conductibilité des métaux, due aux électrons libres, diminue moins rapidement et donc que l'application des métaux à côté de l'hélium liquide semble recommendable pour assurer les contacts thermiques. Mais, quand la chaleur spécifique d'une substance ne disparaît pas très rapidement elle aussi, il semble probable qu'on aura besoin de temps énormes pour refroidir cette substance à dix millidegrés Kelvin par exemple. Malheureusement ceci gêne la réalisation de deux des projets les plus intéressants: celui d'employer les moments nucléaires pour obtenir des températures encore plus basses[1] et celui d'orienter les noyaux de l'atome et d'étudier alors leurs asymétries. L'interaction entre des moments magnétiques nucléaires est certainement beaucoup plus petite que celle entre les moments des ions paramagnétiques et donc, comme la loi de CURIE, pour le paramagnétisme nucléaire doit rester valable jusqu'à des températures de 10^{-5} degrés Kelvin, on a en principe la possibilité d'obtenir des températures de cet ordre. SIMON[2] a donné en 1939 une discussion intéressante sur cette possibilité.

Il sera nécessaire de refroidir un système de spins nucléaires dans un très grand champ magnétique jusqu'à, par exemple, 10 millidegrés par un contact thermique réglable avec un échantillon désaimanté d'une substance paramagnétique normale. D'après les recherches de BLOEMBERGEN, il ne faut pas s'inquiéter sur le temps de relaxation des noyaux, mais comme le système des noyaux aura une chaleur spécifique considérable dans le grand champ magnétique, le problème du contact thermique est très sérieux.

Une fois qu'on aura trouvé moyen d'orienter une grande fraction des spins nucléaires dans un échantillon, il sera peut-être encore plus intéressant de se concentrer sur l'anisotropie du noyau que d'atteindre des températures encore plus basses. Pour plusieurs réactions nucléaires, il faut s'attendre à une dépendance des diamètres effectifs de la direction par rapport au spin et il est bien plausible que les réactions et les transformations nucléaires et radio-actives ne soient pas indépendantes de cette même direction[1]. Cela est de la musique de l'avenir, mais je peu affirmer qu'à Leyde comme dans d'autres laboratoires de basses températures on s'efforce déjà à projeter les instruments pour jouer de cette musique.

Summary

In three chapters the most important topics of paramagnetism are reviewed. In the first chapter a short introduction to normal paramagnetism is given and then the phenomena of paramagnetic relaxation are described and discussed. The second chapter deals with the resonance phenomena occurring when an oscillating magnetic field is applied perpendicular to a large constant field. In normal paramagnetic substances these phenomena are studied with the aid of centimetre waves while the corresponding resonance for atomic nuclei is observable at common radio wavelengths. It is stressed that the observation of nuclear magnetic resonance has opened a number of new domains of research. Special attention is given to the unravelling of nuclear magnetic relaxation. In the last chapter the attainment of extremely low temperatures by adiabatic demagnetization is described. It is indicated how thermodynamic temperatures have been determined down to 3 millidegrees absolute. Finally it is mentioned that attempts are being carried out to align atomic nuclei at the low temperatures reached.

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[1] N. KÜRTI et F. SIMON, Proc. Roy. Soc., A *149*, 152 (1935). – C. J. GORTER, Phys. Z. *35*, 923 (1934).

[2] F. SIMON, Rapport à la réunion d'étude sur le magnétisme (Strasbourg 1939).

[1] J. A. SPIERS, Nature *161*, 607 (1948).

Ecotype, Ecospecies, and Macroevolution[1]

By RICHARD B. GOLDSCHMIDT[2], Berkeley, Cal.

The combined efforts of taxonomists and geneticists have succeeded to a considerable extent in solving that part of the problem of evolution which concerns the subspecific level. The detailed work of innumerable taxonomists following in the footsteps of KLEINSCHMIDT, K. JORDAN, MATSCHIE, and RENSCH has shown that many species are best described as "Rassenkreise", i. e. series, and sometimes clines (in J. HUXLEY'S term), of subspecies replacing each other in an orderly geographical way over the area occupied by the species[1]. In most cases these subspecies or geographic races do not overlap and where they meet they may form hybrid populations, as subspecies are fertile *inter se*. Very frequently it is possible to recognize within the subspecies local populations which are again discernable as subunits, and even these may be sometimes successfully subdivided into other distinguish-

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[1] Paper read at the closing session of the International Congress of Zoology, Paris, July, 1948.

