

One of first people to deal explicitly with the importance of the genotype-phenotype map

**NOTE: USE OF THE WORD "RASSENKREIS"—**

'Rassenkreis' is a German word that literally translates to 'ring of races'. It is used in modern parlance as 'ring species' and also applied literally to refer to situations in which there is a continuous species distribution with clinal variation in a donut-shaped pattern. As the species range expands and the two ends of the growing 'donut' come into contact, the populations on each side are no longer able to interbreed, i.e., they are 'good' species, even though there are continuous, interbreeding populations connecting them. Only a couple of actual examples of a true ring species have been identified and even these do not present so neat a picture.

**BUT THIS IS NOT WHAT GOLDSCHMIDT MEANS WHEN HE USES "RASSENKREIS"!** Goldschmidt's usage is the German, non-literal meaning, which is simply a group of related populations/subspecies that together constitute the range of a species, i.e., a group of related populations within a single species that has some geographic structure to it.

# THE MATERIAL BASIS OF EVOLUTION

BY

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old essays finally grew into four elaborate and completely documented books; two of them, with about ten years' interval between them, on sex determination (Goldschmidt, 1920a, 1931), and two others, again separated by ten years of more analytical work, on physiological genetics (Goldschmidt, 1927, 1938). I had always wished to accomplish the same for the evolutionary part of the essays and I intended to do so after my own chief experimental contribution to evolution, the analysis of geographic variation, was finished. When this finally came to pass (in 1932), other work had come to the fore and I contented myself with embodying some of the generalizations in a short paper and in occasional lectures, delivered at different meetings and in different European and American universities. Only a few of these (Goldschmidt, 1932, 1933, 1935) were published. The appointment as Silliman Lecturer—an honor for which I am deeply grateful—has finally furnished the necessary stimulus to carry out the plan, for which the material has been collected for a long time.

## II. THE PROBLEM

ACCORDING to the deed of this lectureship, "its general tendency . . . may be such as will illustrate the presence and wisdom of God as manifested in the Natural and Moral World." To the naturalist this means the demonstration of law and order in his chosen field. As evolution is our topic, this might mean that a full discussion of the facts, laws, and theories of evolution is to be expected. This, however, cannot be accomplished. No individual can claim such a mastery of all facts pertaining to evolution to enable him to present such a discussion. Moreover, it is not my intention to present an objective review of the present status of the problem of evolution. Though attacking the problem as a geneticist, I do not even intend to discuss evolution from the geneticist's point of view alone. What I propose to do is to inquire into the type of hereditary differences which might possibly be used in evolution to produce the great differences between groups, and the title of this book, accordingly, ought to be something like: The genetical and developmental potentialities of the organism which nature may use as materials with which to accomplish evolution. In the analysis of this problem I shall try to use whatever viewpoint seems to lead to progress. Many of the conclusions which we shall reach will be in disagreement with the views held generally by geneticists or, on a different basis, by taxonomists. I trust that negative and sterile criticism will not be found in our discussion, and that whatever doubt is cast upon established ideas will be based upon ample facts and will be the type of doubt which is the sire of progress. There are many important facts relating to evolution, genetic and otherwise, which will not be mentioned. This does not mean that I underrate their importance, but only that they are considered to be outside the sphere of those problems in evolution which are selected here for discussion. If I may compare the individual facts concerning evolution to individual glass

mosaic cubes, it is not my intention to present a huge bagful of them to be used on a future day for assembly into a figure. I intend to build a smaller but finished picture, using only a selected part of the cubes in the bag. Under such circumstances I shall not try to bring together and to review all literature relevant to the subject. This would be a Herculean task and it would, in addition, tend to drown the general picture in a mass of detail. I shall, therefore, have to select my examples and to use those which best illustrate the argument. It is my wish to make this selection in as fair and open-minded a spirit as possible, and I shall try to include at least all really important facts. This book, then, is no treatise on evolution and does not intend to compete with comprehensive treatises like the brilliant texts by Haldane (1932) and Dobzhansky (1937), and the many other collections of fact presented from different angles, viz.; Berg (1926), Cuénot (1911, 1936), Guyénot (1930), Hertwig (1927), Robson (1928), Robson and Richards (1936), and others.

The problem of evolution as a whole consists of a number of subproblems, with some of which we are not concerned here at all. There is, first, evolution as a historical fact. With all biologists we assume that evolution as such is a fact. There is the problem of selection or survival of the fittest. It may be considered as established, both biologically and mathematically, that given hereditary variations, definite systems of heredity like Mendelian heredity, and differences in regard to survival value, selection may wipe out one type or isolate a new type. This means that there is no difficulty in the understanding of evolution, provided the *necessary* hereditary variations are given. There are the different aspects of adaptation, only some of which will be discussed. It is mainly the problem of the hereditary differences as the material of evolution which we shall discuss.

The information on this topic is derived from different fields of study. The basic knowledge is furnished by the taxonomist who registers the actually existing forms down to the smallest recognizable units, and states their natural

affinities, their ecology, and their habitat. A different kind of information is available to the geneticist. He follows the origin of hereditary differences and locates their actual basis in the germ plasm. But it is evident, though sometimes forgotten, that the methods of evolution cannot be derived, say, from the genetics of coat colors of rabbits, without taking into account the existence of what may be called macrotaxonomy. The laws which are supposed to explain the diversification of species must also account for families, orders, and phyla: differences rat-mouse, cow-whale, horse-lizard, butterfly-snail, must all be explained. This means that the geneticist who comes to definite evolutionary conclusions with his limited material must test them within the larger field of macrotaxonomy, the origin of the higher systematic categories, and admit failure if this test fails.

The same applies, of course, to the taxonomist. He used to derive his opinions upon species formation from studies of closely related species. Nowadays he adds to this the study of the subspecies found in nature and their geographic relations. We might call this microtaxonomy. Conclusions derived from microtaxonomical studies upon the methods of evolution are valuable as generalizations only if they can explain also the facts of macrotaxonomy. It is in microtaxonomy that the geneticist and the taxonomist come together. Macrotaxonomy is practically inaccessible to genetic experimentation, but the range of the subspecies up to, or nearly up to, the limit of the species is accessible both to the geneticist and the taxonomist. The results of both, therefore, may be mutually checked, and definite conclusions seem possible.

The field of macrotaxonomy, however, is not directly accessible to the geneticist, or only to a very limited degree. Here the paleontologist, the comparative anatomist, and the embryologist are supreme. The geneticist must try to apply his findings in microtaxonomy to the materials of macrotaxonomic order which he finds in those fields, provided this can be done. This is where the geneticist faces his most difficult task.

There is, finally, another field which has been neglected

almost completely in evolutionary discussions; namely, experimental embryology. The material of evolution consists of hereditary changes of the organism. Any such change, however, means a definite change in the development of the organism. The possibility and the order of magnitude of genetic changes are therefore a function of the range of possible shifts in the processes of development, shifts which may take place without upsetting the integration of embryonic processes. From this it follows that the potentialities of individual development are among the decisive factors for hereditary change and therefore for evolution.

