YALE UNIVERSITY
MRS. HEPSA ELY SILLIMAN
MEMORIAL LECTURES

IE MATERIAL BASIS OF EVOLUTION

THE MATERIAL BASIS OF
EVOLUTION

BY

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THE SILLIMAN FOUNDATION

IN the year 1833 a legacy of eighty thousand dollars was left to the President and Fellows of Yale College in the city of New Haven, to be held in trust, as a gift from her children, in memory of their beloved and honored mother, Mrs. Hepsa Ely Silliman.

On this foundation Yale College was requested and directed to establish an annual course of lectures designed to illustrate the presence and providence, the wisdom and goodness of God, as manifested in the natural and moral world. These were to be designated as the Mrs. Hepsa Ely Silliman Memorial Lectures. It was the belief of the testator that any orderly presentation of the facts of nature or history contributed to the end of this foundation more effectively than any attempt to emphasize the elements of doctrine or of creed; and he therefore provided that lectures on dogmatic or polemical theology should be excluded from the scope of this foundation, and that the subjects should be selected rather from the domains of natural science and history, giving special prominence to astronomy, chemistry, geology, and anatomy.

It was further directed that each annual course should be made the basis of a volume to form part of a series constituting a memorial to Mrs. Silliman. The memorial fund came into possession of the Corporation of Yale University in the year 1901; and the present work constitutes the twenty-eighth volume published on this foundation.

PREFACE

THIS book presents an elaboration of the material which was used, in less technical and less detailed form, for presentation in eight Silliman Lectures delivered in December, 1939. The manuscript was completed in September, 1939, and the author has tried to include important literature up to October 1. He is greatly indebted to Mr. Richard Blanc, Mrs. Laura G. Rauch, and Dr. D. F. Poulson for assistance in editing the text; further, to a number of publishers for permission to reproduce some of the illustrations. Services rendered by the personnel of Works Progress Administration Official Project No. 465-03-3-192 are hereby acknowledged.

R.G.

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CONTENTS

THE MATERIAL BASIS OF EVOLUTION

I. INTRODUCTION

THE major part of the genetical work which I performed during the past thirty years proceeded along three apparently very different avenues: sex determination, physiological genetics, and evolution. But even in early stages of these lines of research it was recognized that such apparently different topics were linked with each other by some generalizations. These were brought out in a group of essays which I wrote in the winter of 1917—18, while a guest at Yale University (Goldschmidt, 1920). In these essays I showed that the work on sex determination led to conclusions regarding the action of the hereditary material in development. The same work was simultaneously concerned with a problem in evolution, the problem of geographic variation, and this led to a consideration of both these problems, genie action and evolution, from the same point of view. It was recognized that a change in the hereditary type can occur only within the possibilities and limitations set by the normal process of control of development through the action of the germ plasm. These possibilities and limitations were a direct consequence of the solution of the problem of genie action which we had found in terms of reaction velocities. Actually, the discussion of all these problems was tentative, and decisive points were mentioned only briefly, even relegated to footnotes. The idea was to wait for a full discussion until my own experimental work on some evolutionary problems as well as genetic ones would have been finished. It happened that in the following decades the first two parts of this work, sex determination and the action of the gene, came to the foreground, and that I could repeatedly work out in detail my ideas, based upon my own work as well as on the ever-increasing amount of work by others. Thus this part of the

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), Cuenot (1911, 1936), Guyenot (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 frGnl 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, ex-perimental 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.[1] 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).

III. MICROEVOLUTION

THIS term has been used by Dobzhansky (1937) for evolutionary processes observable within the span of a human lifetime as opposed to macroevolution, on a geological scale. It will be one of the major contentions of this book to show that the facts of microevolution do not suffice for an understanding of macroevolution. The latter term will be used here for the evolution of the good species and all the higher taxonomic categories.

1. THE MICROMUTATIONS

WHEN Darwin wrote his first drafts of the *Origin of Species* (essays of 1842 and 1844) he believed that sports, nowadays called mutations, played a major part in evolution. Later he changed his mind and was inclined to assume that it is the body of small variations which forms the material for selection. With De Vries' theory of mutation again the large steps came to the foreground, and though his original material, Oenothera, turned out to be of importance in quite a different direction, the awakening Mendelism took over the theory of mutants as the basic material of selection and evolution. All the earlier Mendelian studies were done with mutant types which differed rather considerably from the original form, most of them recessive and the majority hardly viable under natural conditions, if not actually monstrous. Certainly the optimism created by the discovery of the ubiquity and rather considerable frequency of the mutants ran wild. But soon a reaction set in. Some geneticists realized that the taxonomists, who looked with scorn at these mutations as of possible evolutionary significance, were right, and began to ask themselves whether no better materials were available. Thus Johannsen (1923) expressed his doubts in the following words: "Is the whole of Mendelism perhaps nothing but an establishment of very many chromosomal irregularities, disturbances or diseases of enormous practical and theoretical importance but without deeper value for an understanding of the 'normal' constitution of natural biotypes? The problem of species, evolution, does not seem to be approached seriously through Mendelism nor through the related modern experiences in mutation." Johannsen, however, did not point to any positive possibilities. In the same year Goldschmidt (1923), who had already insisted on this point in the aforementioned essays, wrote: "The extraordinary material of analyzed mutants from Drosophila work demonstrates that the type of gene mutation observed there can hardly play any role in species formation. . . . This does not mean that such mutants could not appear and hold their own in nature. . . . [example follows]. But never thus a new . . . [example] species would be formed. Recently Sturtevant has carried out a very useful comparison between natural species of Drosophila and the experimental mutants. His result, with which every expert in any group of animals will agree is: Species differ in innumerable minor characters, mutants in a few extreme differences. Experimental mutants,, however, show these large differences because only these are checked. But it is to be assumed that also the very small mutational steps, which change the organism very inconsiderably and probably do not disturb its balance, are just as frequent but escape notice. If two basic differences were isolated and such micromutation would recur, finally different species could be produced, different in numerous genes. This does not remove all difficulties, as, e.g., the sterility of species hybrids shows. But one thing becomes clear, rather surprisingly to some people, that the facts have made us return again to Darwin, though with the improvement of an exact analysis of variation." We shall see that the facts which have come to light since forced me to revise my standpoint.

