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EVOLUTION OF THE GERM-PLASM[1]

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A DEFINITION of terms seems to be the first requisite in a discussion of this subject. By "germ-plasm" we mean a distinctive substance, endowed with all the properties of life, but especially with that of reproduction, which here is, in some measure, unique. Equivalence is an inherent characteristic of organic reproduction, and it holds in respect to the germ-plasm itself; but, whereas commonly the influence of a part is continuously the same, that of the germ-plasm is cyclically different. It involves elements which mark the race and so it may be denominated "racial material." It is customary to distinguish between "germ-plasm" and "soma-plasm," both being nuclear, one concerned with racial processes, the other with those of the individual. This distinction is, however, purely arbitrary and may lead to misunderstandings. Such a distinction was suggested by the presumed functional differences between the macro- and micronuclei of certain Protozoa. But if the germ-plasm is defined specifically as "that substance, or organization, which distinguishes a chromosome complex" then it is essentially the same in both germ and somatic cells. Mere observations tell us that the chromosome complement of germ and somatic cells is one, both being derived by direct descent from that of the original zygote. Finally, and in a more abstract sense, the germ-plasm may be defined as "the temporal record of racial experience." However conceived, it has the properties of continuity, specificity and control of organic processes.

[1] Presented at the University of Pennsylvania Bicentennial Conference, September, 1940.

The term "evolution" signifies a process characterized by progressive, continuous and related change, as opposed to one in which sudden, discontinuous or unrelated modifications occur. Broadly conceived, it includes not only the stages of full functioning but also the ones which may be characterized as formative. The germ-plasm did not always exist. Only when the earth reached a certain balance in temperature, moisture, radiation and other physico-chemical conditions was life possible. Organic evolution is therefore clearly a part of cosmic evolution. All the evidence in our possession indicates that the first organic entities were small and relatively simple. Since probably the most significant attribute of life is that it exists only in unit form, our search for the beginning of organic things leads us necessarily to the conception of minute, simple units. That these may still occur as separate and independent bodies is suggested by the existence of such related organizations as the filterable viruses; that they persist as parts of coordinated aggregates follows from our conception of genes. The simplest of known organisms is relatively so complex that we can not conceive it as coming into existence fully formed. We must believe that it is the result of a gradual development from small and simple beginnings, which, by assumption, had the properties of life in essence. Therefore these were units in a continuous series, perpetuated by the inherent power of reproduction. The only continuous living thing we know is the germ-plasm, and we naturally associate it with these early beginnings. Thus conceived, the germ-plasm of an existing animal has within it the direct descendants of successively added units, which have arisen in response to altered conditions, both within and without a series of organisms. Unit organization, perpetuated in a continuous series, addition of new elements in response to changed conditions, incorporation of these into a coordinated union of higher complexity, and finally the formation of the very complex structure we call a cell summarizes the series of events as we must now conceive them. In turn cells became aggregated into coordinated bodies of almost infinite complexity and variety. Originally the germ-plasm was, according to this view, in immediate relation with the environment. Gradually it was removed further and further from this physical contact until now only such agents as radiations may touch it directly. From the very first stage of its existence the germ-plasm has been directive in its relations. At first simple and applied directly to the materials and conditions of the environment, its influence has become more and more complex, involved and remote from the operations of the organism, particularly in the germ cells. Even further than we have thought, this is true also of the somatic cells. During development more and more coordinating mechanisms, neural and humoral, are formed until finally it would seem that, for the nuclear materials, there remain only a few of the most basic functions. Each type of cell becomes highly specialized through modification of its cytosome, while its nucleus may lose its reproductive power or even disappear completely. For the individual there is then an exaltation of the cytosomic elements and a limitation of the nuclear. Only in the germ cells are nuclear potentialities retained. Retention of this power by the germ cells is made certain by various isolation devices which remove them from participation in differentiation during development.

But since the race is only a succession of individuals how can we differentiate between activities which serve only the single individual and those which concern the group? Naturally, this distinction can not be closely drawn, and, in fact, it is largely temporal. A germ cell of one individual generation, isolated from somatic participation, becomes detached and forms a complete organism of the next generation. By some insulating device the germinal elements within the gonad do not participate in somatic processes, but merely perpetuate themselves. On being removed from this inhibition they are free from the limited rôle of mere germ cells and may perform, through their descendants, all somatic activities. The germ-plasm, the record of experiences to be repeated, is contained in all cells—in somatically included germ cells, there inhibited from full expression; in differentiated somatic cells, limited largely to a single expression; and is completely lost only in cells about to disappear. Distinctions between germ and somatic cells, unless early established by some marked change, as in Ascaris, may therefore be gradually established by specific limitations within somatic cells and by the retention of unaltered capacities in the germ cells. Fixation and limitation of function, it is assumed, is due to changes within the racial material through repeated reactions with a specialized cytosome.