This statement of the problem already indicates that I cannot agree with the viewpoint of the textbooks that the problem of evolution has been solved as far as the genetic basis is concerned. This viewpoint considers it as granted that the process of mutation of the units of heredity, the genes, is the starting point for evolution, and that the accumulation of gene mutations, the isolation and selection of the new variants which afterwards continue to repeat the same process over again, account for all evolutionary diversifications. This viewpoint, to which we shall allude henceforth as the neo-Darwinian thesis, must take it for granted that somehow new genes are formed, as it is hardly to be assumed that man and amoeba may be connected by mutations of the same genes, though the chromosomes of some Protozoa look uncomfortably like those of the highest animals. It must further be taken for granted that all possible differences, including the most complicated adaptations, have been slowly built up by the accumulation of such mutations. We shall try to show that this viewpoint does not suffice to explain the facts, and we shall look for explanations which might evade these and other difficulties and simultaneously account for such facts as have to be pushed to the background to make the popular assumptions plausible. At this point in our discussion I may challenge the adherents of the strictly Darwinian view, which we are discussing here, to try to explain the evolution of the following features by accumulation and selection of small mutants: hair in mammals,

feathers in birds, segmentation of arthropods and vertebrates, the transformation of the gill arches in phylogeny including the aortic arches, muscles, nerves, etc.; further, teeth, shells of mollusks, ectoskeletons, compound eyes, blood circulation, alternation of generations, statocysts, ambulacral system of echinoderms, pedicellaria of the same, cnidocysts, poison apparatus of snakes, whalebone, and, finally, primary chemical differences like hemoglobin vs. hemocyanin, etc.<sup>1</sup> Corresponding examples from plants could be given.

1. The important problem of the chemical differences has been emphasized in the reviews by Schepotieff (1913), Pantin (1932), Redfield (1936).

Since Gulick's work was done, a similar case, the *Partulae* of Tahiti, has been studied most thoroughly by Crampton (1916, 1925, 1932). Here we have at least some intimations as to the genetic situation, as in the viviparous forms young from the brood pouch may be compared with the mother. If we take this information together with our knowledge of similar characters in *Helix* (Lang, 1906, 1911), there can be no doubt that the distinguishing qualitative traits are based on simple Mendelian recombinations and that the quantitative traits are inherited in some way. The *Partula* material otherwise closely resembles the *Achatinella* shells. That the composition of the individual colonies (based on local polymorphism) varies in time, as actually found, is not surprising, and will be found in any European *Helix* colony revisited from time to time. That the subspecies spread in recent times from their original area, as found by Crampton, is another interesting detail concerning population problems. Again no relation between environment and subspecific differentiation was found, though for many species on different islands a typical subspecies is described for each valley or area within the distributional area of the species. We shall return below to the same material in another connection.

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The facts discussed in this chapter thus show that there is no reason to conclude that isolation of subgroups within a species leads to the formation of categories other than those formed by ordinary continuous geographic variation. The subspecific variation as obtained by isolation may be less orderly than otherwise, and in some cases may even result in somewhat wider gaps between two adjacent forms; but there is no reason, at least as far as the factual material goes, to suppose that isolation makes subspecies develop into species. The conclusion is the same as that derived from our former discussion. Isolation or no isolation, the subspecies are diversifications within the species, but there is no reason to regard them as incipient species.

There is, I think, in the whole idea of subspecies as incipient species a psychological element. It is taken for granted that species are evolved from each other by a slow

accumulation of small individual steps (by means of selection, of course). If, therefore, a subspecific series is found to exhibit different degrees of small differences, the situation must indicate the presence of exactly the evolutionary process which is postulated. If, nevertheless, the individual *rasenkreise* remain separated by large gaps, and if the most extreme members are still only ordinary subspecies, the preconceived idea forces the neo-Darwinist to look for the most impossible explanations to fill the gaps. One of these which always works is the time-honored phylogenetic idea that the existing gaps were formerly filled by missing links. In other words, the subspecies are incipient species because a strictly Darwinian view requires such an interpretation, and because it is taken for granted that no other possibility exists.

The adherents of such a view derive much comfort from the results of population mathematics, especially Wright's calculations (1931), showing that small isolated groups have the greatest chance of accumulating mutants, even without favorable selection. I do not want to create the impression that I underrate the mathematical study of selection problems, as found in the brilliant work of Fisher, Haldane, Volterra, Wright. Actually, I had tried to work out a special case of selection (nun moth, Goldschmidt, 1920b) with insufficient mathematical equipment before Haldane furnished the proper formulae, and therefore I am fully aware of the importance of this now-popular branch of evolutionary research. But it is necessary to remember an old remark of Johannsen in his criticism of Galtonian biometry; namely, that biology must be studied *with* mathematics but not *as* mathematics. This means that the most brilliant mathematical treatment is in vain if the biological rating of the material is not correct (see Pearson and Mendelism). I am of the opinion that this criticism applies also to the mathematical study of evolution. This study takes it for granted that evolution proceeds by slow accumulation of micromutations through selection, and that the rate of mutation of evolutionary importance is comparable to that of laboratory mutations, which latter are certainly a motley mixture of

different processes of dubious evolutionary significance. If, however, evolution does not proceed according to the neo-Darwinian scheme, its mathematical study turns out to be based on wrong premises.

In our present discussion of isolation and the incipient species, it is the contention that small isolated populations have the greatest evolutionary chances from the standpoint of population mathematics. This contention must fall to the ground simultaneously with the neo-Darwinian concept. But it might also be pointed out that the mathematical conclusion does not agree with many biological facts. Anybody who has seen the regal primrose grow in a single crater of Java, or collected *Apus* and *Limnadia* in their rare and isolated haunts, or has studied the occurrence of innumerable so-called relics, is impressed by their uniformity and their obvious position at the end of an evolutionary blind alley, in spite of isolation in small populations, in addition to generalized, primitive features (Phyllopoda, Anaspides) most suitable for evolution. On the other hand, large isolated populations frequently show most extreme variation. I once observed a population of a *Helix* species in Paestum, Italy, which was so dense that the plants were hardly visible under the innumerable snails. The variation among the snails (of the well-known Mendelian type) was immense, and certainly could not have been greater. There is no factual basis for the assumption that such a Mendelian polymorphism leads beyond the existence of whatever recombinations are possible. Another set of facts which clearly does not agree with the mathematical theorem is found in Vavilov's gene centers, assumed also by Reinig (see discussion on p. 87). Whatever the theoretical interpretation may be, the facts show a small area containing a multitude of species side by side, and numerous mutants within the species. By dispersal of these mutants rassenkreise may be formed, but nothing indicates that species are produced in these centers by isolation and accumulation of mutations.

The contents of this chapter, as well as all the data presented thus far and to be presented below, show that the neo-

Darwinian conception, which works perfectly within the limits of the species, encounters difficulties and is not sustained by the actual facts when the step from species to species has to be explained. Selection will certainly be involved also in the accomplishment of this decisive step, but we shall see that selection in nature probably has much easier work than that required by the neo-Darwinian idea of slow accumulation of micromutations.

## 6. THE SPECIES

Our discussions up to this point have shown microevolution at work within the confines of the species, diversifying the primary form either by adapting the species genetically to diverse conditions of the environment within the area suitable for occupation; i.e., by subspecific, geographic subdivision, or by a diversification which is more haphazard and nonadaptational, occurring in the form of mutations, local polymorphism, and polymorphism enhanced by isolation. In all cases the diversification could be subdivided almost without limit down to differences between individual colonies, showing that taxonomic subunits could be multiplied if it would serve a purpose. Wherever known, this diversification was based on the different types of Mendelian differences, implying origin by accumulation of micromutations. It further turned out that the subgroups, wherever tested, were completely fertile *inter se*, though this would not exclude an occasional lack of actual interbreeding which might be on the same biological level as; e.g., noninterbreeding between Brahmin and Pariah.

Darwin's classic concept of the origin of species, which, as we saw, is the one to which modern biologists have largely returned—we spoke of neo-Darwinism—is found in the following phrases from the *Origin of Species* (Chapter II): "Certainly no clear line of demarcation has as yet been drawn between species and subspecies—that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at, the rank of species: or, again, between subspecies and well marked varieties or between lesser



varieties and individual differences. These differences blend into each other by an insensible series; and a series that impresses the mind with the idea of an actual passage.