The replacement of the typical Mendelizing mutations by the less tangible micromutations whenever questions of evolution are involved has since reappeared many times. Two more examples from experienced authors may suffice. Baur (1925) wrote: "By exercising one's senses in the course of

years one realizes that the conspicuous mutants are only extreme cases. At least equally frequently, and probably more so, minute mutants appear, which are not pathological but quite viable types. . . . These micromutations . . . are of very different types, small differences in the color of leaves or flowers, in the relative length of anthers, in the type of hairiness, size of seed, etc. . . ." It ought to be added, however, that the work on these assumed micromutations of *Antirrhinum* never went beyond such general statements.

One more recent statement of the same views may be quoted. East (1936) writes: "The situation is so peculiar that taxonomists have little interest in the characters with which geneticists deal, maintaining that they are wholly unnatural material for evolutionary processes. Professor C. T. Brues has examined the published descriptions of mutational effects in Drosophila at my request, and finds that only a limited few characteristics of similar type have ever survived in nature and these often in distant genera. . . . [There follows a very appropriate discussion of the fact that nevertheless the rate of *Drosophila* mutation is made the basis of theoretical conclusions.] I suggest that constructive mutations *are numerous* but have ordinarily remained unnoticed simply because destructive mutations are more easily described, catalogued and scored, and therefore have been more convenient in genetic research. There is evidence of a varied nature, nevertheless, in support of the idea that constructive mutations occur with remarkably high frequency." The evidence which East derives from his experience with Nicotiana is actually of the same type as Baur's from *Antirrhinum.*

These statements, then, may serve as a starting point. As far as genetics is concerned, the heritable variations which Darwinism needs as materials of evolution are available in constantly appearing mutants, the more conspicuous of which are deleterious or even monstrous, whereas the small deviations which may be even more frequent are less easy to detect and to isolate. Our task now is to find out how far

these mutants and their accumulation by interbreeding and selection will explain the successive steps in evolution. For this part of our discussion it will not make any difference which theory we accept regarding the nature of mutants. We therefore use for the first part of our discussion the terminology of the classic theory of the gene, assuming the chromosome to be a string of units, the genes, each located at a definite locus of the chromosome and each playing a definite role in controlling normal development. A mutation is a localized change in one of the individual genes and therefore Mendelizes with the original form. The term "point mutation" or "mutant locus" will appear in the same sense as "gene mutation." Doubts in regard to the theory of the gene will appear only later and only where further analysis requires definite ideas about mutation.

2.   THE SINGLE MUTATIONS

THE first step to be taken in order to get acquainted with the materials of evolution in nature is to start with the lowest taxonomic units and to relate natural conditions to genetic analysis. There is no doubt that the type of laboratory and field mutants with which the geneticist works occurs within wild species in nature where for one reason or another such a mutant might even become a frequent occurrence. It is known that occasional albinos are found in many groups of animals. In the year 1910 in one small area in upper Bavaria numerous albinos appeared among the field mice *(Microtus),* so numerous that I saw a dozen within an acre of land, but they were never observed again. A systematic study of *Drosophila* populations in Russia made by Dubinin and collaborators (1934) revealed that quite a number of flies were heterozygous for well-known recessive mutants, which then had a chance to appear as rare visible variations. (A long time ago I had found the same for *Drosophila* trapped in the surroundings of Berlin [Grunewald]. But I did not trust my observations because of the presence of genetics laboratories within not many miles. This source of error is excluded in the Russian work.) Many others have since re-

ported similar findings. It is also known in the cases of other animals and plants that rare but typical mutants may be confined to definite localities where the collector may happen to find them. The taxonomists have never thought of these "varieties or aberrations" as being of importance for evolutionary problems, for they are very frequently of a type which occurs in the same way not only in different species but in different families and orders. Obviously, in these cases one rather generalized process of development is liable to be affected only in a few simple ways (see below). Thus, albinism is found in innumerable mammals and birds, and also in mollusks and insects. Melanism, or partial melanism, or progressive, graduated melanism is a very frequent type of mutant in the same groups. Wherever red pigment occurs, yellow mutants are found, and white ones arise from yellow. I have analyzed genetically many such cases in moths and butterflies showing all the different types of one-factor Mendelian inheritance. The yellow aberration of the Arctiid moth *Callimorpha dominula,* with largely red hind-wings, an example of a mutant found only in rare localities, is a simple Mendelian recessive. The dark aberration of the fritillary *Argynnis paphia,* the form *valesina,* is a recessive with sex-controlled inheritance; the aberration of the gypsy-moth caterpillar with a black dorsal band is a simple dominant mutant. These examples from my own experience could be indefinitely multiplied by adding further facts taken from the large body of published experiments which have used mutants of wild species in both animals and plants.

