Orthogenetic Variation

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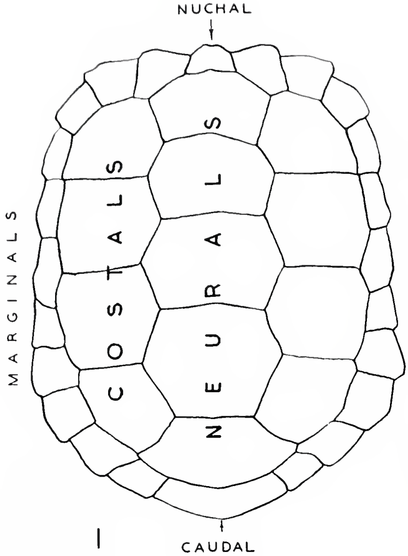
Hans Gadow was the author of a contested hypothesis called "orthogenetic variation." This endeavored to account for an apparent reduction in the number of extra scutes during the growth of turtles. This paper presents later evidence which may prove that some of his assertions were correct, and at the same time it may reconcile a few of the arguments advanced by Gadow's critics.

To orient the reader, it might be said that, except in a few species of turtles, the normal horny scales or scutes covering the bone case or box are arranged and usually designated as shown in Figure 1. Scutes in excess of this complement have been called "extra," "supernumerary," "abnormal," or, as Gadow believed, "atavistic." In this article the scutes will be termed "extra" and the turtles bearing them "abnormal." We do not deny the existence of atavistic scutes, and by "abnormal" we mean only variations from the average.

In arriving at his theory of orthogenetic variation, Gadow (1) studied and tabulated the scutes on a series of 82 marine turtles and showed that the young had from four to seven times as many extra scutes as the adults. For some reason he did not blame the possible handicap caused by abnormalities for the destruction of individuals by their natural enemies. He stated, in so many words, that natural selection remained indifferent in this case. To explain the apparent reduction of extra scutes on growing turtles, he evolved the idea that the individual lost them by: (a) fusion of two or more scutes; or (b) suppression of a scute by its failing to grow amid normally growing scutes. He admitted having no evidence to prove this and said that it would be necessary for some one to watch the growth of marked turtles to prove his theory. In the meantime he said that he appealed to common sense and comparative anatomy to uphold him. He stated: "I therefore call this kind of atavistic variation orthogenetic." Literally that would mean that a turtle is an atavistic variant only as long as it retains extra scutes. He desired a term descriptive of self-correction by an individual while dropping ancestral traits and approaching the so-called normal. He did not use "variation" in its commonly accepted meaning. He might have said, "I therefore call this changing from atavistic toward normal, an orthogenetic change, or orthogenesis." The term "ontogeny" might have been used.

Coker (2) rebutted Gadow's hypothesis by calling attention to the small series of specimens used by Gadow and to the fact that the two largest specimens bore the greatest number of scutes, which would tend to refute his hypothesis at the start. Also there were 44 abnormals from one nest of 47 babies in the total series of 82. Coker submitted a table of 238 specimens of Malaclemmys and said that the percentage of abnormals did not vary with age but that extra or abnormal scutes might be correlated with deep-seated abnormalities which could cause death. Coker did not point out that symmetry was not so vital to palustrine Malaclemys as it would be to a marine turtle in its exacting environ-



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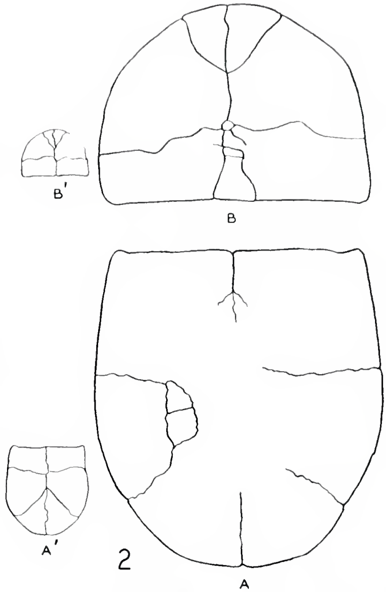