"Hence I look at individual differences, though of small interest to the systematist, as of the highest importance for us, as being the first steps towards such slight varieties as are barely thought worth recording in works on natural history. And I look at varieties which are in any degree more distinct and permanent as steps towards more strongly marked and permanent varieties; and at the latter as leading to subspecies, and then to species. A well marked variety may therefore be called an incipient species."

All these facts have become apparent in our previous discussion, where the modern factual additions to the classic conception were recorded as microevolution *within* the species. We now come to a consideration of the next step in evolution, as set forth in the words of Darwin: "Certainly no clear line of demarcation has as yet been drawn between species and subspecies." Do subspecies actually merge into species as gradually as one subspecies grades into another one? In other words, are subspecies incipient species and is specific differentiation, as well as that of higher categories, a continuation of microevolution, based upon the same principles of accumulation of small mutations, adaptational or otherwise?

Darwin's term, "incipient species," has been frequently used in our discussion. I am not sure that the many authors who use this term stop to think what is actually meant by it. Incipient species must mean that any variation, large or small, within a species has the potentiality of becoming a new species, and, further, that this probability increases with the accumulation of different traits and is therefore greatest in extreme subspecies. If this is true, it follows that subspecific differentiation is a *necessary, obligatory* step toward species formation. This, in turn, means that the differences between two closely related species must be a continuation of the series of differences between subspecies, as we found subspecific differentiation not to be haphazard but

orderly. And since this orderly behavior of subspecific differences is found to parallel geographical or ecological clines, the decisive step from subspecies to species must occur only at the extreme points of the range of the species. Localized species, not forming clines of subspecies, are therefore excluded from further evolution. There is no possibility of other interpretations within the concept of incipient species. Rensch is one of the few who recognized this clearly and actually postulated (see below) that the new species are formed at the extreme end of a subspecific cline and later return to the point of origin to live side by side with the old species.

But geneticists who use the concept of incipient species do it in a different way. They think that a subspecies will be isolated and then have a chance and even greater probability (see above, S. Wright) of producing new mutations, which accumulate until the specific difference is reached. It is usually overlooked that such a conception does not require at all the existence of incipient species. Any isolated group within a population, whether already different from the rest or not, will have the same chance for evolution as any other (provided an equal rate of mutation) if the genetical premises are correct and if the direction toward the new species is not bound to coincide with the direction of subspecific differentiation. The only apparent advantage of a subspecies over any ordinary mutants would be that a few mutations have already been accumulated to start with on the path toward the species. How little that would mean for evolution becomes visible if we remember the numerous species which have needed all the time since the Late Tertiary to produce their subspecies. The difficulty caused by adaptive subspecific traits will soon be discussed. The Darwinian incipient species makes sense, therefore, only if the track leading to specific differences is a continuation of the subspecific clines. Otherwise any isolated population would potentially be an incipient species, and the rassenkreis might at best be called only a model of specific differentiation (i.e., from the point of view of neo-Darwinism).

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F<sub>1</sub> hybrids from a great many different species crosses in *Nicotiana*, describes their behavior in terms which he himself calls "rather heterodox," though he seems to agree with the orthodox opinion that accumulated micromutations make up the specific differences. He finds in these hybrids a "phenotypic reaction pattern" (a term used by Sinnott). If I correctly interpret its meaning, the term indicates that the hybrid reacts as a whole and not as a mosaic of individual genes. Gene changes producing the qualitative effects which are used in ordinary Mendelian work appear different from those which accumulate in specific differences, the latter being quantitative and difficult of demonstration. The former (qualitative, varietal) "are, by their nature, usually incapable of playing a part in natural evolution, though they may be very advantageous in building up knowledge of the hereditary mechanism." (This phrase sounds almost word for word like Johannsen's statement quoted on page 8.)

The pattern of the hybrids shows that each species genome controls "normal orderly," as opposed to "restricted," processes. (I interpret this as meaning the control not of small features at the periphery of organization, but of the general processes of orderly growth and development.) Therefore, East—obviously unwilling to take the step beyond the genes and their accumulated micromutations—concludes that the various genes of each genome produce slight changes in developmental patterns in different organs. He recognizes that the standard type of mutation is without significance for evolution; he realizes that species differences are differences of the whole developmental pattern; and, as individual gene mutations can hardly be recognized on this level, he assumes that a multitude of micromutations must have accumulated to build up the pattern-controlling new genome. I think that these observations, which had been anticipated to a considerable extent by Goodspeed and Clausen (1916) (see below), fall in line with all the data discussed before. All the examples, then, demonstrate clearly that the facts, if closely scrutinized, are not at all what they appear to be in reviews and textbooks. I further think

that the real meaning of the facts will become clear only after the decisive step has been taken of completely discarding the concept of accumulated small gene mutations as the material of macroevolution. The following chapters will show what is meant by this. But one point may already be emphasized here. The facts reported indicate differences between species which are on a chromosomal level and, maybe, frequently even on a genomic level. If species are formed by accumulation of gene mutations, they must possess numerous homologous genes which will Mendelize. Ordinary Mendelian segregation will follow with the usual complications of linkage and crossing over. If, however, whole chromosomes or groups of them segregate, it means, according to all our cytogenetic knowledge, that the homologous chromosomes do not have the same pattern of loci, that they are actually not homologous in detail. We shall later go into the details of this situation. Here we shall note only that specific differentiation has actually turned out to involve a chromosomal reorganization. Assuming, for argument's sake, that the chromosome is a string of genes, we are confronted with the following alternative: Either the mutant genes are alone responsible for the specific differences, and their different order in different species, which accounts for the special features reported, is a chance condition without any significance; or the intrachromosomal pattern is a feature which plays an active part in specific differentiation. In the latter case the reported facts are highly significant. We believe this to be true and shall soon discuss the reasons for our conviction.

## 7. Conclusions

WE have repeatedly indicated in the course of our discussion the conclusions which we have to draw from our survey of the facts of microevolution, and have, I think, covered all important angles of the problem. Only a short summary is therefore needed before we turn to the problem of macroevolution.

A survey of the facts relating to microevolution; i.e.,

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evolution within the species (or whatever two different, nearly related forms separated by "an unbridged gap" may be called severally), has led us to reaffirm the conclusions which we have drawn in former papers: Microevolution within the species proceeds by the accumulation of micromutations, in addition to occasional upshoots of local macromutations, or polymorphic recombinations of such. The lowest taxonomic unit used for practical purposes (that is, for the sake of unequivocal labeling), the subspecies or geographic race, may in many cases be subdivided into subgroups distinguishable with different degrees of certainty, and resubdivided even as far as individual colonies. In addition, what are subspecies in one form may be on the same genetic level as subsubspecies in another, according to the amount of information available, the usefulness of the respective traits for taxonomic description, and the special type of subspecific spreading over smaller or larger areas. The differences between two subspecies are usually clinal, merging into each other, except when isolation produces sharper differences. But the clinal character may be obscured if subspecies located in separate centers form clines of subsubspecies radiating from these centers. The subspecific and lower differences are based upon a number of hereditary traits, most of which do not show the simpler types of Mendelian inheritance. The character of the individual subspecies is the result of a definite combination of these traits, each of which may vary independently within a rassenkreis of subspecies. Many, if not most, of these traits are directly or indirectly adaptational, and their intraspecific variation follows the corresponding variation of the different climatic or other conditions to which adaptation is made. These geographic races are frequently arranged in the form of continuous chains with a continuous linear type of variation of the individual characters. This type is found only when some of the conditions to which adaptation is vitally necessary have an arrangement of a gradient type. If this is not the case, or if nonadaptational traits are involved, a correspondingly irregular pattern of distribution and of traits may occur.

