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by M. V. Turbin

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NUCLEOPROTEINS AND HEREDITY

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One of the most important problems in modern genetics is that of determining the role of intracellular nucleoproteins as carriers of the heredity information of the cell. This has encouraged profound research on the structure and properties of the nucleoproteins and first of all their nucleic component, the polymerized nucleic acids - desoxyribonucleic and ribonucleic acids. Success in this field will lead to the development and increase in our knowledge of the nature of the hereditary factors, and the mechanism of their action in the development of characteristics. Using the terminology of cybernetics in evaluating the results obtained, one may say that an attempt has been made to solve, in a first crude approximation, the problem of discovering the means of "coding" inherited information available for progeny from parents in the structural elements of the sex cells, as well as the means of controlling it in the process of the individual development of the new organism. We may say that the discrete hereditary information is coded by certain structures of the nucleic acid molecules which possess the capacity for replication, thanks to which it is transmitted to all newly formed cells of the organism.

The structure of the nucleic acid molecules determines the structure of the proteins which are synthesized in the cell, in particular, the proteins which have enzymatic properties. The first serve as templates ("dies") in the synthesis of the latter.

Thus hereditary information, included in the germinate zygote cell, is transmitted to all the cells of the organism (principle of intensification) and acts on the biochemical and physiological processes taking place there, on metabolism, and in the final analysis on all the macroscopic properties of the organism as a whole.

This article give a brief survey and analysis of the basic facts and conclusions which prevailed before the development of the above - mentioned concept of the mechanism of the transmission of heredity, and also makes an attempt to give a new interpretation of certain facts in the field of the biology of plant fertilization.

A comparison of the biochemical properties of chromosomes, chloroplasts, and viruses -- structures and particles which are capable of replication within the cell -- shows the presence in them of one common characteristic: they are all constructed of nucleoproteins, include in their make-up polymerized nucleic acids DNA and RNA or both at the same time. The chromosomes are made up principally of DNA and a small amount of RNA; the chloroplasts, of RNA; the chondriosomes and microsomes which carry out the synthesis of enzymes contain RNA; the animal viruses consist mainly of nucleoproteins which are formed of protein and DNA; and the plant viruses, of protein and RNA.

This fact requires an explanation of the properties of the polymerized nucleic acids and their biological functions. Of particular interest in this respect is DNA, which is the basic component of the nucleoproteins of chromosomes; and this makes the problem of the material mechanism of heredity (in which the chromosomes play an inevitable role) closely connected with the problem of discovering the structure and biological role of DNA. Of like interest is RNA, localized in the plasma structures responsible for the synthesis of proteins and entering into the composition of the nucleoproteins of the plant viruses.

As indicated by the eminent English scientist J. Bernal, the greatest importance attaches to the mechanism for the replication of DNA-proteins, since a study of plant viruses gives us reason to assume that the replication of RNA-proteins may take place only in the presence of DNA, inasmuch as there are no known independent organisms which contain only RNA.

While it was recently determined that DNA (and RNA) are individual substances identical in all organisms, we still cannot determine their hereditary specificity. Starting with this view, attempts were made to establish the nonspecific functions of DNA and RNA common to all organisms. It was concluded that they do in a certain fashion participate in the synthesis of protein and play a role in the process of the replication of certain structures of the cell and of the viruses.

With regard to DNA two functions were discerned: the function of template for extending the polypeptide chains into a monomolecular film necessary for the autocatalysis of protein, and the function of a source of energy in the creation of peptide bonds in the process of protein synthesis, inasmuch as in it (as in RNA) there are macroenergetic bonds. However, a further study of the problem led to a basic revision of such phnomena.

It was proven experimentally (by O. Avery and his colleagues) that it is possible to produce basic changes in heredity in bacteria through the transformation of one hereditary type (strain) into another by injecting purified DRN from one strain into a culture of the other.

At first these studies, using pneumococci, were limited to one type of transformation, the so-called capsule transformation, connected with the conversion of acapsular forms of pneumococci into capsular forms. On the basis of the results obtained we could expect that in the future other types of changes in heredity would also be induced. In further research this assumption was fully confirmed and in fact several different types of transformations were obtained with the same test object, in particular changes in the somatic antigen components (proteins), resistance to antibiotics, changes in the enzymatic systems, etc.