[2] University of California, Berkeley, Cal.

[1] Details and discussion from different points of view in: TH. DOBZHANSKY, Genetics and the origin of species (2nd ed., New York, 1941). – R. GOLDSCHMIDT, The Material basis of evolution (New Haven, 1940). – J. HUXLEY, Evolution, the modern synthesis (London, 1942). – E. MAYR, Systematics and the origin of species (New York, 1942). – B. RENSCH, Neuere Probleme der Abstammungslehre (Stuttgart 1941).

able groups down to individual colonies. Though the taxonomist does not apply nomenclatural distinction to these categories below the subspecies, it is important to realize that in many cases, if not in all, further subdivisions would be possible upon the basis of still recognizable hereditary differences. A further important result of this taxonomic work, frequently forgotten by present day evolutionists, is that subspecies and even smaller units are characterized by recognizable differences which are present in every individual. This is obvious, as otherwise the taxonomist could not name and describe subspecies. When the differential characters are of a quantitative nature, the characteristics are means of quantitative series. The individual variants may or may not overlap with those of the adjoining subspecies. Furthermore, a number of such differential traits, constant within the limits of normal variation, combine to characterize the respective subspecies.

Within this basic framework other phenomena have been recognized. The most important of these is the occurrence of additional hereditary traits, i. e., single mutants (including also position effects of chromosomal rearrangements) within subspecific populations, sometimes called *forma* or *varietas*. Such mutants may be floating within the populations, i. e. be present irregularly in heterozygous condition and appear as rare homozygous individuals. There is no doubt that these floating mutants are present everywhere though the taxonomist cannot, as a rule, be concerned with them. Sometimes, however, such mutants within a subspecific or still lower group show a regular behavior to the extent of exhibiting definite frequencies in individual populations. It is this type of diversification which lends itself to statistical study and has thus become the main material of the field of study called population genetics, now so popular. As the students of this field tend to consider their material as the most important one for the study of evolution, it should be made clear that they are working mostly on a level below the subspecific one. The subspecies, which is the lowest category recognized in taxonomic nomenclature, are not characterized (except perhaps for few cases such as Coccinellid beetles) as populations of numerically different mutants, or mutant combinations, but by a series of constant traits present in each individual. Population geneticists, when drawing far-flung conclusions from their work, frequently forget to realize the position of their material within the taxonomic picture.

The genetic basis of the rassenkreis aspect of the animal species was analyzed by the early zoological explorers of this field, SUMNER for *Peromyscus* and GOLDSCHMIDT for *Lymantria*[1]. Much material has been examined since, but it can be stated that no facts or conclusions of basic importance have been added for animals. The decisive facts are: subspecies (and still lower categories, where recognizable) differ in a series of hereditary traits and these differential characters remain typical when the different subspecies are bred under identical environmental conditions. The individual subspecies is characterized by a definite combination of these traits, visible ones which are used by the taxonomist, and invisible, physiological or developmental ones which only the experimenter can analyze. Within a geographically arranged group or cline of subspecies each of the hereditary differential characters varies independently. Thus one might be common to a number of subspecies, another will be different in each of them. One character may show a variation from low to high expression within a cline; another may vary inversely in the same cline, and a third might show its maximal expression within the spatial center of the cline with a decrease toward each end. This shows that the individual differential character has its specific meaning in the evolutionary process within the species, as has the combination of all differential characters. Genetically, the differential traits are based upon all known types of genetical differences, simple mutants, multiple alleles, and, most frequently, multiple factors.

The pioneer work in this field also succeeded in assigning a definite meaning to the subspecific differences. Many of them could be proved to be of an adaptive nature, both visible and physiological or developmental traits. About the same time the botanist TURESSON had shown that different types of plants, like alpine or dune varieties, are genetic types, called by him ecotypes, which are genetically adapted to their specific environment[1]. Thus the subspecies and still lower categories may be called ecotypes. The adaptive nature of their differential traits is usually difficult to prove when morphological characters, i. e., those accessible to the taxonomist, are involved, except in the case of protective coloration. Frequently, if not always, visible traits will be the morphological expression, itself not adaptive, of an underlying physiological and adaptive condition. Physiological and developmental traits are easily recognized as adaptive. A typical example is the diapause in the eggs of the races of *Lymantria* dispar and its reaction to rising temperatures[2]. It could be shown that the different races are genetically different in regard to the temperature sum required to bring about the hatching of the eggs in spring. These differences were exactly those required to fit the normal seasonal cycle of each region, i. e. to ascertain that hatching occurred exactly at the proper time not only to insure food for

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[1] F. SUMNER, 1915–1932, Review: Bibl. Genetica *9* (1932). – R. GOLDSCHMIDT, 1917–1935, Review: Bibl. Genetica *11* (1934).

