both class I and class IV abnormalities are chiefly responsible for the higher frequency of abnormal individuals above the median, the individual class contribution is distinctive.

As can be seen in figure 142, individuals with one or more heterotopic sulci do not appear in the smallest size classes but become increasingly more frequent with an increase in size. This latter tendency is not as pronounced as in class IV. The difference detected by the test involves the relatively lower frequency of class I individuals among the smaller size classes. It is interesting to note in this connection that in the majority of instances heterotopic sulci are found affecting only the later "growth rings" of a particular scale.

On the other hand, individuals with one or more additional scales are present throughout the size range of the sample. Class IV individuals become more common with an increase in size (fig. 142). The difference detected by the test involves the relatively higher frequency of class IV individuals among the larger size classes. The deviation of class IV from all non-class IV in the smaller size classes is not great. Thus, while both class I and class IV abnormalities effect a greater number of individuals above rather than below the median, they do so in different ways. Assuming that the classification of the abnormalities is not ambiguous, there is evidence to believe that the size distributions of class I and class IV individuals are not of the same morphological significance.

A similar comparison was made between all individuals with one or more instances of bilaterally symmetrical abnormalities and the remainder of the sample of *Chrysemys picta*. The size distribution of the symmetrically abnormal individuals was found to be different from all others at the 0.01 level of significance. The form of the size distribution was similar to that of class IV, which is not surprising, since most of the symmetrical abnormalities involved the addition of extra elements to the normal shield pattern.

THE DISTRIBUTION OF ABNORMALITY AMONG SPECIES

It has been found that some species are more subject to abnormality than others. We tested the hypothesis that the frequency of abnormality is independent of the species samples, using the Brandt and Snedecor chi-square method (Snedecor, 1946, p. 206). Only those species in which 12 or more individuals were available

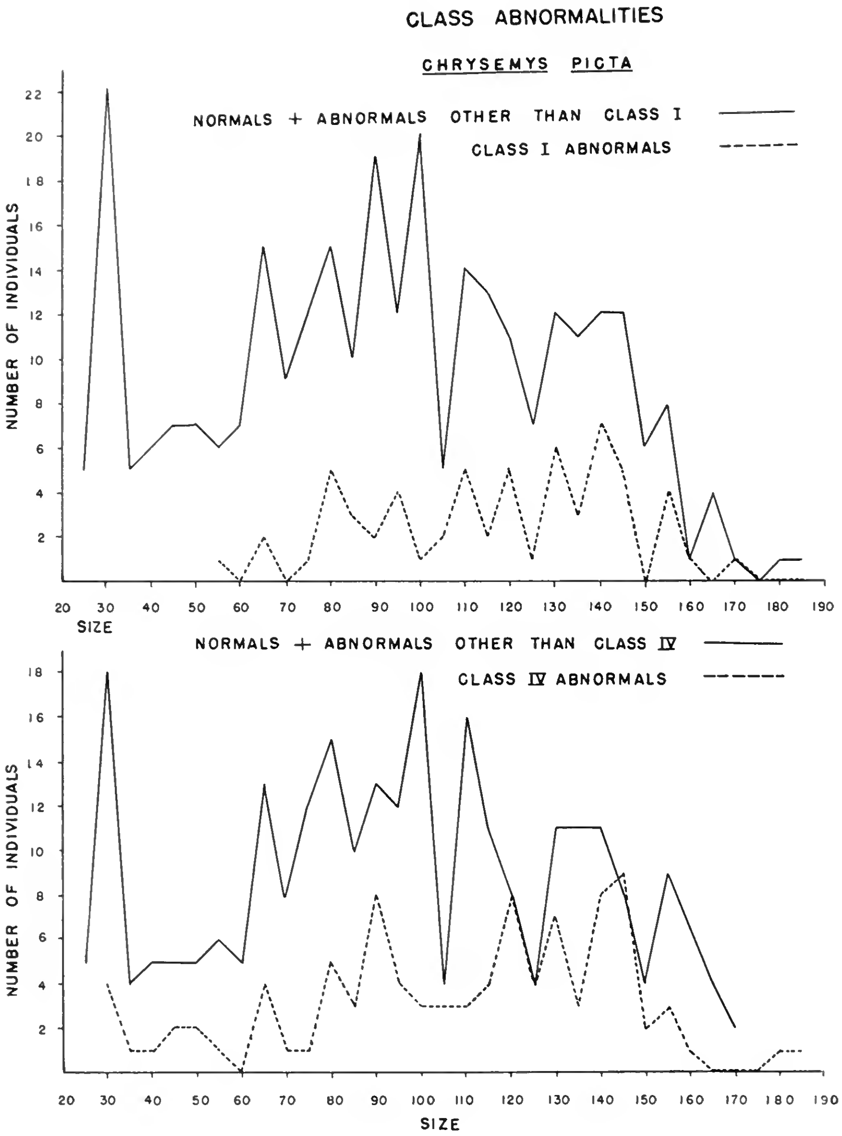

FIG. 142. The size distribution of class I and class IV abnormals in the sample of *Chrysemys picta*.