We have already expressed our opinion that we agree with the taxonomists that these aberrations cannot play any major role in evolution. But this does not mean that they may not contribute to microevolution, to diversification within the species. It is quite conceivable that under definite circumstances such a commonplace mutational type might establish itself either by supplanting the original form or by occupying an independent area. We shall soon meet with such cases of a little more complicated order. I do not know of any simple case in which all the relevant facts are known.

We should certainly suspect such a situation whenever we find two forms of a species occupying different areas near each other and distinguished only by a single Mendelian factor difference. Such cases, however, seem to be very rare (see below, Harrison). In addition, one has to be cautious in assuming such a difference on any other basis than an actual crossing experiment. It may happen that a racial difference looks to all purposes like a simple Mendelian difference without this being so. The following is an example from my own experience. As already mentioned, in the Arctiid moth *Callimorpha dominula* with largely red hind-wings a yellow mutant occurs in the environs of Berlin, Germany, and this is a simple recessive. In Italy a geographic race of the same species is found which closely resembles (in some of its forms, see Goldschmidt, 1924) the yellow mutant, and one might expect that here the yellow mutant has replaced the red form. But a cross between the German red and the Italian yellow form gives an intermediate orange Fi, and in F_2 the whole range from red to yellow is found, indicating a multiple-factor inheritance. This proves, therefore, a completely different origin for the two cases.

Many similar instances could probably be quoted. I wish to emphasize again their importance, as corresponding unanalyzed cases have frequently been used in erroneous generalizations. Thus Kinsey (1936), whose work on gall wasps will be quoted later on, has found forms with small wings which occur as seasonal variations within a race, as well as in the form of definite races or hereditary units at different points of a racial circle. He lists these short-winged forms simply as mutants, and whereas this wing character has formerly been considered as of generic value, he makes this a point of considerable evolutionary significance. As no genetic information is available in this case, his interpretation may be right and it may be wrong. We shall discuss in a later chapter the problem of wing rudimentation in insects, and shall see which possibilities are available. Here we want only to caution against the use of unanalyzed material for sweeping conclusions.

We turn now to another group of cases of this same type which are of significance for microevolution. There is, first, a group of interesting data, for which, however, the genetic facts are more or less unknown; namely, the "mutations" in birds studied by Stresemann (1923-26). These "mutants" are known from nature; in a few cases hybrids are known, and a few crosses made in zoological gardens are available. These mutants are different from the type in color; e.g., melanisms, albinisms, rutilisms, the presence of differently colored spots or bands. They appear in more or less large numbers within the typical population, and in some cases they tend to supplant the original form. The hawk *Accipiter n. novaehollandiae* has a white mutant in Australia; in Tasmania nowadays only the mutant is found. The white mutant of the gray snow goose *Anser caerulescens* has almost supplanted the original form. Only the black mutant of the red-breasted weaving bird *Colius asser ardens* is now found in large areas of West Africa. The egret *Demigretta sacra* is found in New Zealand in the original gray form; in other parts of its area a white mutant is also met with which some day may replace the gray form, just as has happened in other species. In a few cases very rapid suppression of the original form is known. At one time a melanic mutant of the flycatcher *Rhipidura flabellifera* was known to occur only in the southern island of New Zealand. Today it has conquered the northern island, where it first appeared in 1864. Other similar cases are reported for the West Indian bird *Coereba saccharina,* of which the black "mutant" has completely replaced the original form.

But there are also genetically known cases in which a kind of microevolution is based upon a relatively simple type of ordinary mutations. The latter belong in part to the group of the **typical** mutants and in part may be classed with the hardly discernible micromutations which we discussed above. One such case which is rather well known and which actually was the first evolutionary problem I personally attacked with genetical methods thirty years ago[1] is the case of the

melanistic nun moth, *Lymantria monacha* L. This common pest has typically white wings with black **zigzag** bands in a definite arrangement. Up to about eighty years ago this form was rather constant, though occasional melanic individuals were found and much cherished by collectors as rare aberrations. That this type is hereditary was proven in pre-Mendelian days by Standfuss (1896). It has apparently always existed, as it is mentioned even in eighteenth-century literature. During the second half of the last century the number of these melanic aberrations increased and, starting from certain centers within the general area of distribution, spread from there over the whole range. When I started my work in 1909 and obtained my material from large areas infested with this pest, the majority of individuals already showed the different degrees of melanism. It is known that the same phenomenon was simultaneously observed in a number of other moths, and that in all these cases the centers of distribution were found in the areas of high industrialization, both in England and in Germany. Hence the term, "industrial melanism."[2]

The genetic analysis in this case showed that this melanism was the result of at least three mutational steps of unequal value, but all of them dominant. Two autosomal gene mutations increased the breadth of the zigzag bands and produced some pigment between them. The effect of these mutations individually is so small that they might be classed as micromutations. The third gene is sex-linked and produces the deep black of the higher grades. All these genes are additive in action and their different combinations produce the complete series of gradations from white with black bands to completely black (fig. 1).