[1] G. TURESSON, 1922–1936, esp. Hered. *3* (1922), *6* (1925).

[2] R. GOLDSCHMIDT, Arch. f. Entwcklgmech. *126*, 277, 591 (1932).

the larvæ but also to provide them enough time to finish their life cycle. The very intricate correspondence between the meteorological features of the different regions in regard to the seasonal cycle of the food plants and the genetically controlled time of hatching as proven in very extensive experiments on a multitude of races of different origin is really amazing. Many comparable examples have been found, and there can be no doubt that most, if not all, differential traits of subspecies and still lower categories are directly or indirectly adaptational.

Here an important observation must be made, important because it is usually disregarded in the evolutionary speculations of today. No individual or population can survive without a minimal genetic adaptation to the general features of the environment. To use the previous example again: a race of insects with the need for a diapause in development may live for many years without a close adaptation to the seasonal cycle. But if occasional severe winters or very mild winters are a part of the climatic conditions of the region, the first severe or too mild winter would destroy the entire population by inducing hatching at the wrong time, if the genetic control of the hatching reaction were not fine enough to cover rarely occurring extremes. The same argument applies *mutatis mutandis* to all such general features of environment as temperature, moisture, seasonal cycle, or, in special cases, wind, soil and similar general conditions which work directly or indirectly by influencing food, etc. (A beautiful example for such indirect adaptation has been described for *Lymantria*[1].) These indispensable adaptations without which no category of animals could survive are thus a common feature of all life, a minimum condition of existence. It is, in my opinion, a bad logical error if the conclusions drawn from this type of basic genetic "existential" adaptation, as one might call it, are simply used to explain the origin of such adaptations as constitute the material of the major phases of evolution, say adaptation to terrestrial or aquatic life, relation of insects to flowers, adaptation to intra-uterine development, etc. If we look at a species or Rassenkreis, all its essential features of organization are the same all over the geographical range. The same is true for any other species ranging over the same area. But both and all have their subspecific adaptations to climatic factors, frequently resulting in parallel geographic or ecological series. Is it justified to draw conclusions upon the origin of these species, and even the genera, families, etc. from the analysis of this generalized, existential adaptation? I deny it.

The picture of subspecific adaptation is completed by the study of its origin. Nobody doubts, I think, that CUÉNOT's theory of preadaptation is the proper explanation[1]. This means that not adaptive but not deleterious mutants present in adapted populations enable those individuals possessing them to settle in a new niche or area to which they are preadapted by these mutants. This principle is, of course, generally applicable to any type of adaptation. The workings of preadaptation and its positive selective value in new niches are most clearly recognized and studied on the lowest systematic level, i. e. below the subspecific. In the early days of the genetic study of these problems, I analyzed the so-called industrial melanism of the nun-moth[2]. Within a known number of decades and starting in heavily industrialized areas a melanistic mutant known to be present in the population as a rare occurrence began, in the second half of the last century, to supersede the original form in Central Europe. I found this successful phenotype determined by the collaboration of three pairs of dominant factors. This permitted calculation of the mutation pressure needed to account for the phenomenon in the absence of selection. This was so high that it had to be assumed that the melanistic form had a definite selective advantage in the industrialized areas. A definite physiological condition produced by these factors in addition to their visible effect, namely, a resistance to certain metal salts in the food, was assumed to be the preadaptive, selective agent.

In recent years the same problems on the same, i. e. subspecific level, have been studied on a large scale with the refined statistical methods under the name of population genetics. Many details and variants have been brought to light in different organisms, and many different aspects of the selection process in populations in time and space have been ascertained and a subtle technique developed for their assessment. In spite of the brilliance of the attack, the scope of the experiments, and the numerous details of the results, all of which erected a solid superstructure upon the limited facts known earlier and especially led to a quantitative study of selection, I cannot help saying that as far as the general features of evolution are concerned, population genetics has not led beyond the already available information. In spite of many assertions to the contrary, it has also failed to throw any light upon evolution above the subspecific and subsubspecific level of the investigations. To avoid misunderstandings I repeat that the importance of population genetics lies in the light thrown upon the workings of selection, the role of isolation, and the sterility barrier. But there is nothing controversial in these fields as every biologist agrees that selection and isolation are the basic working methods of evolution. Considering, however, the material upon which selection works, the students of population genetics accept it as a dogma

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[1] R. GOLDSCHMIDT, Amer. Natur. *72*, 385 (1938).