But how are we to gain any practical knowledge of such changes as occur during differentiation and development? Surely only by a comprehensive and detailed study of the germinal material during these stages. Here we note that there is a general pattern in all Metazoa, which at once suggests a basic unity of design and function; also that there are characteristic group modifications of such a character as to indicate that this is progressively increased in complexity in the phylogenetic series. Cytogenetic studies have demonstrated that the germ-plasm is a precise organization of particulate, causal elements which are specific in nature and yet general in their attributes. Which is perhaps to say that of a common series of functions, they show, individually, emphasis upon certain ones of these. Such studies have, however, yielded no knowledge of the method by which these causal elements operate. By limited and experimental investigations it may be possible to learn the individual operation of this mechanism, but knowledge of its phylogenetic development can come only from a careful comparison of its expressions in a group of organisms. But for this there is first required a careful analysis of the fundamental relations of organisms so that it is possible to evaluate the differences which characterize groups.

Every organism is a fully developed and coordinated unit. In this measure all organisms are alike. At the same time they differ, even individually. In estimating phylogenetic relationships what relative values have these elements of likeness and unlikeness? Since organisms are completely specific, structurally and functionally, at every stage of development, these qualities must exist even in the one-cell stage. When therefore we seek to discover, in the causal mechanism of the chromosomes, differential conditions between taxonomic groups, what shall we look for? Obviously from the considerations just stated, great differences can not obtain. We see indeed that they do not. Except for the lowest forms all organisms are composed of cells, and these are of a limited number of kinds wherever found. For each distinctive function there is a common form of appropriate cell. The visible difference between members of these types is in no way commensurate with the phylogenetic standing of the organisms in which they are found. High development and perfect coordination of structure and function occur at every taxonomic level. Since, then, individual structural units, as such, are no measure of phylogenetic advance, we must seek elsewhere for a criterion, and the course of individual development offers suggestions. There we witness, in addition to the differentiation of cell types, two suggestive phenomena, *i.e.,* increase in the number of elements, and second in their interrelations, which mean greater complexity.

Such a situation carries with it the need for more extensive and perfect measures of control and correlation. This coordination is primarily provided by the nervous system; therefore in higher forms there is a more extensive development of this system. However, for purposes of regulating internal functioning, this control system does not anywhere differ widely. It is only when the level of ideation and reason is reached that a new problem presents itself, and we have to inquire whether human nerve cells develop new attributes, or whether higher functioning results from increased and bettered interrelations between them. Practically that is not a problem for those who seek an explanation of the relation between the causal mechanism of cells and developmental processes, for these do not immediately involve the subsequent phenomena of ideation. Our problem may accordingly be stated thus: In the presence of a vast series of structurally different types of organisms, all performing a common series of functions, where shall we look in the causal mechanism of the cells for evidences of the required differences? Practically put—does increased complexity of structure in the phylogenetic series, as in individual development, involve more elements as well as increased extent of interrelationships between them? If, as seems apparent, each gene, representing a discrete unit of the determinative mechanism, corresponds to the incidence of some recognizable character in the completed organism, then it would logically follow that more characters mean more genes. This is probably a correct inference, in general terms, but at the same time we have to recognize the possibility of another alternative. If, as is certainly true, each form of organism is completely functional, then it possesses all the needed properties of an organism. All that can happen toward progress is a refinement in the operation of these universal functions. Refinement, we find, commonly involves increased complexity in the mechanism which performs organic functions. Therefore apparently entirely new structures are only altered expressions of previously existing mechanisms. For instance, devices for producing motion in Metazoa consist, usually, of contractile elements attached to skeletal members. Motion results when muscles contract and force the skeletal structures to react against the opposing medium. Depending upon whether this medium is air, water or a solid substratum, appropriate mechanisms develop. In different cases if the same structural elements are involved we speak of "homologues"; if a similar device in form involves different structural elements we refer to them as "analogues." When only the contractile element is involved, greater diversity comes in, and this is further intensified when the usual paired members are replaced by a single median one. In view of the almost infinite range of motor mechanisms developed by organisms, it does not seem possible that they could result from the permutations of a common series of controls in the developing whole. At the same time when we recall that, simple or complex, they are each the result of an infinite number of repeated reactions between organisms and a given environmental requirement, the possibility of multiple modifications of a basic system must be considered.