There can be no doubt that these mutational changes of a type which is found in numerous animals—melanism—led to a definite step in microevolution in this case. This means

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1. **Owing to the** war, the results were published only seven years after the work was **finished** (Goldschmidt, 1920b).

2. For references to melanism in 1785 see P. Schulze, *Berl. Entomol. Wochenschr.,* 57.1912. Schroeder *(Ztschr. Wiss. InsekterMol,* 4,1908) could hardly find a melanic specimen, as a young man, in the same localities where they are prevalent now. Details regarding the spreading of the melanic form may be found in German textbooks on forest entomology.

that here a mutant, or a set of mutational advances in the same direction, led to a new condition in the relations of the species to its environment which permitted the new form to replace the old one, a process which of course is aided by the dominance of the mutants. Obviously, the melanistic forms had a selective value, as the relation to industrializa-
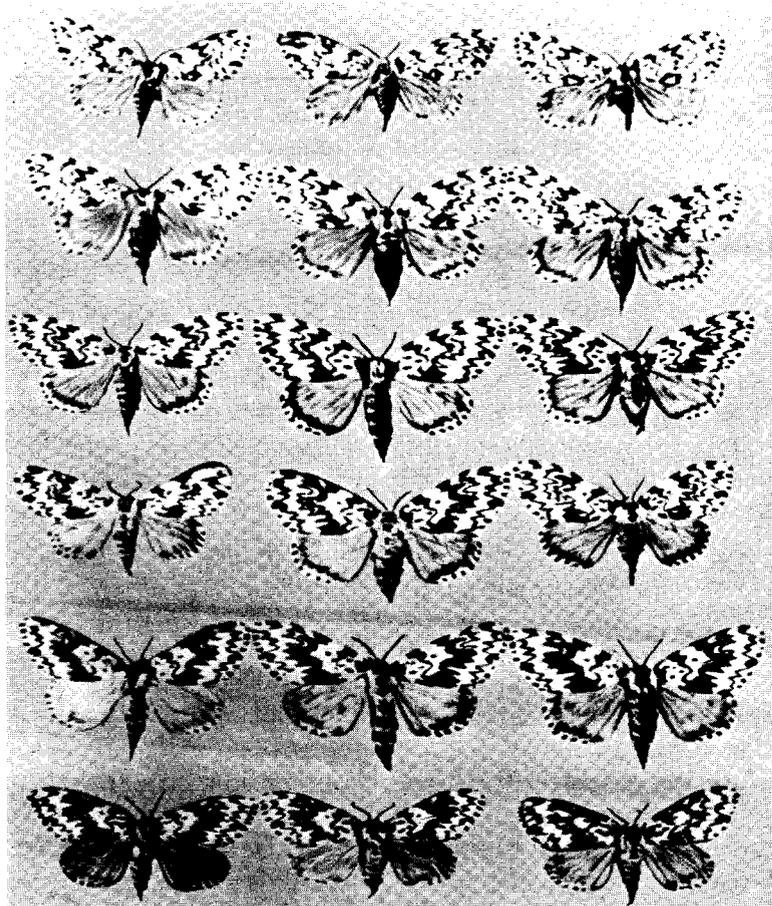

FIG. la. Melanic variation of *Lymantria monacha* $. Each row represents another combination of the two autosomal and one sex-linked dominant mutations. (From Goldschmidt.)

tion indicates, that was of a definite type. (A calculation—see Goldschmidt, 1920b—showed that the quick replacement ot the original form by the melanic one required only a small selective advantage.) We tried to see whether the dark indi-
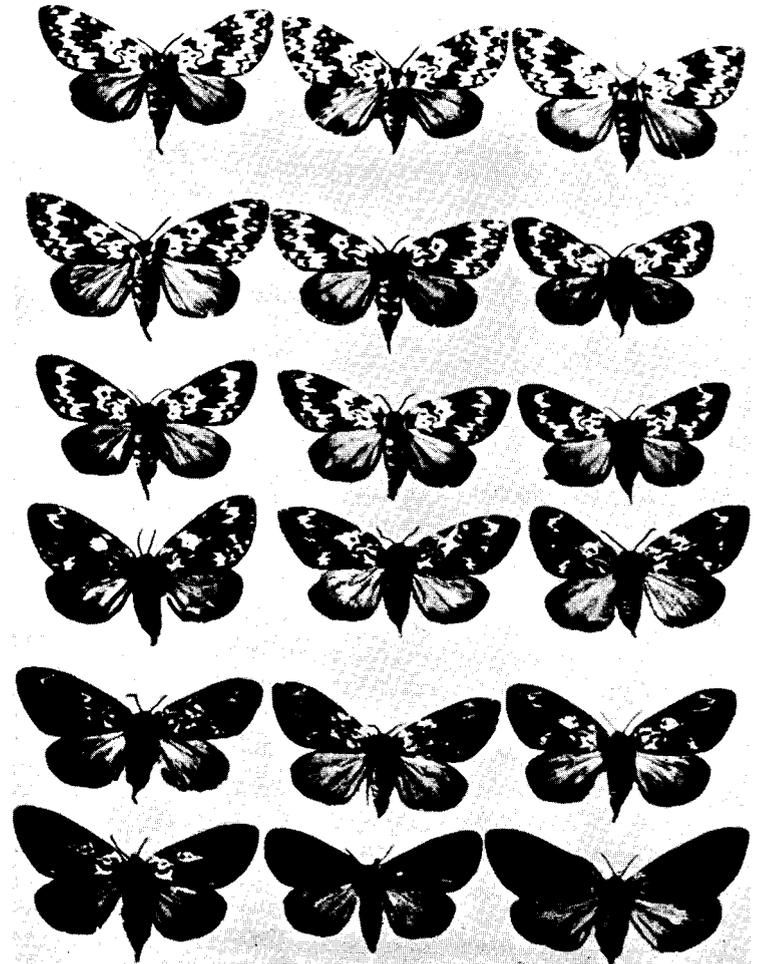