[1] L. CUÉNOT, L'adaptation (Paris 1935).

[2] R. GOLDSCHMIDT, Z. Ind. Abstl. *25*, 89 (1920); Am. Natur. *81*, 474 (1947).

that all phenomena of evolution, on any level, are based upon selection and accumulation of micromutations. This I claim to be impossible and I further claim that population genetics has not offered and cannot offer any information on the material of evolution above the subspecific level. I may say that those studies have taught us the rules of a game (the rules of selection), but the players (micro or macromutants) have not been identified.

Thus the mechanism of evolution on the subspecific level is rather clear. The difficulties arise when we reach the specific level. The taxonomists since DARWIN have always assumed that they are entitled to extrapolate from the subspecies to the species. This means that they take it for granted that at the extremes of a subspecific differentiation enough distinctive adaptational factors are accumulated to make for a transition into the specific level, an assumption of which RENSCH is the modern protagonist. The idea has been phrased thus: subspecies are species *in nascendo*. Much work has been done to prove this thesis, and many authors believe that their data require this interpretation. In the material which I studied I came to the conclusion that this is not the case, nor do I know of any stringent proof for that thesis. I can prove that this is not prejudice on my part by quoting (in translation) from a recent paper by a leading taxonomist and a well-known geneticist, both confirmed believers in this type of origin of species (STRESEMANN and TIMOFEEFF-RESSOVSKY[1]) "On the basis of genetical and population dynamic, ecological features we can visualize theoretically different mechanisms of speciation. Empirical facts from nature, actual observations of this process *in statu nascendi* do not exist". (I add to this that experimental evidence does not exist either. Author.) "Though geographic variation has been considered since DARWIN's time to be the most important first step toward speciation, only very few examples which prove speciation via geographic variation have been found." "...almost the only pet-example for a species *in statu nascendi* being the transgression of area of the titmouse *Parus major major* and *minor* in the Amur region. But even this example needs certain corrections..." Thus we face the confession of confirmed Neo-Darwinians that not a single reliable proof of their basic contention exists, although, if their viewpoint were correct, this should be a most frequent and easily observable phenomenon. I should like to quote again from the contents of this paper to show how two brilliant and experienced zoologists can fall prey to a prejudiced idea. The Northern gulls were described by STEGMANN as a single species *Larus argentatus* PONTOPP. with 19 subspecies which replace each other geographically and form hybrids where they meet. This is a typical Rassenkreis (with one aberrant type in California). Seven members of this series meet and inhabit overlapping areas in the Baltic, Barents, and White Sea regions without forming hybrid populations, "of substantial size". Though it is not possible to group the subspecies of these regions consistently into higher units, the authors propose "for practical reasons" to split this part of the Rassenkreis into *two or three* species. It is emphasized that the so-called isolation of the end members of a cline where they meet is only ecological (as far as known) and not genetic, and that hybridization is possible though no *large* hybrid populations are formed. Now follows the conclusion. "The Formenkreis *Larus argentatus-cachinnaus-fuscus* thus presents a classical example for species formation via extreme geographic races." To make it clear: interfertile races without a "considerable" tendency for hybridizing for purely ecological reasons and therefore being able to exist as overlapping subspecies are called species "for practical reasons". At will two species can be made, or, if you like, three. This makes them a "classic example" for the Neo-Darwinian postulate. I have emphasized this very recent study to show that the contention that subspecies are species *in nascendo* is thus far based upon wishful thinking and not upon facts.

In spite of this failure I think there is one type of animal species to which the earlier reasoning of the Neo-Darwinians applies, and I am ready to acknowledge that I did not make this clear in a previous book[1]. This is what TURESSON[2] has called an ecospecies. In many cases in which an animal type has a large range of distribution and the areas occupied by it are clearly separated geographically as islands, continents, or isolated parts of continents, an arrangement of species replacing each other is found in what parallels a Rassenkreis. This type of arrangement was called by RENSCH[3] an Artenkreis, and is composed of ecospecies. Differences between such ecospecies do not go far beyond those of subspecies and are sometimes so small that a taxonomic determination is not possible without knowledge of where the specimen was collected. We might call such ecospecies glorified subspecies because only their isolation sets them apart from real subspecies. Their origin according to the Neo-Darwinian pattern is not to be doubted. If they can be crossed, which is frequently the case, they show the genetic differences of the subspecific type.