Each of these types of transformation was induced by the action of a particular nucleic acid on individuals of mutant strains under strictly controlled conditions and each of these transformations can be reproduced repeatedly at the desire of the experimenter. Such basic changes in heredity were also obtained with other types of bacteria (Escherichia coli, Pfeiffer's bacillus, Flexner's dysentery bacillus, meningococci, the murine typhus bacteria, etc.)

It must be pointed out that purified DNA as a transforming agent is very active: its introduction into a culture of microbes in concentration of 6 x 10-8 is enough to activate the conversion of one hereditary type of microbe into others. Its activity becomes stronger with depolymerization.

Special research (H. Ephrussi-Taylor and others) has shown that a general result of such transformations in any direction is the disappearance of the agent which was present in the bacteria at first, and in place of this the propagation of the agent introduced into the nucleic acid extract. Thus the transformation is based on the substitution in extraction of one agent for the agent which was first present in the cell, or in other words, transformation consists of replacing the nucleic component of the cellular element which reproduces itself, by nucleic acid of external origin having similar structure and function.

From the fact that induced transformations are caused by highly purified solutions of DNA it appears that these agents are desoxyribonucleates. On the basis of his own observations of the desoxyribonucleinc acid of pneumococci, Avery expresses the idea that these substances are biologically and chemically heterogeneous and that this heterogeneity exists even when isolating DNA from a single pure clone. The correctness of such a comment is indicated by the fact that in desoxyribonucleates recovered from a strain of pneumococci (smooth type III) six transforming agents were recovered in experiments.

Further research has shown that some properties of different transforming agents (TA) relate them to independent genetic individuals. For example, they can be recognized in a number of cell generations, determine the character of dying characters and features

of bacteria, and may undergo mutation changes independently one of the other. They are comparatively independent of each other in their reproduction in the cell, capable also (Ephrussi-Taylor) of the combination of independent agents which cause different cellular characters, which permits the experimenter to distinguish the different individual capsular characteristics from different individual characters of antigen complexes (M protein) or resistance to a certain antibiotic. The agents which cause these different characters, isolated from different lines, may exist in one and the same cell. Along with the independent combination of transforming agents, which are different molecules of DNA, we see cases of a special "coupling" analogous to the coupling of genes located in one and the same chromosome, from which it follows that in certain cases one and the same molecule of DNA (its different parts) effect the development of different characters. Thus there is an established similarity in some functions of molecules of DNA in bacteria and in the chromosomes in the organisms which have quite well formed cell nuclei.

The diversity of DNA is also demonstrated by direct biochemical examinations. It has been found that not only in different organisms in DNA chemically different but that the DNA of a cell (tissue) is the sum of a whole series of different individual nucleic acids (18). A preparation of a composite DNA may be fractionated into a series of fractions of different composition. But in so doing we find a constancy of the composite DNA from which it appears that the ratio of the fractions which make up the acid is more or less constant. Data in support of the concept of the species specificity of DNA were obtained by A.N. Belazerskiy by studying the composition of nucleic acids in different species of bacteria. In this he found that DNA in these organisms has more clearly expressed specificity by comparison with RNA; this means that in experimentally altered strains of bacteria there are more pronounced qualitative differences in DNA than in the original forms, and these changes in DNA are correlated with changes in the entire sum of hereditary characteristics at the same time that RNA in modified bacteria preserves an unmodified composition.

Thus the original concept of the identity of DNA in different organisms was a profound error. In fact, as shown by identical observation results, the DNA has a high genetic specificity, it is different in different types of strains. This conclusion is confirmed by certain other facts. For example, if we infect bacterial cells with virus particles of bacteriophage, it has been established that the bacterial cell is penetrated not by the entire bacteriophage particle but only filaments of DNA liberated by the protein membrane which remains outside the cell. Penetrating the cell (possibly with a very insignificant amount of protein), the DNA assures the propagation of the bacteriophage and the whole

cycle of its development inside the bacterial cell. Thus by penetrating the cell the DNA produces within it the synthesis of its own species specific particles, including their protein component.

