HOMOEOTIC MUTANTS AND EVOLUTION

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(with 3 figures)

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In a series of former publications (GOLDSCHMIDT, 1933-1951) I have defended a saltational point of view of evolution. This means, on the negative side, that evolution of the higher taxonomic categories cannot be explained by the accumulation of miromutational steps which lead only to diversification without evolution, mostly by "existential adaptation" to the standard features of environment (see 1949). On the positive side it means that real evolutionary changes, as involved in the origin of at least the superspecific categories, are brought about by large mutational steps, saltations, which change at once major features of early development, which results in the production of a largely divergent organism. In its general form the saltational point of view is not new as repeatedly emphasized by myself. What is new is its derivation from an integrated study of the facts of taxonomy, geographic variation and its genetic basis, cytogenetics, chromosome structure, experimental embryology, comparative anatomy (including paleontology), and physiological genetics.

Already in former publications I pointed out that the so-called homeotic mutants of Drosophila may serve as good models for what probably happens in saltational evolution. Other evolutionists seem also to have been impressed since by the importance of the subject as SEWALL WRIGHT'S (1950) recent discussions show. (see below). I am returning here to the subject because a new study of one of these mutants has revealed facts which I consider to be of great significance for the problem.

All mutations produce a change in some developmental step which occurs at a definite time and stage of development as well as in a definite region of the embryo. The standard mutants act, as a rule, upon some minor process in the finishing of an organ, say the production or non-production of a pigment precursor, while the part to be pigmented differently from the

1) This investigation was supported by a research grant from the National Cancer Institute of the Public Health Service.
original form finishes its normal development. Other mutants may affect quantitative features of an otherwise correctly determined organ, e.g., the number of facet forming primary cell-divisions in a compound eye. A real macromutational change would affect early embryonic processes of organ determination at the source as it were. If, for example, in an arthropod the early anlage of a segmental appendage is affected by a mutant before its determination as a leg bud is final, with the result that a gill or a mandible is formed, we speak of a macromutation, and we claim that all major evolutionary steps involving a real change of organization cannot be produced in any other way than by an initial single change of determination in early development.

Therefore, apart from the genetical and population genetical aspect of the problem, the center of the discussion must center around the genetically controlled processes of embryonic determination and their change by mutation. We ask: How far can early and basic features of development, especially the processes of embryonic determination, be changed by a single genetic change without upsetting the finely balanced and interwoven web of happenings in time and space which make up embryonic development? What consequences for subsequent development will be entailed by a single genetically controlled, early change in embryonic determination? Do the potentialities of development permit a major deviation of early determination or growth to be worked into a balanced and functional whole? Can the regulatory growth required for such a restitution produce large structural changes which are nevertheless well integrated into a whole? Is it possible thus that a single mutant change at the level, time, and point of organ determination results finally in a complex "normal" structure which is new in itself and is properly integrated in the whole? In short, does macromutation succeed to produce at once large deviations by the process of shift in determination followed by regulative integration? Is, therefore, the origin of a new type of structure by saltation not a minor miracle, as has been said, but a process which is not at all miraculous and within the known features of genetics and development?

At a former occasion (Goldschmidt, 1948; Goldschmidt et al. 1951) I had already presented a case which has many of the characteristics we are looking for. By a genetic change (shortly reported in Goldschmidt et al. 1951) a line of Drosophila was obtained with a tendency towards union of the two first legs. Whether the two imaginal discs were pushed towards the ventral midline and fused more or less, or whether they started development already at this point is not known. But the result shows in the extreme cases: 1. The primary effect of the genic action is the fusion of the two discs.