The important question is now whether this type of microevolution can simply be extended to lead to real evolution. By this I mean evolution of such species which differ from each other not in small quantitative

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[1] E. STRESEMANN und N. W. TIMOFEEFF-RESSOVSKY, Biol. Centrbl. 66 (1947).

[1] R. GOLDSCHMIDT, The material basis of evolution (New Haven, 1940).

[2] G. TURESSON, 1922-1936, esp. Hered. *3* (1922), *6* (1925).

[3] B. RENSCH, Das Prinzip geographischer Rassenkreise (Berlin 1929).

features but in important parts of their organization, ecology and physiology and which actually do occur or might occur together in the same area without interbreeding. It must be realized that forms differing in this way are sometimes called different species (I mentioned at another occasion the *Lymantria* and *Ascaris* species) and sometimes they are distinguished on the generic and even on the familial level, depending upon the known numbers of the different forms and sometimes also upon the whims of the taxonomist, as the words "splitters" and "lumpers" indicate. Let us therefore not insist upon the terms species or genus but upon major organizational differences as opposed to the small quantitative differences of subspecies and ecospecies. It is typical for the former group that fertile hybrids are rare in animals and that there are no intermediate conditions or transitions between the two types. Our problem is to find whether or not the differences between these categories can also be explained on the basis of accumulation and selection of mutants with small effects.

Let us look first at the logic of the situation. If a new species is formed at an extreme end of a series of ecotypes, and if evolution of the ecotypes proceeds by accumulation of preadapted mutants and immigration into the proper niche, the last form which is supposed to be a species is still an ecotype as far as adaptation to its habitat is concerned and differs from other members of the species only in its dislike or inability to mate with nearby ecotypes. Let us suppose that the latter feature is genetic (which is not proven). The new species now will do the same as the old one, i. e. spread by preadaptation. If definite mutant combinations are needed for this adaptation, a reimmigration into the habitat of the old species would mean a return to the adaptive characters typical for that habitat. In other words, it would be impossible for two related species to live in the same habitat and remain different in their existential adaptive characters. The usual answer to this dilemma is that the new species first develops many new characters by mutation. These characters have nothing to do with the specific adaptation of the ecotype. Only secondarily the original ecotype might be produced again by mutation, in the now greatly changed new species. This preadapted form is ready to return to the former habitat where it now exhibits "parallel adaptation". Apart from the artificiality of this conception it is not quite clear why all the detour via the extreme end of subspecific clines is needed if any isolation, say by a sterility mutant, would suffice to start the process of speciation within any adapted subspecies.

Geneticists sometimes point out that the Neo-Darwinian view is proven when it is shown that after crossing of species a multiple factor segregation occurs. This is not a very good argument. First, species showing a basic general difference in organizational pattern do, as a rule, not produce fertile offspring. When offspring is produced, the species involved are in most cases found to be ecospecies, and consequently differ very little from one another. Second, species which actually have been separated for a considerable time must have evolved a considerable number of small mutations which enter the general picture of specific differences without being the ones which originally made for specific diversity. If normal chromosome pairing occurs in the hybrid, these new mutant differences of relative unimportance will exhibit multiple factor segregation. If this is true, it should be possible to distinguish, in favorable material, the actual specific differences from those secondary mutational additions. If the real specific or generic differences are basically produced by large single mutant steps affecting major organizational patterns, they should exhibit simple Mendelian segregation if viable at all. In an earlier book I have registered such cases from the animal kingdom. Since that time the botanists have added a number of new and convincing cases. A beautiful example was studied by DE CUGNAC[1] in two *Bromus* species (even described as genera) where the entire complex of specific differences segregated unifactorially, but for one trait. Other cases were found by OEHLKERS[2] in *Streptocarpus* and LAMPRECHT[3] who studied segregation after interspecific crosses in *Pisum* in more detail than known in any other case, was finally forced to the conclusion that the real species differentiating factors are different from those small overlying mutants, and that they are single, monofactorial determiners of the basic specific pattern.