Similar results were obtained with plant viruses (virus of tobacco mosaic) in which filaments of nucleic acid (RNA) can be partially separated from the protein membrane. A. Hirer and H. Schramm showed that the RNA of the virus of tobacco mosaic when separated by rather mild methods is itself virulent; this means that it retains its infectiousness even after total removal of proteins. If it is placed on the leaf of a susceptible plant it not only reproduces but causes the synthesis of the specific protein component of the virus. Accumulated data in support of the statement that the RNA of the virus of tobacco mosaic is infectious and is the genetic determinant of the virus were obtained by H. Frenkel' -Konrat and R. Vil'yams in research on the nature of the "progeny" of virus reconstructed from protein and nucleic acid of different strains of the virus of tobacco mosaic.

This method for obtaining the reconstructed "hybrid" virus includes the separation and combining of the protein and ribonucleic components of two viruses which depend on different genetic series. In this case one manages, so to speak, to "Package" purified nucleic acid taken from one strain of the virus of tobacco mosaic inside the protein of another strain. It was shown that symptoms of infection caused by the "hybrid" virus are always characteristic of the strain from which the RNA was taken. The "progeny" of these reconstructed virus particles include at the same time RNA and protein from the virus from which the RNA was taken. In fact, the authors point out the presence of a slight difference between the "progeny" of a mixed virus and the viruses which were the source of the RNA, which indicates a certain slight effect of protein on the process of virus replication. This research clearly demonstrated that the RNA is the genetic determinant of the virus. The acid (RNA) can be skillfully separated from the protein membrane. It has also been determined that the propagation of this virus requires only that a filament of RNA with a small amount of protein penetrate the cell.

The discovery of these facts which indicate the great role of the DNA (and RNA) in heredity is stimulating interest and a detailed study of its physical and chemical nature. The results of such a study helped to elucidate the details of the structure of DNA, which is of real significance for understanding the mechanism of the replication process of the nucleoproteins of chromosomes and viruses. On this basis a three-demensional model of DNA was proposed which gives a more satisfactory interpretation of this process than many other hypotheses. In particular, it coincides wholly with the new views on genes which have developed on the basis of the study of the relation of the "position effect" and "pseudoalelism" which were mentioned above.

In brief, the essence of this new concept of the structure and function of DNA amounts to the following: In hydrolysis the molecule of DNA and RNA breaks down into fragments which combine with the nitrogen base, sugar, and phosphroic acid, and have been given the name of mononucleotides (or simply nucleotides). A molecule of DNA and RNA is a composite (polymer) complex which is made up of a great number of nucleotides. The degree of polymerization of the DNA may be judged from its molecular weight which is designated by values from 500,000 to 1,000,000 and from some data above. This means that it can be composed of 500 or more mononucleotides. The degree of polymerization of RNA is much less.

Nucleotides from which a polymer molecule of DNA is built are distinguished from each other by the base which is utilized in their composition. A total of four bases are found: two purine -- adenine and guanine, and two pyrimidine -- cytasine and thymine, and there are four corresponding varieties of mononucleotides each of which includes one of these bases. RNA is also built from four varieties of nucleotides. Of the four bases which it contains, the three in common with DNA -- ademine, guanine, and cytasine -- include the pyramidine base of uracil instead of thymine. In addition, these two nucleic acids are different in sugar: the nucleotides of DNA contain the sugar deoxyribose while the nucleotides of RNA contain ribose.

The method for distinguishing the nucleotides in the polymer molecule of DNA can be diagrammed thus:

Base -- sugar
Phosphoric acid
Base -- sugar
Phosphoric acid n-times
Base -- sugar
Phosphoric acid
Base -- sugar

This means that particular nucleotides are interconnected by oxygen molecules formed from hydroxyl groups of sugar of one nuclectide and the phosphoric acid of another adjacent nucleotide with the liberation of a molecule of water. The base in each nucleotide is joined to the sugar by a glucoside bond through one of the nitrogens of the base.

Thus the skeletal base of a molecule of DNA is made up of a long chain of alternating sugar and phosphoric acid radicals. X-ray structural analysis has established that individual adjacent nucleotides are 3,4 Å distant from one another, which corresponds to the distance between two adjacent amino acid radicals in a polypeptide chain. DNA molecules are long thin filaments which have axle ratios equal to approximately 300.