FIG lb. Melanic variation of *Lymantria monacha* $. Each row represents another combination of the two autosomal and one sex-linked dominant mutations. (From Goldschmidt.)

viduals were larger or stronger,[3] but with negative results, though these individuals were more viable in breeding, an experience also reported by Harrison (1920) for British melanic moths. Thus we concluded that the difference must be a physiological one. The relation to industrialization seemed to offer a clue. The nun-moth caterpillar feeds on fir trees, which undoubtedly deposit in their tissues various chemicals, especially metal salts, from their surroundings. The idea arose, therefore, that the melanic forms were in some way changed in regard to their metabolism, and that this enabled them to feed on the poisoned food of the industrial districts. For a considerable time we performed experiments in this direction, but the susceptibility of the animals to infectious diseases prevented a solution. I am convinced, however, that the actual explanation cannot be far from this one. (As a matter of fact, Harrison [1920] conceived the same idea in regard to cases of melanism found in England, which, however, he interpreted in a Lamarckian sense.) I am encouraged in this belief by the knowledge that these animals are rather sensitive to the chemical composition of their food. One of the close relatives of the nun moth is the gypsy moth, which is much hardier and omnivorous. For years we tried to make the breeding of a winter generation possible by using artificial food. Once we were very successful with shredded pine needles; but the following winter the same method was a complete failure. It turned out that we had taken our material from a different tree which had a higher content of rosin in its needles. The general correctness of this interpretation, aside from the special features, is demonstrated by some recent work along similar lines. A number of authors (**Kühn** and collaborators, 1934, for Ephestia; Timofeeff-Ressovsky, 1934, for *Drosophila)* have shown that genetic strains of different viability exist, among them also some with increased viability. More specific is the finding by Kiihn and Von Engelhardt (1937) that a melanic mutant of the geometrid moth *Ptychopida seriata* is better adapted to lower temperature and higher humidity.

3. A positive claim made in Goldschmidt, 1917, was later corrected.

An interesting account of the formation of local forms (races) involving melanism, as in the former examples, as well as other traits of pattern and color, has been given by J. W. H. Harrison (1920) for local races of the geometrid moth *Oporabia autumnata.* In the short time between 1885 and 1919 a certain region in England changed its character completely in regard to the food trees of the species and corresponding microclimatic conditions. Two very different ecological habitats were formed, separated by a half mile of heather, one a coniferous wood, the other a birch wood with some alder. The two habitats now actually contain separate races distinguished by size, choice of food, color and markings, time of emergence. Breeding experiments showed the differences to be hereditary. For one of the characters, hatching time, an adaptive value to microclimatical conditions of the habitat could be demonstrated. In the same species there are also melanic forms, the evolution of which, as already mentioned, is interpreted by Harrison in a Lamarckian sense. A more probable explanation has already been presented. (A good review of industrial melanism, especially the English material, is to be found in Ford [1937].)

To return to our main topic, microevolution by mutation. A mutant or a combination of mutants with similar effect had actually changed the species in such a way as to give to the new type a physiological advantage under proper environmental conditions. When, in the case of the nun moth, these were furnished by the chemical effects of industrial smoke upon food plants, the mutant began to replace the original form. The result is that a white nun moth has become a more or less black one. *Here this type of evolution ends.* The same conclusion, *mutatis mutandis,* probably applies to the ornithological examples already mentioned.

A good example of a situation such as is discussed here can be derived from a comparison of *Lymantria dispar* and *monacha.* We have already reported on the melanic varieties of *monacha,* their adaptational value, and the positive results of natural selection which has slowly replaced the light race by the dark one within man's memory. In *dispar,* the