were used in the analysis. The hypothesis was rejected at the 0.005 level of significance ($Pr\{X^2(_{34}) \geq 122.98\} < 0.005$).

In view of the relationship of abnormality and size it has been necessary to assume that the species samples are random with respect to size. In most instances this assumption seems warranted, but in at least one case, *Terrapene carolina,* the size distribution of the sample suggests the presence of some bias. However, the difference in the frequency of abnormality between the small and large size classes of this species is trivial when compared to the large differences found between species. Therefore, such bias has been neglected, and it is concluded that the difference between species demonstrated by the test reflects the actual circumstances.

In addition to the differences in the frequency of total variation, preliminary studies indicate that particular abnormalities occur more frequently in some species than in others. In *Chrysemys picta,* a single and medial inframarginal on one side occurs 26 times in a sample of 355 individuals. In the remainder of the sample—all other species—this abnormality was observed only 25 times. Similar distributions are evident with respect to other specific abnormalities.

It was found that the frequency of abnormal individuals was different in the various genera and the six families represented in the collection. The hypothesis that the occurrence of abnormalities is independent of generic membership was rejected at the 0.005 level of significance ($Pr\{X^2(_{18}) \geq 82.98\} < 0.005$). A similar hypothesis was rejected in the test of the distribution of abnormalities among the families ($Pr\{X^2(_5) \geq 38.36\} < 0.005$).

Aquatic, semi-aquatic and terrestrial turtles exhibit different frequencies of abnormality. The hypothesis that abnormality is independent of these mode of life categories was rejected by a chi-square test similar in arrangement to that used with the taxonomic groups ($Pr\{X^2(_2) \geq 14.49\} < 0.005$). To test such a hypothesis it has been necessary to assume that each of the mode of life groups is as taxonomically heterogeneous as any other mode of life category. This assumption is warranted in all the groups in the sample, with the possible exception of the semi-aquatic turtles. Although 17 species and subspecies fell into this category, all were members of a single family, the Emyidae. However, this large family includes many forms of each of the modes of life, so the category "semi-aquatic" does not coincide with a single taxonomic group.

Dissecting this result further, we have found that the frequency of abnormality between semi-aquatic and terrestrial turtles is not significantly different ($Pr\{X^2(_1) \geq 0.62\} > 0.30$). The aquatics with a much lower frequency of abnormality are different in this respect from both terrestrial and semi-aquatic turtles ($Pr\{X^2(_1) \geq 14.01\} < 0.005$).

DISCUSSION OF RESULTS

The results of the above analysis are listed below under appropriate headings, together with a discussion of the findings. The terms "variant," "variation," or "abnormal" are used to denote a shield condition of any kind deviating from the normal pattern of the species.

A. *General aspects of shield variability*

1. Of 2,220 specimens studied 43% possess one or more shield variations.
2. Heterotopic sulci are the most common kind of abnormality observed.
3. The posterior half of the shell is slightly more variable than the anterior half.
4. The most variable scale of the shell is the abdominal scute of the plastron. The next most variable scales are the two last marginal scutes on either side of the carapace.
5. There is a tendency for multiple variations to occur on adjacent scales in an individual.
6. There is a tendency for coincident variations to occur on paired scales of the shell.
7. These two latter tendencies appear to be responsible for the fact that the plastron and carapace are not bilaterally independent with respect to normality or abnormality.
8. There is evidence to suggest the independence (with regard to normality or abnormality) of the carapace and plastron.

The greater variability of the posterior portion of the turtle shell corresponds with the common observation that the thecal, or bony shell also shows the greatest degree of variation in this region. There are many examples (see also Parker, 1901) where both the bony shell and the epidermal shields are abnormal in the same individual. In view of the very high variability of the epidermal shields, many such occurrences must be coincidental. Furthermore, cases are known where individuals exhibiting profound thecal abnormalities possess perfectly normal epidermal shields. Thus, there is no evidence to suggest that there is any relationship between the variability of the thecal and the epidermal shields. However, there is phylogenetic evidence to the effect that the posterior part of the bony carapace has never been fully stabilized. The incorporation of the sacral complex of the vertebral column into the shell presents, morphologically, a much more complicated situation than exists anteriorly. It may well be that the variability of the shield cover reflects in a general way the relative phylogenetic instability of this area although the differences between anterior and posterior areas reported here are slight.