The series of subspecies, or rassenkreis, is separated by a gap from the next one; while the characters of subspecies are of a gradient type, the species limit is characterized by a gap, an unbridged difference in many characters. This gap cannot be bridged by theoretically continuing the subspecific gradient or cline beyond its actually existing limits. The subspecies do not merge into the species either actually or ideally. Border cases which have been interpreted in a positive way can be brought into line with these conclusions. Nor can the gap be bridged by the assumption of slow accumulation of micromutations independent of subspecies formation. Microevolution by accumulation of micromutations—we may also say neo-Darwinian evolution—is a process which leads to diversification strictly within the species, usually, if not exclusively, for the sake of adaptation of the species to specific conditions within the area which it is able to occupy. This is the case for microevolution on the subspecific level of formation of geographical races or ecotypes. Below this level, microevolution has even less significance for evolution (local mutants, polymorphism, etc.). *Subspecies are actually, therefore, neither incipient species nor models for the origin of species. They are more or less diversified blind alleys within the species. The decisive step in evolution, the first step toward macroevolution, the step from one species to another, requires another evolutionary method than that of sheer accumulation of micromutations.*

tion créatrice, etc.), the second, the one presented here. We shall have to discuss later on how modern paleontologists have come to a similar conclusion.

### 3. THE REACTION SYSTEM

WE have repeatedly used this term, which is also found in one of the quotations from Dobzhansky, to express the following viewpoint: According to the theory of the gene, each individual gene exercises a definite influence upon the development of morphological and physiological characters. These influences are mutually interdependent and the end result is the specific type. Although a definite visible trait will be controlled by many, if not all, genes, nevertheless certain genes will be predominantly concerned with definite and localized actions, so that the action of the individual gene is, after all, the decisive feature. A mosaic of individual actions is thus assumed to produce the final whole. It is sometimes denied that modern geneticists still think of the gene in such a way. The best proof that the theory of the gene necessitates this atomistic assumption is found in the cases of deficiencies opposite a so-called hypomorphic gene. In the absence of the allele, such a "wild-type gene" produces the type of mutant character ascribed to the same gene when mutated! For example, a single wild-type gene at the vestigial locus in *Drosophila* causes a kind of vestigial effect if the allele is absent due to a deficiency covering this locus.

The idea of the reaction system in the sense in which this term will be used is opposed to the idea of integrated genic action. It means that the germ plasm as a whole; i.e., predominantly the chromosome complex, controls the general features of development which lead to a definite type, the species in question. This idea dispenses completely with the individual gene and its individual action, with the attending difficulty of integrating mosaic action into a unified whole. It considers only a single unit action of the whole germ plasm, with more or less independent action of the individual chromosomes. Whether the intricate pattern of this germ plasm is a pattern of genes, or whether there are no genes

at all, is another problem; the point here is that the germ plasm as a whole controls a definite reaction system, which, then, is not a mosaic of separate effects but a single developmental system controlled as a whole by one agency. (The important problem of how such a conception tallies with the facts regarding definite actions of sections of the chromosomes is discussed in Goldschmidt, 1940 [in press]. We shall not go into these technical details here.) It is certainly difficult for many geneticists to think in such terms, as most of them are so completely wrapped up in the axiomatic belief in the atomistic gene theory that they are unable to think in other terms. But embryologists, physiologists, and probably taxonomists will, I trust, not find any difficulty in accepting such a conception, and may even welcome it.

The term reaction system was introduced into genetics by Goodspeed and Clausen (1916), who realized at that early date, right at the height of the new triumph of the theory of the gene, that something more than the additive action of individual genes must be involved in genetic determination. It is highly significant that they derived their new concept from experiences with species hybrids. As a matter of fact, these authors did not take the decisive step away from the gene mosaic conception, but they tried to expand it by adding the new idea of reaction system. "For if this conception of genic interaction be valid then it should not be possible, in certain cases at least, to shift and recombine the elements, from which systems have been built up in the haphazard way that some advocates of Mendelism have attempted to do. *If, for example, it is possible to obtain hybrids involving not a contrast between factors within a single system, but a contrast of systems all along the line, then it is obvious that we must consider the phenomenon on a higher plane, we must lift our point of consideration as it were from the units of the system to the systems as units in themselves.*"<sup>3</sup> These conclusions were derived from a set of facts which we might have mentioned above when discussing species hybrids and emphasizing their peculiarities, espe-

3. Italics mine.



evolution. Unfortunately, this question cannot be answered. There are many cases known in which cytoplasmic differences can already be found at the level of microevolution. We mentioned before cytoplasmic differences between geographical races of *Lymantria*. Other cases will be found reviewed in Goldschmidt (1938). But there is no indication that whatever differences exist are of essential value to evolution. (We speak, of course, only of cytoplasmic differences which are not under chromosomal control. Most of them probably are, as the inheritance of serological features proves.) Actually, recently experimentation has shown that tissues of different orders (Amphibia and fishes, Oppenheimer, 1939) may be combined into a whole, which would hardly be possible if the cytoplasmic constitution were so very different. For the present, therefore, the evolution of cytoplasm—not under chromosomal control—may be neglected.

##### 5. EVOLUTION AND THE POTENTIALITIES OF DEVELOPMENT

WE emphasized before that direct genetic information stops almost at the point where macroevolution begins, though a considerable body of evidence is still available right on the borderline. But where the higher categories begin, and especially where huge differences of the entire architectural plan are involved, direct genetical information ceases to exist, though indirect information may be found, as we shall see. But this does not mean that no exact method for further analysis is left. Exact analysis is not confined to experiments in hybridization, as some geneticists want us to believe, but may be based upon any body of reliable facts. Such a body of facts was used in my essays of 1920, when I tried to link them with definite genetical conceptions. These facts were mainly taken from the realm of development; in the widest sense of this word.

Evolution means the transition of one rather stable organic system into a different but still stable one. The

genetic basis of this process, the change from one stable genetic constitution to another, is one side of the problem. No evolution is possible without a primary change within the germ plasm; i.e., predominantly within the chromosomes, to a new stable architecture. But there is also another side to the problem. The germ plasm controls the type of the species by controlling the developmental processes of the individual. Whatever may be our conception of the germ plasm, mosaic of genes or chromosomal pattern, the specificity of the germ plasm is its ability to run the system of reactions which make up the individual development, according to a regular schedule which repeats itself, *ceteris paribus*, with the purposiveness and orderliness of an automaton. Evolution, therefore, means the production of a changed process of development, controlled by the changed germ plasm, as well as the production of a new pattern of germ plasm. A change within the germ plasm, therefore, is of evolutionary significance only if the subsequent different processes of development are again properly integrated to produce a balanced whole, the new form. It is, therefore, of decisive importance for the understanding of evolution to take into consideration the potentialities of the developmental system for a more or less radical change. In other words, the *action* of the germ plasm, the genes, or what you will, in controlling orderly development has to be taken into account when we try to link genetical changes with the resulting evolution. Continuing the line of argument derived in the foregoing chapters, we must find out further whether the developmental system is capable of being changed suddenly so that a new type may emerge without slow accumulation of small steps, but as a consequence of what we called a systemic mutation.