In describing the physical and chemical properties of nucleic acids and comparing them with other specific cellular pollymers (proteins, polysaccharides, blood groups, etc.) biochemists have established the following different properties of the first, connected with their biological functions. Nucleic acids (as the proteins) differ from other natural polymers by heteropolymerism, i.e., they are from a number of different monomers (primary "bricks"), linked in each type of nucleic acid (protein) in a characteristic order. The sequence of position of mononucleotides in the polynucleotide chain is not just any periodicity, but these polymers have a very pronounced arhythmic sequence. However, this sequence is strictly determined for each type of nucleic acid.

A particular feature of nucleic acids, observed by Chargaff (18), is the marked balance between the individual component parts. For example, in studying quantitative correlations and the order of alternation of four varieties of nucleotides it was found that for such a molecule the number of nucleotides included in adenine always equals the number of nucleotides in thymine and the number in guanine equals the number in cytasine. The sum of the purine nucleotides equals the sum of the pyrimidines. Thus we have found a paired relationship between one purine base (adenine) and one pyrimidine base (thymine) and the corresponding other bases -- purines and pyrimidines (guanine and cytasine). As for the quantitative relations between these pairs of bases, it is different in different organisms but is characteristic for each concrete organism. The order of alternation of bases as mentioned can be different in DNA of different species and in different parts of one and the same polymer molecule.

A significant feature -- the balance between the individual component parts -- is a characteristic property of nucleic acids which does not exist in other cell-specific polymers, and, in the opinion of some modern biochemists, it is precisely with this chemical property of the polymer nucleic acids that their role in hereditary "information" is connected.

In studying the reaction of DNA to changes in the pH, some characteristics were discovered in changes in its dissociation which lead to the concept of the presence in DNA of hydrogen bonds among the bases, which act within its structure.

Taking into account data on the X-ray structural analysis of DNA and its physicochemical properties, Watson and Creek (14) proposed a three-dimensional model of the DNA molecule which elucidates its detected properties and makes possible a new approach to the problem of the mechanism of the replication of particles of nucleoproteins and the problem of the nature of genetic specificity of DNA. According to this model, the molecules of DNA contain two polynucleotide chains which twist around a common axis, going parallel and having an identical right turn of the spiral (Fig. 1). The common diameter of the molecule equals 20 Å

and the distance from the atoms of phosphorus to the axis of the molecule is 10 Å.

The phosphorus-sugar skeletons of both chains of the DNA make up the external part of its structure while the bases are wrapped up inside this structure. The latter, being connected with the sugars by glucoside bonds, are located perpendicular to the molecular axis and stand opposite each other. An analysis of the spatial distribution of the bases and the possibility of the development of hydrogen bonds between them, which join two chains into a single structure, leads to the conclusion that not every combination of bases corresponds to the scientific data.

The dimensions of the purine bases (adenine and guanine) are approximately 7 Å, while the dimensions of the pyrimidine bases (cytasine and thymine) are approximately 5 Å. With the diameter of the entire structure at 20 Å, the distance between the sugars is approximately 12 Å. This means that for the placement of two purine bases this distance is small but for two pyrimidine bases it is large, hydrogen bonds which are effective only at a short distance could not be established between them. Thus the opposing bases in a pair of DNA chains, connected into a single structure, may be composed only of one purine and one pyrimidine base. From the fact of the existence of the pair relationship of bases it follows that these pairs may be adenine-thymine, guanine-cytasine, and the components of these pairs, as already mentioned, are represented in DNA in ratios of 1:1.

The existence of a strict regularity in the form of the existence of fixed pairs of bases, which connect the two chains of the DNA into a common structure, has no effect on the nature of the subsequent location of the different nucleotides; any sequence of pairs of bases along the axis of the common dual structure of the DNA is possible.