The tendency for multiple variations to affect adjacent scales probably reflects the actions of mechanisms that govern the growth of a relatively complicated, geometrical pattern of shield areas. At least in some instances, adjacent abnormal shields suggest positive or negative compensatory growth of one or both elements to maintain a closed shield mosaic.

The tendency for coincident variants on paired scales and the apparent dependence of the condition (with regard to normality or abnormality) of one side of the shell on that of the other side, may be related phenomena possibly connected with that mechanism of growth that controls the bilaterally symmetrical development of the organism.

As has been pointed out earlier, the variational independence of the carapace and plastron is not a surprising result. Throughout the history of the order the carapace and plastron display a notable phylogenetic independence of each other. This is most clearly demonstrated by turtles that have undergone profound marine specializations that are usually accompanied by gradual reduction of the bony shell. In some forms the carapace is almost entirely reduced while the plastral plates are thick and large bones (e.g., the Protostegidae), whereas in others (e.g., the Toxochelyidae and some cheloniids) the reverse situation prevails. As to the epidermal shield cover, an interesting example of the independence of carapace and plastron is seen in the modern *Chelydra* where the carapace mosaic is entirely normal but where the scute pattern of the plastron differs notably from that of the usual condition. In *Macrochelys* the pattern of the *Chelydra*-plastron is further modified and moreover is so highly variable that Boulenger (1889) felt compelled to illustrate four different shield conditions in this species.

B. *Relationships of shield variation*

1. There is a relationship between the frequency of shield variations and the size of individuals.

   (a) Heterotopic shield furrows are rare in the very young, their frequency of occurrence increasing with an increase in specimen size.
   (b) Supernumerary scales occur in all size ranges, but likewise increase in frequency with specimen size.
   (c) Bilaterally symmetrical variants occur in all size ranges, their frequency increasing with increase in specimen size.

2. There is a relationship between the frequency of abnormality and mode of life: aquatic species vary less than do semiaquatic and terrestrial forms.
3. There is a relationship between the frequency of abnormality and the systematic categories:
   (a) There is a different frequency of variation in different species, genera, and families.
   (b) The frequency of occurrence of specific kinds of variations differs with species.

The character of the shield variability as summarized above permits, we believe, an inquiry into the nature (teratological, somatic, genetic) of these variations. The observation that semiaquatic and terrestrial forms vary more than aquatic forms suggests that many of the abnormalities are due to the effect of the environment. If this is so it may be that fewer abnormalities are produced in the growth of aquatic forms because of the relative uniformity of this environment with regard to temperature, humidity, insolation, etc., as compared to the terrestrial biotope.[1] On the other hand, the environmental effects upon epidermal growth may be the same in both aquatic and terrestrial environments (basking behavior of aquatic turtles; search for cool and moist shelter by terrestrial forms). If this latter possibility is actually the case we would have to assume genetically determined variation, selected against in the aquatic environment. The observed age distributions of abnormality in the aquatic forms is not that expected for such selection. It is difficult to conceive of any advantage or disadvantage in adaptation associated with the kinds of variations studied here.

The observation that the frequency of abnormalities increases with the size of the individuals supports the view that most of the abnormalities (heterotopic sulci) are related to environmental

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[1] Abnormalities caused by the healing of wounds (such as are frequently seen in *Terrapene* and are incurred in brush fires) are readily recognizable and have not been recorded.

factors. The age distribution observed is that expected if the number of abnormalities in a population is a function of the period of time individuals are exposed to inducing agents. It is conceivable that such a distribution could arise through the action of specific genetic factors acting late in life. While such genetic factors have been recognized elsewhere (notably in man) they could not be as common as those acting early or throughout life.

All of the variations studied here, however, cannot be considered to be environmentally induced. The distribution of abnormality among species suggests the action of specific genetic control in at least a few types of abnormality. *The fact that certain abnormalities occur more frequently in a single species than in all other species combined seems to indicate some form of genetic predisposition.* In addition, the possibility of atavism cannot be entirely dismissed in such cases as the late ontogenetic development of a supernumerary inframarginal scute in an emyid turtle, a structural element typical of a more primitive level of turtle scutellation. These aspects of the problem will be analyzed in much more detail in the further analysis of the sample.

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