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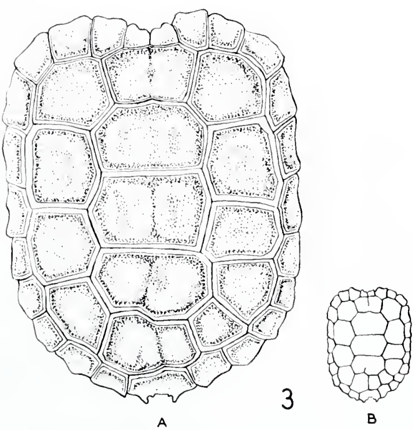

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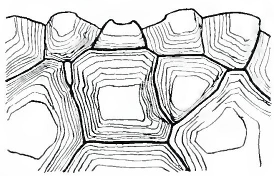
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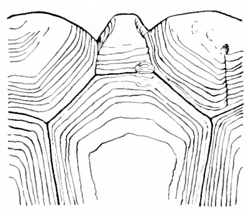
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Fig. 1. Normal scutes of carapace of *Gopherus agassizii.*

Fig. 2. *A*, posterior lobe of plastron of *Terrapene triunguis* (13,165, Field Museum), showing that the normal sutures as shown in *A'* have disappeared or wandered, making false scutes; *B*, anterior lobe of plastron of *T. carolina* (18,649, Field Museum), showing that normal sutures as shown in *B'* have wandered and thereby formed false scutes.

Fig. 3. Yearling of *G. agassizii*. *A* shows that some sutures did not develop although they had been indicated by aeroles when the specimen first hatched as shown in *B* by the split nuchal, and first, fourth, and fifth neurals. Note the double ocellation in the second and third neurals indicating a primordial double row. Specimen alive in writer's possession.

Fig. 4. Anterior portion of carapace of *G. agassizii*, showing an extra costal, anterior to number one on the right side, and a corresponding scute on the left which is being crowded out. Specimen alive in writer's possession; presented by Dr. F. B. Sumner.

Fig. 5. Anterior portion of carapace of *G. agassizii* showing extra scute, which is being crowded out at the right rear of the nuchal. This may have originated as a split nuchal, as in Fig. 3. Note the "radial suture" on the first right marginal. Specimen dead in possession of writer.

(Illustrations by Norman Bilderbach, by courtesy of Dr. C. G. Abbott, San Diego Soc. Nat. Hist.)

ment, nor did he state whether his examples were reared in capitivity or had been wild specimens exposed to normal dangers. Lastly, his oldest specimens were only three or more years old. He then took up "fusion and division" which had been Gadow's next point and illustrated his article with specimens of partial fusion and partial division and ended by saying that finally there is no actual fusion or division at all. We shall see in Gadow's next paper that he thought Coker had admitted fusion. He evaded Gadow's idea of a crowding out or suppression of scutes by saying that where the outer scute layers scale off, the record of a scute which had not developed would be obscured and that such cases are unexplained and probably abnormal. We believe that scaling off of outer layers of scutes is normal in Chrysemys and explained as the usual shedding of a reptile skin. To clinch his argument Coker stated that sutures remain distinct. We have found that sutures sometimes wander or disappear in old turtles as described with Figure 2.

Gadow (3) later, in 1905, disputed Coker and championed the term "orthogenetic variation," for which he claimed authorship. He admitted that his specimens had been too few, but said that Coker's were too young—largely embryos. He stated that Coker had charged him with the claim that embryos "should begin to mend their ways before they are born" and denied the assertion, although in his first paper he had said: "In several newborn specimens such a fusion is still incomplete." This remark might lead to the assumption that he believed in embryonic scute fusion; so it is not clear why he was so ready to deny it. He seized upon Coker's remarks on fusion by saying: "Would it not . . . support my hypothesis . . . that the number (of scutes) can be reduced? I should feel grateful (to Coker) and glad to accept 'fusion' instead of my suggested 'squeezing out'." As has been pointed out, Coker did not admit of a fusion of scutes "once formed," but we do not understand what Coker meant by "once formed" as no question is likely to arise about unformed scutes.