This leads us to the decisive problem. Since early Darwinian days it has been emphasized that no major adaptation can be understood on the Darwinian concept of accumulation of small hereditary differences because the selective advantage could not become manifest until considerable adaptation was accomplished. Therefore a number of biologists were led to assume that major adaptations, actually all major pattern differences at least above the specific level, must have originated in single large steps. The early Mendelians (BATESON, DE VRIES) held similar views, but later the geneticists developed into Neo-Darwinians, even Hyper-Darwinians. They tried to overcome the old difficulties of the origin of major adaptations by different means, e. g. the assumption that heterozygous mutants could be safely accumulated until a good preadaptive combination was assembled (FISHER[4]). Another assumption made was that under definite breeding conditions mutants may be accumulated

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[1] A. DE CUGNAC, C. R. Soc. biol. Paris *132*, 404 (1939).

[2] F. OEHLKERS, Ber. Dtsch. bot. Ges. *58* (1940).

[3] H. LAMPRECHT, Agri hortique Genet. *2* (1944).

[4] R. A. FISHER, The genetical theory of Natural Selection (Oxford, 1930).

without the interference of selection, thus permitting new combinations to be available for preadaptation (WRIGHT[1]). One can visualize the working of such systems on the lowest level of evolution. I cannot possibly see how major adaptations and differentiation of the higher systematic categories could be explained thus by haphazard accumulations. As far as I know, nobody has tried to work this out in concrete terms and with concrete examples. I am sure that such a trial would result in failure[2].

While the majority of geneticists are content to accept the Neo-Darwinian idea and not to inquire into its consequences above the level of, maximally, ecospecies, beyond taking the extension to all evolution as granted, I was led by failure to discover in my experimental material any indication of speciation via the subspecies to reconsider the whole problem critically. I was forced to the conclusion (as had done many non-geneticists before me) that major systematic differences and adaptations can only originate in single major steps which establish at once the main features of the new organizational and physiological pattern. If the new types resulting from such macromutation fit into a new niche, selection and selective addition of minor mutants will perfect the adaptive features. I tried further to prove that these ideas are in accord with the facts (as opposed to the interpretations) of genetics as well as of comparative anatomy and experimental embryology. Needless to say, I did not succeed in producing a higher category in a single step; but it must be kept in mind that neither have the Neo-Darwinians ever built up as much as the semblance of a new species by recombination of micromutations. In such well-studied organisms as *Drosophila*, in which numerous visible and, incidentally, small invisible mutants have been recombined, never has even the first step in the direction of a new species been accomplished, not to mention higher categories. Thus the discussion will be decided in favor of that party which can show best how the actual process may have occurred on the basis of the type of genetic changes which are actually found, and their evaluation in regard to evolutionary potentialities. I think that the Neo-Darwinians have nothing to offer in this respect except a refined knowledge of the action of selection. Otherwise they must postulate as a dogma that this selection acts always upon individual micromutations or groups of them, and that all organization can be conceived as being based upon accumulation of more and more of such micromutants. The adherents of the saltatorial concept of macroevolution, however, can produce a number of remarkable facts which permit visualization of the much simpler and more plausible way of evolution they assume.

At this point of our discussion a word should be added about the results of the only science which actually sees parts of evolution in action, i. e. paleontology. During the past years some important discussions of our problem have taken place among paleontologists. One of these discussions occurred here in Paris[1], another in Germany[2]. The result is in so far disconcerting as about the same number of experienced paleontologists expressed themselves in favor of the Neo-Darwinian as of the saltational point of view of evolution. But it is also encouraging to see that some leading paleontologists agree completely with the views which I have upheld and are marshalling important bodies of fact in favor of such views.

A large array of such facts outside the field of paleontology were compiled by me in an earlier book. Quite a number of new ones have since come to light. I may mention shortly two examples from the plant kingdom. A long time ago LOTSY found among types segregating from a species cross in the snapdragon group one which he considered a new species, *Antirrhinum rhinanthoides*, because it had the decisive characters of the genus *Rhinanthus*. Subsequently STUBBE[3] proved that this rhinanthoides type was a simple mutant which recurred in *Antirrhinum*. He found further a number of simple mutants which, in one step, produced characters typical of different genera of the same family. In one case both the flower form and the number of anthers were changed to those typical of another genus. In another mutant of this type the number of anthers was reduced to a figure characteristic of other genera. STUBBE and WETTSTEIN[4] actually used for these occurrences my term of "hopeful monster" meaning that what appears as a mutant monstrosity in the species might become the start of a new genus if the first decisive step fits a niche in the environment and is perfected and isolated subsequently. A similar phenomenon has been described by BURGEFF[5] in the liverwort *Marchantia* where again typical generic features of other members of the family appear as simple mutants. He also accepts my evolutionary interpretation. Recently GUSTAFSON demonstrated in SVALÖF amazing macromutations of cereals, one of them as perfect a new type as anybody could desire.