Such an analysis may be carried out in complete independence from the detailed conceptions which we developed concerning the architecture of the germ plasm and its changes. It does not make any difference whether a single macroevolutionary step is caused by a major change within

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the chromosomal pattern, a systemic mutation, or by a special kind of gene mutation with generalized effect, if such is imaginable. The decisive point is the single change which affects the entire reaction system of the developing organism simultaneously, as opposed to a slow accumulation of small additive changes. As a matter of fact, when I first tried to derive ideas concerning macroevolution on the basis of specific genetic changes (Goldschmidt, 1920), I did so within the classical theory of the gene by making use of the concept of gene quantities and their relation to reaction velocities. But all the facts reported above which push the systemic mutations into the foreground point to the necessity of regarding these as the effective agents of macroevolution. In the following discussions we mean, therefore, systemic mutations when we speak of genetical changes, though we admit the possibility that the same facts may be discussed, at least theoretically, in terms of single large gene mutations.

#### A. The Norm of Reactivity and Its Range

In early Mendelian days Woltreck introduced the term "norm of reactivity" (Reaktionsnorm) to describe one of the basic conceptions of genetics. The genotype cannot be described simply in terms of the phenotype, since the description must contain the whole range of reactivity of the phenotype under different external or internal conditions. A genetic condition controlling, for example, large size, is in fact a condition which produces large size, provided that a series of environmental conditions is present, like nourishment, temperature, light, normal production of hormones. The genotype is, therefore, the inherited norm of reactivity to the ensemble of conditions which may influence the phenotypic expression. This concept of norm of reactivity, under natural as well as under experimental conditions, is founded on a huge set of facts which are of basic importance for the discussion of our present problem, the potentialities of development.

#### a. Examples

We do not need to discuss the innumerable modifications produced by the environment which furnish the material for the statistical treatment of nonhereditary variation. But within this group of facts we meet one rather general feature which parallels features of evolution. Species and varieties

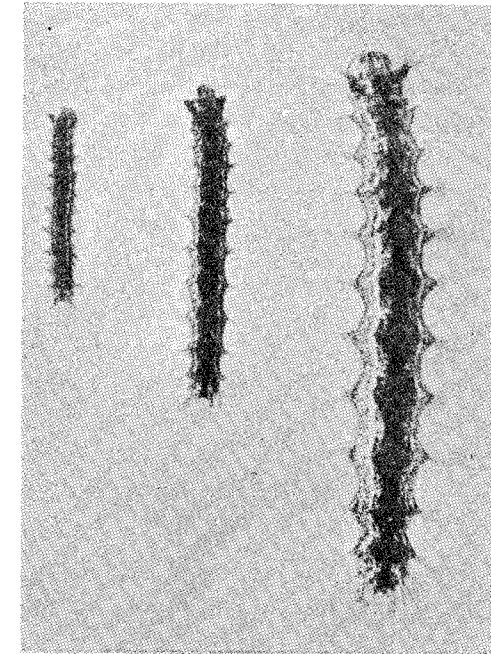


FIG. 39. Three sister caterpillars of *Lymantria dispar*, of equal age (stage), raised in normal, optimal and pessimal conditions. (From Goldschmidt.)

differ in many cases in typical size and proportions. But frequently, though not always, the range of modificability of one species under experimental conditions transcends the maximum of the ranges of all species combined and studied under natural conditions. For example, a stunted large species may be not only smaller than a luxuriant small

There are numerous developmental processes which must be, in a general way, identical throughout large groups and which by their very nature cannot vary except in a few directions. Let us take eye pigmentation. The chemistry of the melanin pigments allows for the presence or absence, or presence in different quantities and at different times, of the basic ingredients, chromogens and oxidases. The absence of pigment may be caused not only by the absence of the chromogen or its precursors, or the absence of an oxidase, of a coferment or of a proper substrate, but also by a shift in morphogenetic processes which might perfect the eye too early for the pigment, or the pigment too late for the eye. Innumerable developmental upsets may exist which in the end cause an unpigmented eye. In insects white-eyed mutants have actually been analyzed in such different groups as Lepidoptera, Diptera, and Hymenoptera. The claim that this proves the presence of the same gene for eye pigmentation in the three classes is obviously absurd, though frequently advanced. We know, further, from the work of Ephrussi and Beadle, Caspari and Kühn (literature in Goldschmidt, 1938) that eye pigmentation requires the presence of a substance, most probably a chromogen-precursor,<sup>5</sup> which is absent in certain mutants. This substance (or substances) is identical in the different insect groups, probably because it is necessary in the chemistry of melanin (eye pigment) formation. Does this then mean identical genes for the production of pigment? The same argument might be used for hair form in mammals, or for any other comparable case. But we always reach the conclusion that the phenomenon of parallel mutation does not give any information about the genotype of the two or more contrasted forms, beyond the general statement that eye pigment or hair form, etc., is inherited. But it does give information as to the embryonic, morphogenetic, and physio-

5. This is not the opinion of the authors named, who call the substances hormones. I am sure that the substances will turn out to be chromogen precursors, which can be hydrolyzed into the real chromogens. Whatever chemical information is thus far available points to such an interpretation.

logical processes and their intrinsic limitations as regards possible aberrations from the typical line of events.

#### *d. Norm of reactivity and hormones*

The last-mentioned examples, and others which will be mentioned in the following chapters, show that the range of the norm of reactivity is directly dependent upon the possibilities of shifting the relative speed of some simultaneous developmental processes. There is another group of facts concerning a large range of developmental potentialities, a range which on the phenotypic level is comparable to macroevolutionary changes. We mean the effects caused by an utterly simple change of internal environment; namely, a change in the features of production of active substances, especially hormones. The determining stuffs produced in development and responsible for orderly serial differentiations may be of two types: different substrates for the embryonic differentiation (embryonic segregation, fields, stratification; see Goldschmidt, 1927, 1938), and active substances controlling morphogenetic processes. The latter vary considerably in significance and bear different names, the merits of which have been discussed by J. Huxley (1935). But their type of action is in a general way very similar to that of hormones, in that definite substances induce definite and often complicated morphogenetic processes if brought into contact with a definite substrate. Wherever these determining substances of a hormonal type (using the term hormone in a generalized sense) control differentiation, a change in differentiation may be brought about by changes in the quality, quantity, time and place of formation, direction, and speed of transport of the substances in collaboration with an otherwise unchanged general developmental system. Since these substances produce an immense morphogenetic effect when called into action (see the so-called organizer of the amphibian egg), small changes of the type just indicated may lead to large results, provided that the general harmony of differentiation is not interfered with. This simple argument shows that any hereditary

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change in the production of these substances may have an immense effect of a macroevolutionary order if it leads to the development of a viable and properly balanced whole. Expressed differently, if the norm of reactivity of embryonic development is such as to allow for changes induced by a changed activity of hormones (that is, hormones in the widest sense, including all determining substances), a single hereditary change affecting these hormones in one of the different ways indicated above may produce an immense evolutionary effect.

Discoveries regarding the active substances of the organizer type, so important for experimental embryology, cannot yet play an important role in our present analysis, except in the way of rather generalized information. What we mean by this may be shown by an example. Embryonic undetermined skin transplanted from an amphibian donor species which has typical larval structures, like a horny beak, to the prospective mouth region of a host species devoid of such organs is induced by the inductive substances of the host to oral differentiation, which, however, assumes the characteristics of the donor; i.e., a horny beak, etc. The host inductor substances then control differentiation at a definite point, but the genetic constitution of the material controls the specific type of the differentiation. This shows that a genetical difference in the reacting system may produce a huge departure without a change of the inductive materials which initiate differentiation (Spemann, Holtfreter, Schotté; see Spemann's Silliman Lectures, 1938). The inductive substances are known to be rather unspecific and perhaps are even identical over large taxonomic groups. We know nothing about taxonomic differences in inductor material and therefore cannot discuss their eventual origin.