Coker (4) still later, in 1905, regretted that Gadow had misinformed unsuspecting readers of Volume 8 of the 1901 Cambridge Natural History by saying that certain shields are squeezed out or suppressed by their enlarging neighbors and that the ultimate result is the formation of fewer but larger shields. We point out later that Gadow was probably correct, but he had no proof for his statements.

Newman (5) summarized Gadow's work and stated that he could see no difference in proportion of abnormals between young and adults in his series of 476 specimens of Graptemys and 188 of Chrysemys. He stated that a scute, whether normal or extra, is a separate and definite entity, resulting from a definite embryonic primordium. The writer cannot fully subscribe to this statement. A scute is not an organ, but merely an epithelial area of a size first dictated by the necessity of pliability, and later, as turtles developed a bony box, the reduction of the number of scutes was limited by the necessity of enlarging to keep a growing box covered. Newman criticised Gadow's tables by saying that a large proportion of new-born specimens came from one nest, the whole brood of which was abnormal and that the others were taken in small sets from various collections and he believed that such specimens had been preserved chiefly because of their abnormalities. Neither Newman nor Coker made allowances for the higher mortality of prolific sea turtles. This point would have mitigated some of Gadow's statements, although he checkmated himself with the statement that natural selection remained indifferent to abnormalities.

Parenthetically, the writer wonders at the statements of Gadow that natural selection remains indifferent to an abnormality and of Coker and Newman who subscribe to the same idea when they unqualifiedly state that they found no difference in proportion of abnormals among young and adults. Coker (2) said that it was hardly conceivable that the success of a turtle in the struggle for existence would hinge on whether it was the possessor of ten or eleven costal scutes. He went on to say that probably extreme cases were correlated with deep-seated abnormalities which might cause failure to survive and that natural selection could not be ignored. Such statements and findings seem tantamount to professing belief in creation and abjuring evolution. The writer believes that an infinitesimal variation is immensely important in geological time. Authorities supposedly agree that the ancestors of turtles had more scutes and that the survival of the fittest evolved the present form. Since atavism is an established fact, some extra scutes on turtles may prove to be atavistic. Variation must be constant and radial or the living universe would be static; consequently variations of even less than the present normal number of scutes should be expected. The fittest have always survived in the long run; so it is impossible to believe that individuals with either more or less than the normal number of scutes should have the same chance of survival as the normal. The "normal" may be shifting to more or less scutes than we now consider normal, but it would take years and great numbers of specimens to prove this.

Coker (6) stated that external pressure on soft turtle eggs might cause abnormalities. The present writer found that about 10% of over 300 specimens of Gopherus examined were abnormal, but the eggs of this turtle are brittle and so hard as to be insusceptible to warping by any pressure they would normally receive. Coker reviewed all the authors who wrote about extra scutes and summarized Gadow as follows: (1) Variations are reversions to ancestral conditions. (Parenthetically let us point out that Gadow (3) had stated that there is also a "beyond the type," meaning a variant with less than the normal number of scutes.) (2) The hypothetical explanation is that these atavisms are stages in ontogeny or arrests of development.

Coker said that when Gadow regarded these atavisms as arrested development in adults and ontogenetic recapitulation in the young, his position seemed untenable on the basis of any facts then at hand. However, Coker discussed radial sutures appearing in the periphery of abnormally large scutes by saying that these radial sutures may indicate post-natal attempts to perfect a previously inadequate adjustment. This is apparently just what Gadow meant in his hypothesis and what Coker was endeavoring to discredit.