We have presented this model of the structure of DNA in only the most general features, omitting a number of its less important details. It makes possible the clarification of the process of spontaneous twinning of the reproducing particles of nucleoproteins by the following method. As was pointed out above, the structure of DNA consists of two mutually complementary chains of nucleotides. The hydrogen bonds which connect the pairs of adjacent bases of these two chains enclosed within the structure, are weak, their energy does not exceed the energy of thermal motion at room temperature. Then, too, destruction of the hydrogen bonds is comparatively easy, whereupon the dual structure of the DNA divides into two isolated filaments. The bonds which are freed thereby may be points of attraction for free nucleotides or their predecessors from the cellular cytoplasm. Nucleotides which are attracted to the chain will be attached (through a hydrogen bond) to nucleotides of the single chain, forming special pairs of bases,

and adenine will be attached to thymine, guanine to cytasine. Thus the sequence side by side with a similar single chain of polynucleotides will find a base of another identical chain. Then bonds are formed between the sugars and phosphoruses which form the skeletal base for a second new chain connected with the first in such a manner that the dual structure of the DNA is restored with the same sequential arrangement of the specific pairs of bases which existed in the original dual structure. In the same way the second single chain, by attracting nucleotides from cytoplasm and placing them in a certain order, is able likewise to renew the original dual structure. In short, there is a replication of the original dual structure of the DNA.

However, this explanation, which is striking in its simplicity, requires further analysis, inasmuch as it has certain real defects. For instance, there remains unsolved the role of the protein component of the nucleoprotein and the mechanism of its renewal. It was established by direct research that there was a coincidence between the periodicity of structure of the DNA and the polypeptides in the nucleoprotein from which it follows that the protein component of the latter also participates in the spiral structure of the DNA. This structure thus has not two but three elements; two polynucleotide chains of DNA and one chain of polypeptide.

In the triple structure, as D. Blokh admits, two chains belong to DNA and (in accordance with the earliest considerations are joined by hydrogen bonds, and the third (polypeptide) chain is twined around the two polynucleotide chains in such a manner that the adjacent amino acid groups, located in opposition, form ionic bonds.

The doubling of such a structure starts with the destruction of the hydrogen bonds between the bases of the polynucleotide chains. After the rupture of the hydrogen bonds the bases rotate around the glucoside bonds 180 degrees, thus protruding from the intramolecular space. Under these conditions there takes place attraction of the nucleotides of each polynuclectide chain for the corresponding nucleotides from the cellular cytoplasm, i.e., attraction of thymine by adenine and of cytasine by guanine.

These pairs of bases are joined to each other by hydrogen, and, finally, side by side with the perpendicular polynucleotide chain an additional identical chain is formed. In this case both original chains are held firmly in place, thanks to their ionic bond with the protein common to both chains. The joined nucleotides will thus have a configuration rolled out along a glucoside bond. The polymerization of the joined nucleotides leads to the appearance of two new polynucleotide chains. Joining a polypeptide chain (hiatone) to them leads to the doubling of the original triple structure of the nucleoprotein (deoxyribonucleoprotamine). The old and new structure at first will be joined through hydrogen bonds between the old and new polynucleotides. But then there will be a separation of this

complex which includes two identical triple structures, each of which is composed of two polynucleotide chains and one polypeptide chain. The separations will take place thanks to the rupture of the weak hydrogen bonds between the old and new polynucleotide, and also thanks to the rotation of the bases around the glucoside bond under normal conditions and the creation of hydrogen bonds inside the two old and two new chains of polynucleotides.

In the light of these new concepts of the structure of DNA and the mechanism of its doubling a new solution is being worked out for the problem of the genetic specificity of DNA and the material basis for the functional differentiation of chromosomes. Earlier, when DNA was considered identical throughout the body and the features of its structure which provided for genetic specificity, were not known the problem of the nucleoprotein component responsible for hereditary specificity could have only one solution, the recognition that this component was protein, which was found in the make-up of the nucleoproteins. In this case for interpreting the functional differentiation of chromosomes, its parts corresponding to genes, it was necessary to admit the existence of a large number of proteins (of the order of many thousands) which could be the centers for the formation of a corresponding number of biologically active substances (enzymes or their predecessors) which emerge from the cell and control the corresponding biochemical processes.

The determination of the fact of the genetic (hereditary) specificity of DNA creates a new basis for interpreting the role of the nucleoproteins of chromosomes in heredity, with the physical-chemical side of this problem being simpler than was first thought. From the presented interpretation of the structure of DNA one may draw the full conclusion that only one part of its structure, its side chains of purine and pyrimidine bases, can be responsible for the genetic specificity, inasmuch as the skeletal portions, made of up alternating sugar and phorphoric acid, are indentical throughout the entire length. As for the bases, they, as indicated, are identical in DNA of a different origin, and this means there is only a possible difference in the sequence of their alternation.