One of the examples of this type which I used formerly is the occurrence of homœotic mutants in *Drosophila*, e. g. those in which halteres are transformed into wings or wings into halteres by mutation, a step which involves the major difference between the Diptera and other insects. I have since studied another case which is so amazing that I beg to discuss it in some

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[2] S. WRIGHT, Genet. *16* (1931).

[1] See my analysis of a special case (mimicry) in: Quart. Rev. of Biol. *20* (1945).

[1] See review in: La Revue scientifique (1947).

[2] Published in: Die Naturwiss. 1942–1944 (SCHINDEWOLF, BEURLEN, GROSS, HEBERER).

[3] H. STUBBE, Biol. Centrbl. *60*, 113 (1940).

[4] H. STUBBE and F. v. WETTSTEIN, Biol. Centrbl. *61*, 265 (1941).

[5] H. BURGEFF, Biol. Centrbl. *61* (1941).

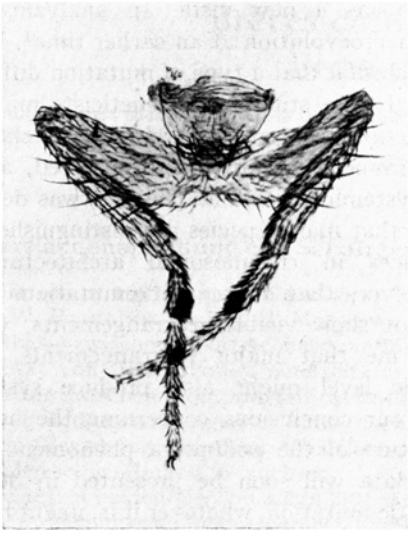

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 1–3. – Photos of different grades of concrescence of forelegs. *1* beginning, *2* intermediate, *3* extreme.

more detail. A group of homœotic mutants of *Drosophila* was found, all of which transform the wing, via all transitional stages, into a leg-like, trisegmented structure. (It is not relevant to the present discussion that individual factors have a lesser effect than a combination of many as regards the penetrance of this character; there exists also one dominant mutant with full penetrance.) This is in itself a macromutation to which the conclusions which were drawn from other homœotic mutants apply. The podoptera factors, as they are called, produce other pleiotropic effects, among them irregular effects upon the legs, which become individually more or less abnormal, duplicated, or absent[1]. While this effect is very variable and ordinarily of low penetrance, affecting usually only a single leg, the introduction of the dominant mutant *Hairless* into the podoptera genotype results in a high percentage of flies with all legs transformed into short stumps of characteristic structure. Thus, in two steps, a very extreme deviation from normal has been accomplished. By outcrossing podoptera to a line with recessive markers another modifying factor—in itself without visible effect—was introduced which again increased the leg effect of podoptera considerably, adding a tendency toward formation of biramous legs. In addition this combination produced regularly, although in a small percentage, a tendency of the first legs to unite into a single structure located in the ventral mid-line of the body. While still showing its origin from a pair of legs the structure became flattened, assumed a new but perfect pattern of bristles, and was bent forward as if belonging to the mouth parts.

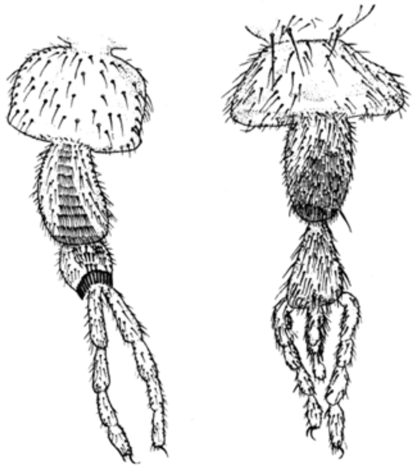

Fig. 4. – Drawings of two characteristic types, showing the new pattern of bristles and hair. One is a male. Notice the typical organ formed by the two sex-combs.