nearest relative of *monacha* but with different ecology, melanic variations also occur. They nearly duplicate the *monacha* series (fig. 1), but for details of pattern. In addition, the genetic basis in both cases seems to be very similar though not identical, as far as information goes. But this
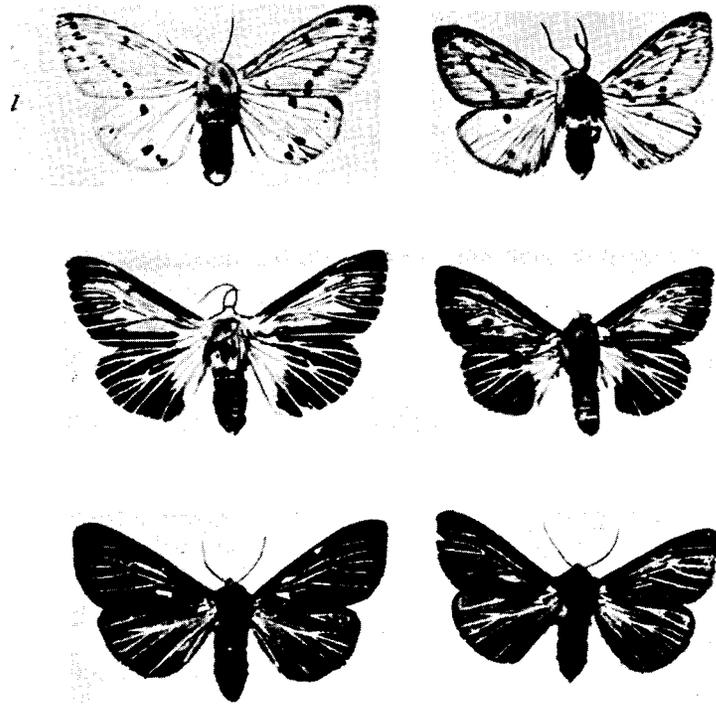

FIG. 2. *Spilosoma lubricipeda,* type form, melanic form *(zatima)* and hybrid in between. (From Goldschmidt.)

melanism is extremely rare and has been found only once, by Klatt (1928). It never occurred in the hundreds of thousands of individuals of all races which I have bred. Obviously, a very rare set of mutations is involved here, and it is, in addition, without positive selective value thus far.

The next question is whether this simple diversification by Mendelizing mutants could not carry an evolutionary process one step farther. We have already seen that in many instances a definite mutant is not found everywhere over the area of distribution of a species, but sometimes only in definite localities, as is well known to collectors. From a genetical point of view this might be a purely chance situation. If a mutant occurs in a well-isolated population and if there is no counterselection, it may hold its own and be present in the population. This, however, will hardly be the explanation if the mutant is present in different localities but only in those of a similar type. There is, for example, the Arctiid moth *Spilosoma lubricipeda,* a small moth with yellow wings and a few black dots, which is found all over central Europe. This has a dominant mutant called *zatima,* (Fi is actually intermediate) with almost black wings. This mutant frequently appears among the type form on the coasts of Holland, the Friesian Isles, and especially Heligoland[4] (fig. 2). There, undoubtedly, the regular presence of a definite mutant in the population has a relation to a definite geographic situation with rather definite climatic features, and the simple problem of mutations of hardly any evolutionary significance begins to widen its scope, though strictly within the sphere of microevolution.

3.   LOCAL POLYMORPHISM

THE next step is best introduced by a phenomenon which we might call local polymorphism. Just as a definite locality might typically harbor a definite mutant, such a locality might also be inhabited by a group of interbreeding mutants if the situation is as described before; i.e., considerable isolation and no selective value of the mutants. A group of mutants appearing under such conditions and interbreeding freely among themselves and with the original species will lead to a stable population (under average environmental

4. The genetics of the case has been worked out by Federley (1920) and Goldschmidt (1924). There is a difference of one major gene and, in addition, a series of modifiers for the degree of melanism.
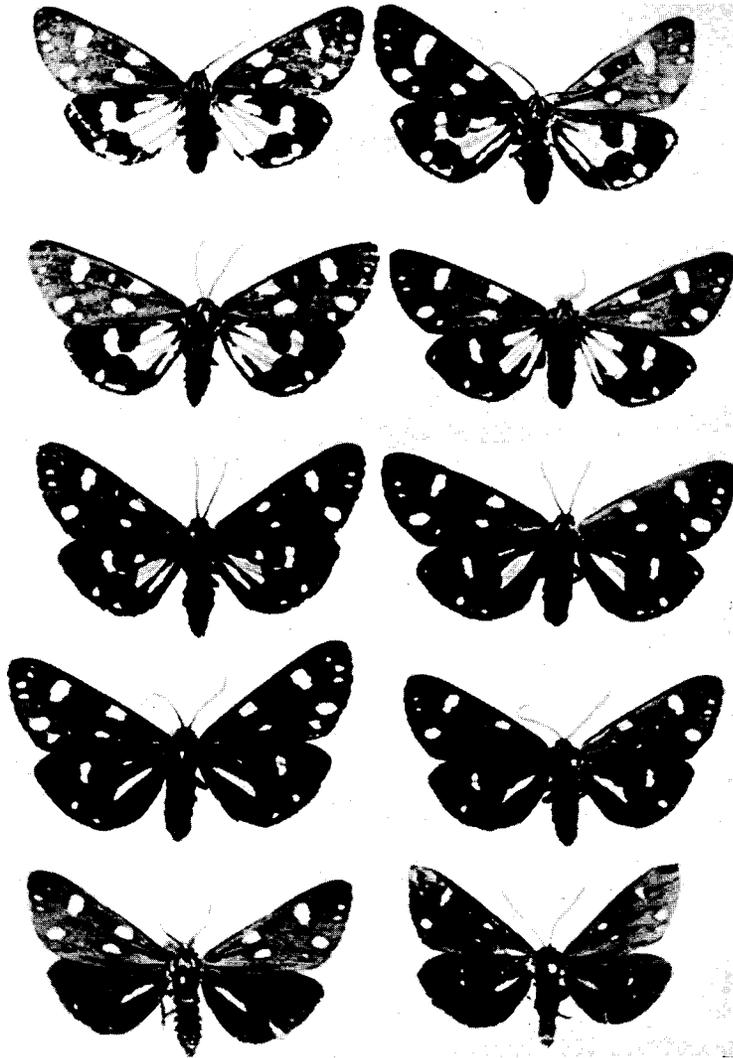
FIG. 3. Polymorphic series of *Callimorpha dominula* from the Abruzzi. (From Goldschmidt.)