A more concrete insight of evolutionary significance may be derived from a study of the effects of that group of determining stuffs which are called hormones proper. The gist of our argumentation becomes easily visible if we look at the well-known case of metamorphosis in Amphibia. In the classical studies of Gudernatsch (1912) it was shown

that metamorphosis in frogs is controlled by the thyroid hormone. Experimental administration of this hormone produces metamorphosis long before the normal time of onset; absence of the thyroid prevents metamorphosis. In addition, the absence of the hypophysis prevents normal metamorphosis and produces giant neotenic larvae.<sup>6</sup> The innumerable details which have since been added to these basic facts are not of importance here. One of the extensions of this line of work is the study of the role of the thyroid in the metamorphosis of urodele amphibians. The classical case is the Mexican axolotl, which reaches maturity without metamorphosing, a hereditary condition which is absent in its nearest relatives. Feeding with thyroid makes the axolotl transform into the *Ambystoma*, a transformation which involves an immense morphogenetic change from gills to lungs, with all the concomitant changes in all systems of the body. (The complete literature is listed in Marx, 1935.) Now, it is generally known that a whole group of Amphibia, the Perennibranchiata, remain in the axolotl stage of development and do not metamorphose. It has not been possible to force them into metamorphosis by hormone treatment (except for minor changes: Noble), and it seems that they are genetically unfit for complete metamorphosis. This is best demonstrated by the experiment of grafting *Proteus* skin onto an axolotl and inducing metamorphosis. The typical metamorphic skin changes do not extend to the graft (Schreiber, 1939). We shall not discuss here the old problem as to whether the perennibranchs are phylogenetically primitive or whether they are derived as neotenic larval forms from metamorphosing Amphibia. The point of our argumentation is independent of such speculations. The

6. For curiosity's sake I might mention that I was the first to realize this fact. I had obtained giant neotenic frog larvae in an experiment and on dissecting them, could not find the hypophysis. Comparing this observation with those on certain human abnormalities based upon hypophyseal action, I concluded that it was reduction of the pituitary which had led to the neotenic growth. I suggested, therefore to my student Adler that he extirpate the hypophysis in tadpoles, an experiment which produced the expected result (1914), later elaborated by Allen, Klatt, and others.



amazing that these tissues, if given a chance, are not mixed in an irregular way, but may arrange themselves into a kind of bilateral, orderly pseudoembryo. (An example of regulation which is unsuccessful because of mechanical hindrance is, I suppose, the embryoma.) Holtfreter emphasizes in connection with these experiments that some facts indicate that the direct cause of the initiation of regulation is a rather simple chemical one. Finally he discusses experiments in which the regulative ability of a given embryonic tissue is not determined by its immediate chemical or physical environment, but by some action of the whole germ, whereas normal embryonic induction is a localized one. He adds this important statement (original in italics): "It may be assumed that these strange processes of determination surpass the usual principle of action by contact, and occur not only in experimentation, i.e., after material disturbances, but probably are important also for normal development." And further: "One thing is sure, that here a mutual relation between the parts is involved, and not only a one-sided one, as is the case with induction. The system as a whole is here taking a part in controlling all partial processes." I may add to the last statement that I have derived the same conclusions with regard to one regulative process, regeneration, from a general analysis of genetic control of development (Goldschmidt, 1927), by explaining regeneration in terms of redistribution of all determining substances, according to the given physicochemical conditions of the system as a whole.

We have gone into some of the details of regulation because they are of utmost importance in a discussion of the potentialities of development with regard to evolution. We have discussed many cases in which a hereditary change (a mutation) has produced exactly the same shift in the processes of individual development as has an experimental disturbance of development. In the experiments on regulation it is always an operative disruption of continuity between embryonic parts which sets regulation in motion. A comparable disruption may also be produced by a genetic

change. We have reason to believe that many genetic changes result in a relative shift of the rate of interlocked developmental processes. Such a shift, if produced in early developmental stages, at the time of still labile determination, may act in the same way as an experimental disruption by operation; except that there is no disruption by crude separation of the parts, but a disruption by separating interlocking processes through the shifting of one integrating process. (Simile: the disruption of the function of a motor by breaking a shaft, as against dislodging it from the synchronizing mechanism.) What will be the consequence of such a mutation? In many cases the result is an upsetting of the developmental mechanism; i.e., lethality. In other cases a certain amount of regulation takes place and the result is some kind of monster. However, effective regulatory processes may be induced if the change occurs under proper circumstances (see the conditions for regulation, above). In this case the single genetically produced change of an embryonic feature results in a whole series of changed developmental processes—in other words, in a completely new type of development; i.e., a departure of a macroevolutionary order of magnitude. To take a fictitious example, a genetic change in vertebrate development which shifts the differentiation of the gill arches will lead to regulation of the developmental processes of the aortic arches, the gill pouches, and many other cephalic structures. The actually existing series of large anatomical differences between taxonomic groups does therefore not require an evolution by simultaneous selection of numerous small mutants of the determiners for every single organ, a necessary hypothesis on the basis of the neo-Darwinian view, or the current theory of the genes. A single mutational step affecting the right process at the right moment can accomplish everything, providing that it is able to set in motion the ever-present potentialities of embryonic regulation. It is needless to say that this statement also contains the explanation of atavism as well as of the positive and negative features of embryonic recapitulation. We shall have to return again to

this important problem of embryonic regulation as a phenomenon of evolutionary significance.

We may conclude this chapter by stating that it has been shown before that the potential range of effects of single mutational steps coincides with the range of the individual norm of reactivity as determined largely by the range of shifting individual developmental reactions. Now we may add that this range is immensely enlarged if the norm of reactivity includes also the power of regulation.

#### *f. The sexual norm of reactivity*

In discussing the alternative norm of reactivity as well as the relation of hormones to determination, we did not mention the sexual alternative and its relation to hormones. This subject will now be discussed, as we consider it to be of great significance in the present connection. We have reported upon a number of cases which demonstrate the range of developmental potencies based upon the general type of developmental processes (we mean such types as permit a certain amount of shifting without interfering with the harmony of the resulting organism). The sexual alternative furnishes a case in which the developmental processes within a species may become so different that the resulting organisms, the two sexes, may exhibit differences of a macroevolutionary order of magnitude. As I pointed out in the essays (1920) to which I have repeatedly referred, a morphological difference of the magnitude found between the female and male genital armature in Lepidoptera (see fig. 25) would suffice for at least generic distinction if found as a somatic character distinguishing two different forms. This argument could be easily extended all over the animal kingdom. This sexual difference, however, is based upon a genetic difference—if we take only the most frequently found situation—i.e., the mechanism of the X-chromosomes, which creates within the same species two different genetic situations which determine differences in development. But these developmental differences are also based upon a definite norm of reactivity of the embryonic primordia, an

alternative norm of reaction. Let us explain the situation by means of some examples. The anlage of the tissue on either side of the cloaca in mammals has an alternative norm of reaction. Under the influence of female determination it develops into labia majora; under male influence, into a scrotum. In Lepidoptera a group of cells in a certain abdominal segment develops into an ovipositor (labia) if the individual is genetically female, and into a clasping hook (uncus) if it is genetically male (see fig. 25). In both cases it can be demonstrated that the corresponding groups of cells in both sexes have an alternative potency of development. The decision over the alternative, which is usually brought about by the action of genetic determiners, according to female or male chromosomal constitution, may also be enforced within the same genetic constitution either as a consequence of a special genetic situation (zygotic intersexuality) or as a consequence of environmental influence, including action of hormones. The sexual difference, then, furnishes examples of developmental potencies of a large range within the same species, of a genetic control of these potencies via the existence of an alternative norm of reaction of the embryonic primordia, of the realization of these potencies within the same individual either by environmental influence of a simple nature or by genetic determination, and, finally, of the realization of both these potencies within the same individual in the special cases of intersexuality, both on a genetical and an environmental basis. This shows that the sexual alternative exemplifies within a single organism different aspects of the developmental norm of reactivity which are otherwise found in different forms, and that this happens sometimes with realization of an extreme range of morphogenetic possibilities. We may therefore expect to find in this field good models of large morphogenetic (as well as physiological, chemical, psychological) changes of the type occurring in macroevolution.