Inasmuch as the biologically active substances (enzymes), secreted by the chromosome in the cell, are protein bodies, it is necessary to explain by what means the specific alternation of four bases in a polynuclectide chain can be the base (template) for the formation of many specific polypeptides (enzymes). In order to explain this the following idea was advanced which is based on the information theory. The proteins are built up from 20 amino acids and are distinguishable from each other by their composition and sequence of location in the polypeptide chain. Corresponding to 20 amino acids are combinations of three which can be made from four bases. The problem of synthesizing specific enzymes (proteins) under the influence of chromosomes from the

point of view of the information theory is a problem in the transmission of hereditary information from the chromosomes, where it exists in the form of long polynucleotide chains, to the enzymes, which are polypeptide chains. The mathematical side of the question amounts to a procedure of converting a long number, recorded in the quaternary system (corresponding to the four types of bases in polynucleotide) into long words written with 20 different letters (corresponding to the 20 amino acids from which the polypeptide chains are constructed). This can also be achieved by admitting a correspondence between each of the 20 existing amino acids and one triple base from the 20 possible threes which can form the four existing bases (adenine, guanine, thymine, and cytasine).

In view of such a correspondence within the DNA spiral, perhaps a protein molecule (enzyme) can be built in which the order of location of amino acids will be identical specifically to the order of location of the purine and pyrimidine bases. In other words, the alternation of the basic three bases, located in a certain sequence in one and the same sector (locus) of the polynucleotide chain, will determine the alternation of certain amino acids in the polypeptide chain being synthsized. The number of isomers of the polynucleotide chain, which are distinguishable from each other by the sequence of alternation of the 20 possible triple combinations of bases, is as endlessly great as the number of different isomers of polypeptides which are distinguishable one from the other by the sequence of alternation of the 20 amino acids which are a part of their composition.

If we accept this statement that the synthesis of one amino acid requires the action of three nucleotides, i.e., corresponds to a sector of the polynucleotide chain, which is made of up three nucleotides, it is possible to determine the approximate size of that portion which can be the "template" for protein (enzyme) synthesis and that of other products (vitamins and sterols), by means of which a given sector could exert an effect on the biochemical processes in the cell, i.e., by the distinguishing mark of the physiological action (genes). In the opinion of N. P. Dubinin (8), a portion of the polynucleotide chain in which are located from 12 to 600 nucleotides may correspond to the gene. The number of possible juxtaposed four bases in a system made up of 12 nucleotides, will equal 4^{12}, i.e., more than 150 million. With the condition that the portion of the polynucleotide chain which corresponds to one gene will be made of up 12 nucleotides, then for 50-200 genes we would need from 600 to 1,000 nucleotides. And if this portion (gene) were made of up 1,000 nucleotides, then for a like number of genes we would have to have approximately 50,000,000,000 nucleotides. According to the computations of certain authors, DNA in one chromosome

includes more than 40,000,000 nucleotides. These computations, cited from the work on N. P. Dubin, indicate that any possible variation in the hereditary specificity of organisms is completely provided for by the diversity of possible juxtaposed four bases in the DNA structure.

In connection with the mentioned concepts of the structure and mechanism of replication of the DNA and its role in the synthesis of protein, the problem is once more posed regarding the biochemical structure of the gene and the genetic discreteness of chromosomes. DNA, which exists in the composition of chromosomes, has a continuous undivided structure which is constructed of the basic nucleotides and is charaterized by a certain order of alternation of the nucleotide bases in its make-up. The sequence of bases, or more accurately, the sequence of the location of the 20 possible triple combinations of bases, determines the synthesis along the length of the polynucleotide chain of certain amino acids which are located in strict sequence and pass through two stages. The first stage consist of the extension of certain amino acids by the appropriate triple combinations of bases of the polynucleotide chain, and the second in the formation of peptide bonds between the adjacent amino acids, the condensation of the latter into a polypeptide chain which is characterized by the specific location of the amino acid groups. In this the formation of peptide bonds may also take place under the influence of nonspecific enzymes.