conditions) in which the different types and their recombinations are represented. The population thus is polymorphic. The same type of polymorphism would result if a series of mutant stocks of flies in a laboratory were mixed up. An example of this type—if I may be excused for preferring examples with which I have experimented myself— is the local polymorphism of the Arctiid moth *Callimorpha dominula.* I have already mentioned the yellow Italian form of this species. In a small area of the Abruzzi mountains at the base of the Gran Sasso d'ltalia this species occurs in a series of forms ranging from the typical ones through all intermediate grades to almost black ones (fig. 3). For many years a collector who specialized in this form found during the proper season all the forms on the same spot and provided me with living material. The genetic analysis (Goldschmidt, 1924) showed a multiple-factor inheritance, different combinations of genes giving the different types.

There is only a small step from this localized polymorphism based upon recombination of Mendelizing mutants to a similar phenomenon on a larger geographic scale. A long time ago the French conchologist Coutagne (1896) noticed that each individual colony of *Cepaea (=Helix) hortensis* which he studied had its special character. In all colonies he found a considerable variation with regard to color and the types of banding. The same material has been studied since by many authors and in a general way the same results were obtained. (A fine review of the facts and a discussion of their significance have been recently presented by Diver [1939].) Today we know from Lang's genetic studies that all these diversities are based on Mendelizing mutations and that therefore a population containing many such types presents a typical case of polymorphism by interbreeding and segregation of mutants. But in Coutagne's case the individual colonies were typically different with regard to the types found as well as to their relative numbers. There can be no doubt that in view of the considerable inbreeding in these mollusks the composition of a colony may be mainly due to the mutations which by chance happen to be present

and are preserved in similar proportions for lack of positive or negative selection. But it is also conceivable that occasionally one or the other mutant is better or worse adapted to physiological conditions of soil, water, etc., which would result in a selection with regard to the composition of the colony. I do not know of any positive evidence in this respect, but there are other cases of the same kind which might lead to the belief that the distribution of the mutants in the population is not purely a chance distribution.

Unfortunately, there are not many cases in which the genetic basis is known. One is the following. The different color patterns of the ladybird beetle *Harmonia axyridis* are mainly based on three pairs of genes, the different combinations of which characterize the forms which have been called *frigida, 19-signata,* etc. (Tan and Li, **1934**). Dobzhansky (1933) studied the distribution of these forms in different populations (see fig. 4). Table 1 is an excerpt from his material.

TABLE 1

DISTRIBUTION OF COLOR TYPES IN POPULATIONS OF A LADY BEETLE

From Dobzhansky.

Region	*succmea frigida 19-signata*	*aulica*	*axyridis*	*specfabilis*	*conspicua*
		Mutant forms, per cent			
Altai	.05		99.95		
Irkutsk	15.1		84.9		
W. Transbaikal	50.8		49.2		
Amur	100.0				
Vladivostok	85.6			6.0	6.8
Manchuria	79.7			11.3	8.6
Japan	27.2		11.0	14.3	47.4

It is not possible to say whether the absence of some mutants in definite localities is a matter of pure chance or whether they are not fit to exist there. But it seems probable that such types of distribution which in a similar way seem to occur also in other Chrysomelid beetles (work of Timofeeff-Ressovsky, 1932, and Tower, 1918) are indicative of an underlying rule.

Such a rule, however, has hardly anything to do with problems of evolution, although it might seem to be the case if large geographic areas are checked as a whole, as was done in the foregoing example. In Coutagne's *Cepaea* colonies the different colonies may have been within easy reach of each other. Rensch also has recently (1933) made a similar survey for the garden snail *Cepaea hortensis.* Table 2 gives a part of his results.
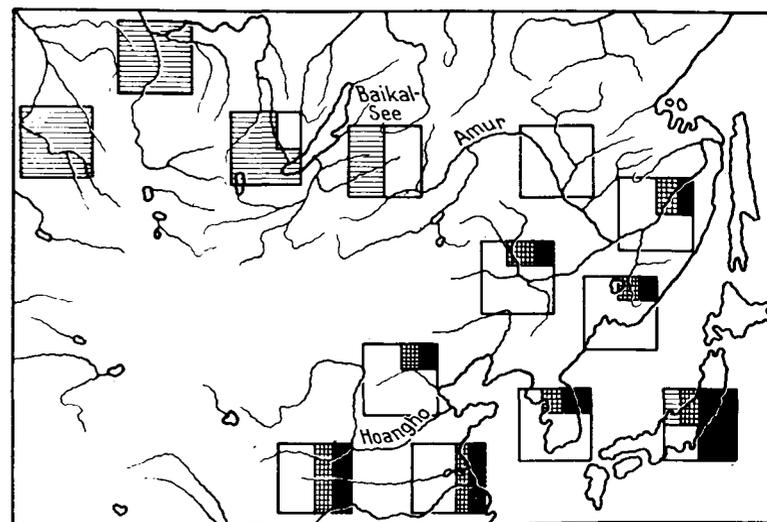

FIG. 4. Geographical distribution of four color types of the ladybird *Harmonia axyridis* in Asiatic populations. White = *signata,* shaded = *axyridis,* crosshatched = *spectabilis,* black = *conspicua.* (Diagram after Dobzhansky from Timofeeff-Ressovsky.)