Perhaps the problem might be stated specifically in this way: Since all organisms exhibit a common series of functions, and since functions are performed under the control of a recognizable series of agents within the chromosomes, there must exist a nuclear mechanism common to all organic types. Logically, this would follow, and observation tells us that, at least in its major features, such a situation does exist, for cellular structure and behavior are essentially the same wherever found. Moreover, in the earlier and relatively simpler processes of development, strong likenesses prevail through all forms. But beyond this, what are we to expect? Does each advance in complexity, each new structural element mean additional gene controls or are they due to what might be called the better education of members of an existing system through new experiences? When it appeared that each character was due to the influence of a particular control there could be but one answer to this question, but now that it is known that each structure results from the operation of the entire integrated system, in which genes are merely differentiators, producing successively different results as development proceeds, then the picture is not so clear and simple. There must also be considered the facts that the cellular mechanism is always much the same, the number and size of the chromosomes are independent of phylogenetic stages, that different results follow upon changes of position of the genes in the series, and that probably the result of gene action varies with the time of its incidence. All these considerations emphasize the need for a most careful study of all elements of the problem. Present knowledge would suggest, certainly, the existence of a basic and prevalent causal mechanism and at the same time the probability of the addition of new members in response to the demands of new conditions. Since, however, each gene modifies the action of the whole system, and therefore produces many effects, an equal number of additional elements would not seem to be required. The course of evolution indicates that any change, to become established, requires innumerable embodiments and great periods of time. Above all things it appears that any successful change must be completely conformable to conditions within the system and also to those in the environment. The participation of chance or accident is strictly excluded. It is true that biparental reproduction intrinsically implies variation, but this is always within definite limits and concerns the permutations of existing elements rather than the addition of new ones.

These considerations are of a very practical character when programs of study are concerned. It is a truism that we see what we are looking for, and this is particularly so of microscopical studies. Therefore, as students of cytogenetics we are much concerned to know whether we should seek additions to the chromosome mechanism or whether we should turn our attention toward the detection of modification within a prevailing type. For many years my students and myself have concentrated our studies upon the conditions found in the germ cells of one family of insects—the Acrididae—seeking to establish the relationships existing between observable changes in the structure and behavior of chromosomes and the associated body characters. Many of these have been noted and found to be constant under given conditions. They involve varied features of chromosome structure, behavior and relations, but represent, not additions of new things, but modifications in a persistent system. They involve such matters as differences in chromosome associations and in fiber attachment, variations in relative time of extension and concentration of individual chromosomes, forms and sizes of chromosomes, relations to chromomere vesicles, etc.

This Orthopteran family is a distinctive group, with clear and sharply marked characters. Such variations of form as exist in subfamilies, genera and species are due to modifications of proportions and relations of the members of the family complex of characters. Logically, therefore, there would not be expected in the control mechanism of development any marked changes or any additions, and these are not found. The picture here is entirely consistent with our present assumptions in cytogenetics. It is a question, however, as to what might be found in comparing the conditions in this limited and well-defined animal group with others of very diverse nature. Without any guiding principle to indicate the best method of investigation, it has seemed wisest to learn as definitely and fully as possible what we can of the modifications shown in one organic group. After enough correlations between taxonomic characters and germ-cell structure have been studied, there will doubtless emerge the outlines of some principle underlying all the observed conditions, and eventually this will become generally applicable. However difficult such studies of broad comparative character may be, they are absolutely essential to an understanding of the true nature of living processes. No amount of pseudo-philosophical speculation, based upon hasty and imperfect studies, can take their place.

We are certain of the continuity of the germ-plasm and of its general nature as the material record of racial experiences. It seems evident that the hope for an understanding of racial and individual development waits upon a fuller knowledge of the nature and behavior of the visible elements which embody the germ-plasm; and upon the inferences concerning the activities of the ultimate conceptual units revealed by genetical and embryological studies. Only long, continued, systematic, comparative, cytological studies can provide the needed information. A continuation of the exceedingly fruitful cooperation between cytologists and geneticists, which has marked the years of the present century, will, in time, inform us of the intimate nature of the germ-plasm.