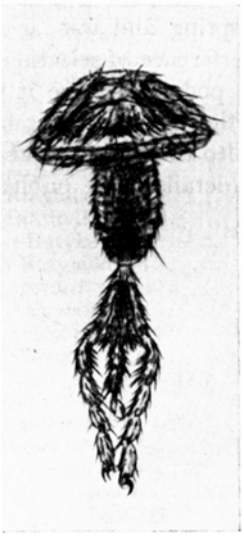

Fig. 5.

Fig. 6.

Fig. 5 and 6. – Photos of some after-mountings.

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[1] Morphology described in: R. GOLDSCHMIDT, J. Morphol. *47* (1945). Genetical analysis is in press.

Its similarity to the labium of Orthoptera is simply amazing (see figures). Here, then, a paired organ, the forelegs, were transformed, in one major step, plus the action of a modifier, into a structure which, if typical for a group, would be considered to be on a class level. Needless to say, this fly with segmented appendages instead of wings, and a pair of legs assuming the structure of a mouth part, is only a monstrous *Drosophila*. But it is clearly what I have called a "hopeful monster". If such a monster were formed in nature and found a proper niche to which it were preadapted, the major step toward formation of a new class would have been accomplished. We saw that the presence of the podoptera factors did not only affect the wings in a macromutational way, but simultaneously created the conditions under which the introduction of modifiers present in the population could immediately produce a still more extreme change. All the conditions are thus present for the eventual selective improvement of a completely new type of organism at a very rapid rate.

The genetic details of this case permit some further statements on the mode of macroevolution along the lines of this model. The mutant characters under consideration have only a low penetrance. This means that the majority of individuals, homozygous for the mutant, are phenotypically normal. Thus the extreme departure can be carried on through generations without succumbing to negative selection until the proper niche is found. We know, however, that the podoptera characters may be built up quickly to 100% penetrance by introduction of supplementary factors. If we take this as a typical feature of these macromutations, we may expect the same to occur in nature, once adaptive value has been established and selection sets in. From this point on selection in a population begins to operate, while the decisive step toward macroevolution was performed in a mutating individual and its direct offspring and was accomplished without the active interference of selection.

During the analysis of the podoptera case it was found that the best interpretation of the genetic facts puts the podoptera mutants into the heterochromatic sections of the chromosomes (details to be published soon). This opens a new vista. In analyzing the problems of macroevolution at an earlier time[1], I was led to the conclusion that a type of mutation different from the usual type studied by geneticists must be involved. I thought that sudden architectural changes within the chromosome must have occurred, and I called them systemic mutation. The idea was derived from the fact that many species are distinguished by such differences in chromosomal architecture. I realized, however, that those macromutations then known did not show visible rearrangements, which indicated to me that major rearrangements on a submicroscopic level might also produce systemic mutation. If our conclusions concerning the heterochromatic nature of the podoptera phenomenon are correct (the data will soon be presented in detail), heterochromatic mutation, whatever it is, might be the basis of macromutation and macroevolution. Much work will be needed before this problem can be solved. But it will be beneficial to realize that, in view of the failure of Neo-Darwinism to explain evolution occurring above the level of the ecospecies, science will be better served by attacking these problems with an open mind instead of from the standpoint of a school sworn to an inflexible dogma.

Summary

Der Autor tritt erneut der Ansicht der Neodarwinisten entgegen, daß geographische, erbliche Varianten Vorstufen neuer Arten seien. Für deren Entstehung sowie für Merkmale höherer Einheiten kommen nur plötzlich große und nicht einzelne summierende Mutationsschritte in Betracht. Mikromutationen liefern lediglich das Material für die Entstehung von Rassen und Unterarten. Nicht nur größere systematische Unterschiede, sondern auch Anpassungsmerkmale kommen durch Großmutationen zustande. Als Beispiele werden unter anderem zwei Mutationen bei *Drosophila melanogaster* angeführt. Bei der einen sind die Flügel in Halteren, oder umgekehrt, diese in Flügel, umgebildet. Bei der anderen, vom Autor aufgefundenen, sind aus den Flügeln beinartige Organe geworden. Diese Mutante ist außerdem deswegen von Bedeutung, weil sich nach Kreuzung mit anderen Mutationen Merkmale entwickeln, die an den letzteren nicht erscheinen.

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[1] R. GOLDSCHMIDT, The material basis of evolution (New Haven, 1940).