As we emphasized just now, the morphogenetic range of the sexual alternative is based upon the alternative norm of reaction of the primordia of the sexually different organs.

of the urogenital apparatus from that of reptiles to that of mammals, which is hardly of a larger morphogenetic latitude than the hormonal effects just described. It is not necessary to continue this enumeration, as it is obvious that the norm of reactivity of development, in the case of hereditary disposition to alternative development, permits a morphogenetic shift of the order of magnitude of large evolutionary changes, and this under control of a single chemical compound, the respective sex hormone.

In order to prevent misinterpretation of the purport of this discussion, let me emphasize once more that the genetic difference between the basis of evolutionary change and of sexual change is found in the presence of the alternative norm of reaction in the latter case. But this difference is not one of principle but only of degree. In the chapter on regulation we saw that under definite experimental conditions many groups of embryonic cells may change their prospective fate. Though this is not the same thing as the sexual alternative, the latter involving a special genetic provision for different types of differentiation, the former the general potency of regulation, it is certainly an indication that the sexual alternative is a specialized case of the general potency of development to proceed in a different direction if the proper stimulus is provided. In both cases different types and degrees of reactivity are found, and in both cases the stimulus has to work on a system which is genetically capable of reacting more or less completely. Therefore I think that the facts relating to the sexual alternative may serve as a model to demonstrate the ability of developmental processes to change on a large scale as a result of a single event which may be compared, with regard to evolution, to a single mutational change affecting major features of development.

#### *B. Mutation Affecting Early Development*

One of the important points in the evolutionary discussions of my essays of 1920 was the following: I had come to understand the action of the genes in controlling develop-

ment in terms of relative velocities of the integrating processes of differentiation. I had found that certain conditions of the genes, which I interpreted as different quantities of that material (for discussion, critique, and changed outlook, see Goldschmidt, 1938), were linked with an action occurring at a definite time in development. This suggested the idea that a single mutation of the type considered to involve the quantity of the genes might act upon an early embryonic process by changing its rate relative to the rates of the other integrating processes of differentiation. If at all viable, such a mutation could accomplish in a single step a huge evolutionary departure. I pointed out briefly that facts taken from the field of comparative anatomy of vertebrates, as, for example, the history of the visceral skeleton, could thus find an easy explanation. The same applies to orthogenesis and the law of recapitulation. I called this conclusion obvious and did not go into further details. Later I returned briefly to the same point (Goldschmidt, 1923, 1937), using a few other examples by way of illustration.

Originally my idea had been that evolution generally proceeds by the accumulation of micromutations, but that occasional mutations affecting early embryonic differentiation via change of rates may account for some major evolutionary changes which could not be accomplished slowly. This viewpoint was accepted by others and enlarged upon in the writings of Haldane (1932a), Huxley (1932), and especially de Beer (1930), who elaborated it in detail. But when my own work on geographical variation later led me to the conclusion that geographic races are not incipient species, and that the origin of the higher categories cannot be explained in terms of micromutations (Goldschmidt, 1932, 1933), I began to realize that the large departures, produced in a single step by what we call systemic mutations, offer the only feasible method of macroevolution on and above the specific level. I have since found out that the general idea of evolution in large steps based upon early embryonic changes has been proposed before; but I think that only the linking of such an idea with the facts of genetics and phys-



type of change. The reason is obviously to be found in the relation between the genetic basis and the physiology of development: a genetic change affecting the rate, time of inception, time of determination, range of regulatory ability of embryonic processes, may occur in a single step without requiring a rebuilding of much of the genetic material. The genetic change is probably a permutation of some of the genetic elements controlling development, whatever theory of such changes we choose to accept in detail, and does not require the origination of new genetic determiners or determining systems. On the other hand, a genetic change involving a huge qualitative departure which would completely revolutionize the processes of development from their very initiation, would wipe out the possibility of recapitulation and would mean such an immense departure that it probably could rarely if ever lead to a viable product. A viable product would be a new phylum. Recapitulation, then, is an ubiquitous fact, unavoidable because of the method of evolution by large single mutational steps affecting rates, etc., of embryonic processes occurring at a definite time, and because of the mechanism of development built upon a timed system of serial processes, the order of which is unalterable.

#### *d. The hopeful monster*

In a former paper (Goldschmidt, 1933) I used the term "hopeful monster" to express the idea that mutants producing monstrosities may have played a considerable role in macroevolution. A monstrosity appearing in a single genetic step might permit the occupation of a new environmental niche and thus produce a new type in one step. A Manx cat with a hereditary concrescence of the tail vertebrae, or a comparable mouse or rat mutant, is just a monster. But a mutant of *Archaeopteryx* producing the same monstrosity was a hopeful monster because the resulting fanlike arrangement of the tail feathers was a great improvement in the mechanics of flying. A fish undergoing a mutation which made for a distortion of the skull carrying both eyes to one side of the body is a monster. The same mutant in a much

compressed form of fish living near the bottom of the sea produced a hopeful monster, as it enabled the species to take to the life upon the sandy bottom of the ocean, as exemplified by the flounders. A dog with achondroplastic bow-legs was a monstrous mutant until man found the proper niche for it—to follow the badger (dachs) into its den—and selected the hopeful monster as a dachshund. Here, then, we have another example of evolution in single large steps on the basis of shifts in embryonic processes produced by one mutation. I think that this idea of the hopeful monster has come into its own only recently. Only now is the exact basis for an appraisal of its evolutionary significance available. This basis is furnished by the existence of mutants producing monstrosities of the required type and the knowledge of embryonic determination, which permits a small rate change in early embryonic processes to produce a large effect embodying considerable parts of the organism.

Actually, the idea expressed in the somewhat unconventional but plastic term "hopeful monster" is not a new one. We may refer back to Darwin, who pointed out that under domestication monstrosities occur which resemble normal structures in widely different animals. But Darwin did not regard them as interesting, as he believed that they could survive only under rare and special circumstances, and that they would be swamped by cross-breeding with normal forms. We know now that these criticisms are not valid. The idea under discussion has since cropped up again and again. Professor R. R. Gates has kindly drawn my attention to a little-known and in many respects rather amateurish book by Bonavia (1895) in which a whole chapter is devoted to the subject and from which Gates (1921) quoted in his book. Bonavia pointed out that monstrosities might actually have played a large role in evolution by providing specific adaptations in a single step. He even anticipated the idea of preadaptation when he declared that such monsters might have been able to occupy new habitats and there continue a special evolution. He also insisted strongly upon the possibility of single large steps in evolution for which the mon-

sters provide the proper material, and he mentioned a number of writers on evolution who had realized this. He even had a vague idea of the embryological basis of large sudden deviations, when he wrote that "a little more atomic disturbance here, a little less there, during the embryonic stage may produce a *new compound*,<sup>9</sup> which then may be called a species, a genus, or even an order, as the case may be." He actually used as an example the long tail of Archaeopteryx, which he suggested might have been reduced in one generation to the short tail of the modern bird. This statement is remarkable, as the existence of an Archaeopteryx stage in the development of birds has only recently been discovered, and as the numerous tail-reducing mutants in mammals and birds, as well as the experimental production of related abnormalities, belong to present-day biology.