We believe that these radial sutures are caused by a purely mechanical law which is here discussed. Theoretically, one single horn scute would have been the turtle's ideal covering, but horn, being dead, cannot stretch; so it was impossible for all the scutes to fuse into one sheet and keep the box covered as it grew. Mechanically there was a minimum number of scutes below which evolution could not go. In terms of geology a cooling, shrinking magma splits into hexagonal pillars, similar in cross section to the scutes of a turtle. An example more frequently seen is in the hexagonal cakes formed in drying mud. An interesting analogy is the "turtle stone" formed when the cracks of dried mud are filled with sand and the whole solidified and later broken and rounded by the elements. Growth from within or radial expansion is the opposite of the geological phenomena mentioned, but the result is the same. Now if it were possible to remove the scutes from a young turtle and cover it with a brittle unyielding substance, its growth would probably crack this coating into figures similar to normal scutes. The numerous marginals cannot efficiently reduce further because the plan and cross section of a turtle change, the hatchling being flatter and more nearly circular than the adult. Since the greatest change of shape occurs along the margins, smaller scute units are required to accommodate it. A like explanation for the growth of the plates of the inner bone box is not necessary because bone grows by introsusception, whereas dead horn cannot. The turtle early found the smallest number of scutes which could cover the bone case and still accommodate growth. The radial sutures which Coker mentions as post-natal efforts to carry out a plan may have been mechanical adjustments based on a law of minimum sutures or fractures.

The figures may serve to coordinate some of the above views.

Figure 2 is of two aged specimens of Terrapene in the Field Museum. The plastrons are greatly worn. The writer's interpretation is that with age and the consequent cessation of expansion, the normal growth stimuli of the malpighian layer are changed fortuitously, allowing the sutures to wander or disappear. If this interpretation be correct, sutures are not always fixed, especially when they disappear altogether, as in Figure 2, A, *T. triunguis* (No. 13,165). The extra areas which have appeared, as in Figure 2, B, *T. carolina* (No. 18,649), by reason of the fortuitous wandering of the senile sutures should not be classed as scutes, being merely divisions that were not represented by the original aeroles. Figures 2, A′ and B′ show the normal sutures on the plastron of a vigorous specimen.

Figure 3 is of a baby specimen of *G. agassizii* which the writer saw hatched. Figure 3, B, which was made at the time of hatching, shows a double aerole at the rear of the neural series. The quadrangular scute at the rear of the fourth neural can be considered as the sixth right costal because there is a faint indication of the fifth neural to show pairing or longitudinal division as in the nuchal. Figure 3, A, shows the same specimen at the age of one year. Two aeroles, or the last neural, developed as one unit, appearing to prove Gadow's assertion of loss by fusion. The writer believes that it shows an atavistic scute, but no growth was needed at the extra suture to comply with the law of minimum sutures. This case is altogether different from Coker's theory of partial fusion of scutes once formed.

Figure 4 is of a 10 cm. female of *G. agassizii*, with about six growth rings, which was presented to me by Dr. F. B. Sumner. This specimen has a medium sized extra scute between the first costal and first neural on the right side. At a corresponding position on the left side, there is a narrow scute which I interpret as having been a very small original aerole that did not increase in size. It may have grown higher from successive layers of horn having been deposited underneath and then broken off by some mechanical agency. This narrow, slit-like area, which probably was a well marked aerole in the hatchling, is seemingly disappearing, thus reducing by one the number of original aeroles and proving Gadow's hypothesis of "suppression" of extra scutes.

Figure 5 is of an old specimen. It shows what the writer interprets to be the right half of a paired nuchal which did not expand, while the left half grew normally. What may have been the right half is now a high, wart-like process which could conceivably be broken off. Probably the aeroles of this specimen showed an evenly divided nuchal as in Figure 3. Normally the nuchal is single in this species.

Summary

1. The term "orthogenetic variation" as used by Gadow appears to be meaningless.

2. Turtles occasionally show fewer scutes when adult than appeared in the hatchling due to: (a) the development of two aeroles as one scute, (b) the failure of a small aerole to expand, resulting in its being crowded out by the normal development of adjacent scutes, or (c) the wandering or disappearance of sutures in aged turtles, thus obliterating the original scutellation.

3. In addition to the reduction of extra scutes mentioned in (2) above, a sufficient series must show a higher mortality in abnormal than in normal turtles.

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