This table shows no order or geographic relation of any kind. Obviously, the situation in each locality is controlled by chance presence of mutations and perhaps also by chance selection in favor of or against individual mutants or combinations. In a general way such a situation has as many or as few possibilities for microevolution as in the former examples. There is reason to believe that this type of polymorphism is a typical feature of life in more or less isolated colonies. Wherever such conditions of life were studied, espe-

TABLE 2

COLOR AND BANDING OF CEPAEA SHELLS IN ONE LOCALITY

1 2 3 4 5—0 presence or absence of bands 1-5. These are Mendelizing traits.

Per cent individuals

Locality	yellow 00000	red 00000	yellow 00305	yellow 10305	yellow 10345	yellow 12045	yellow 10045	12345
East Prussia	32.3							67.7
Ruegen	32.9			26.5	1.2			40.3
Ruegen	36.2		.4	23.5	1.7	.4		37.8
Warnemiinde	77.7							22.3
Ratzeburg	70.3	14.9	2.7	5.4				6.7
Berlin—Buch				10.9		1.4		87.7
Berlin—Spandau					1.1			98.9
Berlin—N 1				72.5		1.1		26.4
Berlin—N 2				65.3		.7		34.0
Berlin—3				45.3		1.9		52.8
Berlin—4			45.6		19.3		7.0	28.1
Weimar	52.0	5.5						42.5
Czechoslovakia	.1	22.2					.5	77.2
Vienna	93.7					.4	.6	5.3

cially in mollusks, the same phenomenon was found (see **Diver,** *loc. cit.*). I shall only mention at this point the Achatinellidae of Hawaii (according to Welch, 1938), because this family of snails will be used later to demonstrate other important types of variation. The facts reported by Lloyd (1912) upon rat colonies in India, and by Hagedoorn (1917) for Java, probably belong to the category of facts discussed here. A huge amount of material relating to Chrysomelid beetles *(Leptinotarsa)* is to be found in Tower's monograph (1918), though it is rather difficult to understand some of the details. But the examples already discussed illustrate the point sufficiently. In plants a parallel case can be found in Gregor's work on *Plantago* (1938).

We have already indicated that we cannot see that the different types of hereditary variation discussed thus far, the mutants of the ordinary type, have any meaning for an understanding of evolution. It is true that here we have a means for diversification within a species, which under conditions of selection might also be termed a kind of microevolution. But it is always the same little change of tune which is produced in these cases, melanisms, albinisms, rutilisms, and

their like. I cannot see that they could be conceived better as the beginning of an evolution or as a model of this. They are a rather unimportant type of variation (as the taxonomists correctly interpreted) which becomes important only as material for genetic experimentation (see the quotation from Johannsen, p. 9) because it is a material taken from nature of the same type and significance as the mutants of domestic breeds or laboratory animals. If we were to use such cases as the last ones mentioned as a starting point for evolutionary deliberations it would be as though we visited numerous dog shows in different countries and took the relative representation of different breeds in these as a starting point for an analysis of species formation.

4. SUBSPECIES AND GEOGRAPHIC VARIATION

A. *The Taxonomic Facts*

UP TO the end of the last century the species concept in taxonomy was handled in two different ways. Either any recognizable form was made a new species, thus enlarging their number immensely, or only a relatively small, well-established group of species was recognized, and aberrant forms assigned to them as far as possible. I remember distinctly the shock which it created in my own taxonomic surroundings (I was an ardent coleopterologist at that time) when Matschie claimed that the giraffes and other African mammals had many different subspecific forms characteristic for different regions which he could recognize with certainty; when Kobelt claimed that the mussel *Anodonta fluviatilis* was different in each river or brook; when Hofer stated that each Alpine lake contained a different race of the fish *Coregonus;* or when Heincke claimed the same for different schools of herring. The ornithologists, Kleinschmidt, Rothschild, and Hartert, soon followed by the lepidopterologists (Jordan), were the first to base upon these and related facts a new principle of classification and to work up their own fields accordingly. Rensch (1934), who is one of the present-day protagonists of these principles,

Goldschmidt, one of the world's great geneticists, delivered the prestigious Silliman lectures at Yale University in 1939 and published his remarks in 1940 as The Material Basis of Evolution. His intent was to inquire into the types of hereditary differences that produce new species. Goldschmidt used a wide range of research to formulate his own picture of evolution. Contrary to most scientists, he insisted that the neo-Darwinist theory of micromutations was no longer tenable as a general theory of evolution. Instead, Goldschmidt claimed, macroevolution accounted for the larger steps in e