The polynucleotide chain itself is not divided into specially strictly delineated parts, corresponding to specific genes, but its particular parts, which are distinguished by the order of alternation of the three bases, can be, as it were, the template for the synthesis of protein molecules (gene products).

This interpretation of the genetic functional differentiation of chromosomes, which is developed on the basis of a study of the structure of the DNA, conforms well to the new interpretations of the gene which we examined in another article, and which were worked out on the basis of facts obtained from a study of the phonomena of "position effect" and "psudoalelism" by means of hybridological analysis.

The above-outlined interpretation of the role of DNA in the replication of nucleoproteins of chromosomes is satisfactorily grounded on factual observations of the structure of the DNA, and for this reason can serve as an acceptable hypothesis which provides a solution to the problem by first approximation. Independent of possible modifications in the future in accordance with new experimental data, which will no doubt be obtained in the near future and which will give us more profound information on the structure of nucleic acids and protein and their interconnection and biological function, we must admit that this hypothesis already includes a number of really important and sufficiently well established

concepts. It may stimulate the search for new ways to solve thorny problems in genetics and contribute to overcoming nihilistic attitudes toward the gene theory of heredity by setting up new research and discovering possible errors in observing certain facts or errors in their interpretation.

In conclusion we shall try briefly to inspect certain new data on the biology of the fertilization of plants which relate to thorny problems in modern genetics.

In the study of the biology of fertilization, Soviet investigators in recent years have had no small success in the following problems: selectivity in fertilization; interaction of pollen in pollination by pollen mixtures; role of autogenous and foreign pollen in the restoration of progeny by self-pollinating and cross-pollinating plants; biological role of repeated pollination; effect of repeated pollination; effect of the age of the reproduction elements on the properties of the progeny; importance of the amount of pollen applied; effect of self-pollination on the hereditary properties of hybrids; biological role of cross-pollination, in particular, its effect on fertility and vitality in inbreeding, ordinary self-pollination, and in remote hybridization; the problem of the multiple effect of fertilization in plants and analogous problems in the biology of animal fertilization.

Of particular interest is the problem of the biological effect of pollination by pollen mixtures and the mechanism of the interaction of pollen. Let us cite some examples from our work. For instance, in research with different varieties of hard and soft wheat it was determined that although wheat is a typical representative of the group of self-pollinating plants, in strict self-pollination (under isolation) it gives much worse results than with natural pollination when the possibility is not excluded that the pollen from other plants fall on the stigma. In the first instance, as compared with the other, there is a reduction in the precentage of seed germination and a reduction in absolute weight.

An analysis of control data showed that the difference in the mentioned variants with regard to seed germination is caused by the presence in one of them and the absence in the other of the possibility of supplementary cross pollination. Careful observations of a great number of plants of many wheat varieties showed that the structure and biology of flowering of the wheat flower contribute to supplementary cross pollination, the possible frequency of such cases being marked by the fact that the number of open flowering blossoms in wheat during the entire blooming period is 60-90% of the total number. With supplementary artificial pollination of wheat we find a positive result which indicates the presence of interaction of autogenous and foreign pollen in plants.

Analogous data were obtained from research with tomatoes and other self pollinating plants which have practical importance for seed production of these plants.

For rye and in part for other cross-pollinated plants it has been established that cross-pollination of castrated plants gives poorer results than the pollination of noncasterated plants when the interaction of autogenous and foreign pollen is possible. The real difference between wheat and rye relative to the biology of pollination and fertilization is both in the fact that the first sets seed from its own pollen while the second by cross-pollination, as well as in the fact that these plants (wheat and rye) differ greatly in degree of self-fertility.

An important contribution in solving the problem of the interaction of pollen was the discovery of the biological effect of foreign supplementary pollination, i.e., the addition of pollen of other species to pollen of the maternal species. This effect is seen most clearly in inbreeding of plants with the application of supplementary pollination with foreign pollen. For example, in rye seeds setting increases in this case 10-12 times by comparison with ordinary inbreeding. Analogous results were obtained in certain other variants of pollination.