The facts and conclusions regarding the hopeful monster are so obvious that there is no need for a long discussion. Only a few points might be briefly mentioned. Certain types of monstrosities occur rather easily as mutants in different groups of animals of comparable architecture. For example, mutants reducing the extremities are known to occur in man, in mammals, and in birds. Hairlessness and tail-lessness occur as mutations in different species of mammals. Bulldog-head is known as a mutant in vertebrates from fishes to mammals. Wing rudimentation occurs in many groups of insects and birds. Reduced eyes occur as mutants in insects, crustacea, mammals. Telescope eyes occur as mutants in fishes. All these types of monstrosity and many others are considered in other cases as taxonomic traits characteristic of forms adapted to special conditions of life. Therefore there is no reason to assume for such taxonomic traits an origin by slow selection of micromutations instead of origin in one large step. Sometimes it is argued that the existence of different degrees of monstrous features is proof of an origin by gradual evolution. Cormorants are poor fliers. Cormorants living on the islands near the Pacific Coast of North America show slight signs of wing rudimentation (Grin-

9. Bonavia's italics.

nell). The Galapagos cormorant is flightless. But we know that mutants producing rudimentation and other monstrosities may have a partial effect in one case or a maximum effect in another. The interpretation of this case is clear. A single mutant may produce any degree of wing rudimentation. If such a mutation occurs in a hawk, for example, the resulting monster will not survive. But if it occurs in such a bird as the cormorant, which is already organized for catching its food while swimming under water, the monstrosity will not be deleterious and might even be of the "hopeful" type if it enhances simultaneously the swimming and diving capacity (by lessening friction). Whether a complete or a partial reduction of the wing can take place depends upon the habitat. Obviously a cormorant on the Pacific Coast cannot survive without flight, but needs a certain amount of it to change its fishing grounds; an island cormorant finds enough fish with very little flying; and a Galapagos cormorant can do well without flying at all. The three different degrees of mutation, all of the type of the hopeful monster, have fitted the respective mutants to three different niches characterized by the distribution of fish supply. Only one more example need be mentioned. Rumplessness is an ordinary mutant in fowl, producing deformity and shortening of the rump; it is based on a genetic disturbance in early development and may also be obtained as a phenocopy by cooling the embryo during a critical period (cf. literature in Goldschmidt, 1938). The eventual appearance of this mutant monstrosity in a bird which has to be a good flier in order to survive would certainly not fit it for survival. But the same monstrosity may enable another bird to start a line of running birds occupying grasslands or steppes. Thus, the combined facts of genetics, embryology, and taxonomy demonstrate that the hopeful monster is one of the means of macroevolution by single large steps.

### C. A Few Facts from Botany and Paleontology

In our discussion of the potentialities of development in relation to evolution, the plants were almost completely



## V. CONCLUSION

THE THESES presented in these lectures have been derived from a large body of research in diverse fields of biology, undertaken, at least in part, with the problem of evolution in mind. They have developed and changed with the progress of my own work and with increasing acquaintance—much of it firsthand—with material studied by others. The result as it stands today, and which we have tried to base upon a large body of diversified facts converging toward a single center, may be expressed in a few sentences. Microevolution within the species proceeds by accumulation of micromutations and occupation of the available ecological niches by the preadapted mutants. Microevolution, especially geographic variation, adapts the species to the different conditions existing in the available range of distribution. Microevolution does not lead beyond the confines of the species, and the typical products of microevolution, the geographic races, are not incipient species. There is no such category as incipient species. Species and the higher categories originate in single macroevolutionary steps as completely new genetic systems. The genetical process which is involved consists of a repatterning of the chromosomes, which results in a new genetic system. The theory of the genes and of the accumulation of micromutants by selection has to be ruled out of this picture. This new genetic system, which may evolve by successive steps of repatterning until a threshold for changed action is reached, produces a change in development which is termed a systemic mutation. Thus, selection is at once provided with the material needed for quick macroevolution. The facts of development, especially those furnished by experimental embryology, show that the potentialities, the mechanics of development, permit huge changes to take place in a single step. The facts of physiological genetics and their explanation in terms of coordinated rates of processes of differentiation furnish the insight

into the possibilities of macroevolution by single steps. A considerable role is assigned to such genetic changes as affect early embryonic processes and automatically entail major deviations in the entire organization. The general picture of evolution resulting from such deliberations is in harmony with the facts of taxonomy, morphology, embryology, paleontology, and the new developments of genetics. The neo-Darwinian theory of the geneticists is no longer tenable.

A theory of evolution, which in the last analysis is based upon the control of velocities of reaction by catalysts which in some way or other must make up the hereditary material, may appear to some evolutionists to be too mechanistic and too simplistic. I think that all theories of evolution tend to reflect the scientific trends of their time. I have lived to see the purely morphological period of biology with its evolutionary corollary, the construction of phylogenetic trees, invention of missing ancestors, and a philosophical outlook variously termed mechanism, materialism, monism. The following period of experimental biology was skeptical of, if not actually hostile to, evolution, as it could not be attacked in laboratory experimentation. Mechanism became unpopular and vitalistic and teleological trends invaded evolutionary thought in the form of creative evolution, emergent evolution, psycho-Lamarckism. The rise of genetics brought back a mechanistic attitude; evolution started to become an exact science. Just as there is no room for transcendental principles in experimental physics and chemistry, in the same way a factual attack upon the problems of evolution can work only with simple mechanistic principles. Genetics showed the evolutionists that evolution can be attacked scientifically only on the basis of known analyzable processes, which are by their very nature relatively simple. But, just as has been the case in chemistry and physics, mechanistic analysis of evolution will sooner or later reach a point where an interpretation in terms of known processes will meet with difficulties. In such a situation chemistry and physics have never invoked transcendental principles on the assumption that nature is so frightfully complicated that it

cannot be understood otherwise. The actual developments have shown that this is not the case. The modern development of the electronic theory has shown that rather simple principles govern the most complicated phenomena of matter. Of course, there is always an unexplained residue on which the investigator may train his personal metaphysical predilection, but certainly no chemist would look to metaphysics for an explanation of a difficult phenomenon, say catalysis. In the same way the evolutionist, who meets with difficulties in mechanical interpretation at a lower level, may enjoy letting loose his metaphysical yearnings. But as an investigator he can only work under the assumption that a solution in terms of known laws of nature is possible.

We frequently encounter the idea that life phenomena are infinitely more complicated than those of inorganic nature and that they therefore cannot be understood on the same basis. Applied to evolution, this outlook would mean that one has to look for very complicated features, preferably such as require a metaphysical interpretation. I cannot agree with this. If life phenomena were not based on very simple principles, no organism could exist; if embryonic development were not controlled by a few simple basic properties and laws of matter, an organism could never be developed in a series of processes unrolling with the precision of clockwork. If evolution had not been made possible by relatively simple features inherent in the material basis of organization, it would never have occurred. I said before that evolutionary theory reflects the philosophy of the time, meaning by philosophy not the metaphysical speculations of some thinkers, but the general attitude toward the solution of the riddles of nature as based upon the results of scientific research. This philosophy is today simplistic and cannot be otherwise, in view of present-day knowledge of the constitution of matter. A few principles expressible in simple numerals govern the essentials of physics and chemistry. In biology a group of chemical substances, many of which are closely related and none too complicated in constitution, the vitamins, hormones, and Atmungsfermente,

etc., control the most decisive processes of life, and heredity will have to be referred, at least in a general way, to the properties of proteins. This shows that a simplistic attitude is not a flaw but the ideal goal for a theory in science and, therefore, also for a theory of evolution. I quote again: *Frustra fit per plura quod fieri potest per pauciora.*