It has also been established that the foreign supplementary pollination effect can be observed only when using foreign pollen taken from species related to the maternal (for the grasses, species of the same family) including those which do not cross with the latter. Data obtained give us reason to state that foreign pollen acts only when it germinates on the stigmas of flowers of the plants under investigation. The most reliable mechanism of its action is its secretion of biologically active substances which effect the germination of the pollen of the maternal species and in some cases increase the fertilizing capacity of the latter, and the period of action of the foreign pollen is the progamic phase of fertilization.

Taking into account the data of modern genetics on the role of the nucleoproteins in the phenomena of heredity, it is possible to state that the biologically active substances which aid in effecting the interaction of pollen in the pollination of plants by a pollen mixture and, in particular, in supplementary pollination by foreign pollen, can be represented as high molecular weight compounds of the type of the nucleoproteins or the polymerized nucleic acids; although this does not exclude the physiological role in this process of the low molecular weight compounds of the type of the carotenoids and others. This mechanism of the interaction of pollen in the pollination of plants by pollen mixtures can also serve to interpret known cases of the production in the heredity of hybrids of characters of several types of

copollinators, as well as examples of the effect of multiple pollination on the properties of hybrid progeny of plants which indicate the possibility of the repeated effect of fertilizing elements on the ovum of plants immediately after their fertilization.

SUMMARY

(Translated from the Russian.)

The work contains a survey of the latest data on the role of the intracellular nucleoproteins in heredity, analyzes data on the structure of DNA and RNA, modern concepts of the polymerized nucleic acids as bearers of hereditary information. The conclusion is also drawn that the concept of the structure and function of the nucleic acids, and of the role of DNA, in particular, in the process of the reduplication of the nucleoproteins of the chromosomes, is sufficiently grounded on factual observations to serve as a hypothesis providing a solution to the problem in first approximation. Regardless of the possible modification of this hypothesis in the future in connection with possible new experimental data, it makes it possible to gain deeper knowledge of the structure of the nucleic acids and protein, their interaction and biological function. The hypothesis aims at seeking new ways for solving thorny problems in genetics, keeps us from a nihilistic attitude toward the gene theory of heredity, and facilitates setting up verification experiments and detecting errors in the interpretation of experimental facts.

The article gives a brief review of some new data on the biology of the fertilization of plants, related to thorny problems in genetics and, in particular, to the question of the biological effect of pollination with pollen mixtures and the mechanism of the interaction of pollen in certain species of self-pollinating and cross-pollinating plants. The supposition is expressed that the biologically active substances which assist in effecting the interaction of pollen in the pollination of plants by pollen mixtures, in particular, in supplementary pollination by foreign pollen, can be represented as high molecular weight compounds of the type of the nucleoproteins or polymerized nucleic acids, although this does not exclude the physiological role of the low molecular weight compounds of the type of the carotenoids and others in this process.

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FIGURE APPENDIX

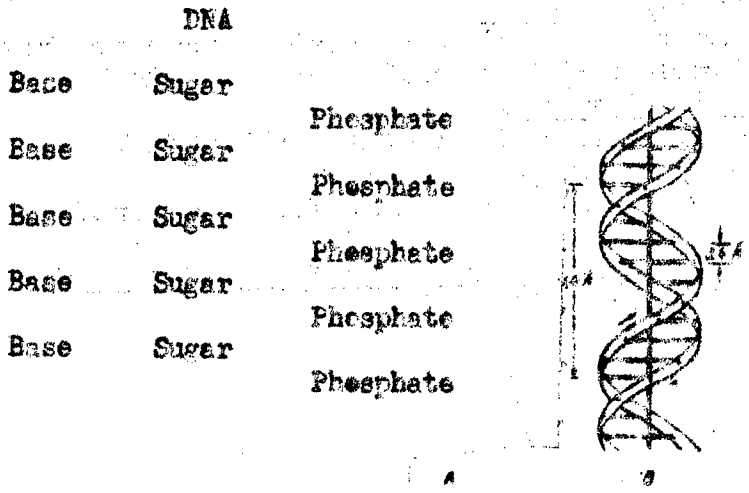

Fig. 1. A--Chemical formula of the a single chain of DNA.
B--Two runs--two phosphate-sugar chains, two horizontal band-pairs of bases which these chains contain at times; vertical lines are eight filaments.

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