The Germplasm and its Architecture.¹

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THE individuals of a generation die, but life is transmitted to its successor through the exercise of the function of reproduction. This handing on of the torch of life, in the more highly organised forms, consists in the union of the gametes, egg and sperm, to form the zygote, the new individual and the next generation, specific to the highest degree and embodying all the possibilities of individual development and of racial perpetuation. Each of the sexually distinct parents contributes but a single cell, so minute as to be far beyond the limits of the unaided eye, yet these gametes are the only material link between the generations, and across this, the narrowest of bridges, everything organic that one generation can receive from its predecessor must pass. The zygote exhibits none of these details of structure and of function which, when the individual has assumed its definitive form, will enable the observer to describe and to classify it, yet in this fertilised egg there must surely be something that predetermines much of the individual's future morphological, physiological, and psychological limitations.

That offspring do in general resemble their parents is so familiar a fact that its significance is either overlooked or over-emphasised. It has been accepted, without wonderment, that a multitude of characters is faithfully transmitted from generation to generation; that like tends to beget like; that it can be predicted confidently that every individual conceived will sooner or later exhibit those details of form and of function which characterise the species, the race, even the family to which it and its relatives belong. The doctrine of homogenesis still satisfies the biologist. It has equally long been recognised that no son is the 'carbon copy' of his father, that each individual is the first and the last of its identical kind; that indeed variation is universal. It may be assumed that out of accumulated anecdotes concerning the similarities and dissimilarities in characterisation exhibited by related individuals, there soon arose the notion that in their distribution there were suggestions of an orderliness, a regularity, that many characters were indeed being inherited and that the mode of their inheritance was not a haphazard affair but was surely subject to certain rules. Thus it would soon become inevitable that the human mind, in its inherent desire to trace and to describe order in Nature, should seek some mechanism which in its functioning could account for this observed orderliness. A consideration of the observed facts of organic inheritance enabled man to form a general theory of inheritance, a speculative thought-model of what the architecture of the hereditary material might be.

The question to be answered was, "How is it that like begets like?" In the latter half of the eighteenth century it was customary to appeal to

vires formativæ, hereditary principles, hereditary tendencies, by the aid of which the seed grew into the likeness of its parents. In an age when materialism was not gross and when the microscope was most imperfect, it was inevitable that scientific men should resort to merely verbal explanations, which at best were gestures of respectful ignorance and of admiration. But improvements in techniques and additions to knowledge quickly eroded such purely metaphysical hypotheses.

During the seventeenth, eighteenth, and the earlier part of the nineteenth centuries, the most favoured explanation of the facts of inheritance and of development was some form of the theory of preformation and evolution. According to this, the egg, or the sperm, contained within it a perfect but miniature model of its parent, preformed though invisible, which required only to become unfolded, evolved, in order to reveal itself. This theory of ontogeny was extended to include phylogeny also, and it was taught that within this miniature was a second, and within this a third, and so on in increasing numbers until all the future generations were supplied; within mother Eve it was estimated were some two hundred thousand million homunculi, one within the other, like the components of an infinite juggler's box of which there is no end. Ovist and animalculist debated violently, yet both were agreed in this, nothing was generated, and what was thought to be generation was but merely the enlargement of that which had pre-existed in an invisible form. Haller it was who declaimed, "Es gibt kein Werden"—there is no becoming—and the theory held sway until it staggered under the blows of Wolff's demonstration of the gradual development of the apparently simple into the manifestly complex. Wolff demonstrated that development was epigenetic, taking the form of a true series of transformations, and was not merely the enlargement of what previously had been invisible.

Just, however, as the preformatists could not easily account for the origin of their miniatures, so Wolff was unable to explain the demonstrated fact that the end-result of epigenetic development was an individual similar in characterisation to its parents, save by an appeal to the aid of a *vis corporis essentialis* by which the plastic organic material controlled its own destiny. Wolff was not unique in this; it has ever required the severest intellectual ascetism to banish from the scientific mind this tendency to explain by an appeal to a metaphysical conception, and since his time this inherent force has been recreated by many who have been at pains to give it another name; purposive striving, emergent evolution, creative evolution, are examples, for man ever creates his gods and imprisons them in the machines that he invents.

These theories in their sequence were signposts along the road we are travelling, for out of them emerged the firm conviction that the future in-

¹ Evening discourse delivered at the Leeds meeting of the British Association on Sept. 5.

dividual must be materially implicit in the gamete, and that not only did this single cell contain the rudiment of the next generation but also those of all succeeding generations as well. Soon the conception arose that the germ-cells were distinct from the rest of the body; that they were to be looked upon as centres of contributions from the different parts of the body. The central problem of heredity came to be that which was concerned with the manner in which the various heritable qualities of the individual got into the germ-cells produced by that individual. Theories of pangenesis, which had flourished from the time of Democritus, were revived and extended but soon gave ground as the conception of germinal continuity, finding support in the newer facts of cytology, gripped the mind. It had been shown that in certain instances it was possible to distinguish between those cells of the segmenting zygote which were destined to become the reproductive organs and those which were to become the body of the individual. The distinction between the ontogenetic and the phylogenetic became more and more emphasised as time went on, and soon it became evident that in the fact of material continuity between the reproductive elements of generations must be found the solution of the problem as to how it is that like tends to beget like.

To Weismann is mainly due this replacement of pangenetic theories by genetic. He taught that the germ-cells were to be regarded merely as parts of an unbroken line of germplasm, the bearer of the heritable qualities; that this germplasm, in certain circumstances, usually the union of two of its constituent germ-cells, frothed up and produced a great excrescence, the somatoplasm, the body of the next generation, and continued its existence therein; that the germplasm was immortal, the body mortal; that the germplasm had existed from the very dawn of life, whereas the body was formed afresh in every generation; that when the zygote divided, some of the resulting cells were set apart at once and took no further part in the building of the body, but remained, later to become the germ-cells of the individual.

Weismann postulated that what is actually continuous is the germplasm of definite chemical and specific molecular constitution, that a continuity of actual germ-cells is rare, but that a continuity of intact germplasm is the rule. According to such a genetic theory of inheritance, an individual is like its parents, not because it is produced by them but because both parent and offspring are produced from the same stock of germplasm. The somatoplasms of father and son are developments at different times from one and the same continuous stream of germplasm. Organic inheritance, all that the individual possesses in virtue of the hereditary relationship, implies a rhythmical repetition of a definite, and on the whole, similarly repeated series of events leading to the production of an individual which liberates germ-cells capable of initiating the same process.

The problem of organic inheritance thus became

restated. It was now concerned with the manner in which the heritable qualities of an individual were represented in the germ-cells which in their union produced the individual; the need for critical experimental investigation of the problem of heredity and variation was recognised and the stage was set for the re-entry of Mendel. When the records of his work of some forty years before were brought to light in 1900, it was recognised that in them was confirmation and extension of the essentials of Weismann's hypothesis, but that no longer was it necessary to invoke a hypothetical mechanism for the distribution of the hereditary factors, for by this time independent cytological investigation was disclosing a satisfactory mechanism within the living cell.

Mendel had taken for his problem the question as to the exact manner in which the definite and true-breeding varieties within a species are related one to the other. He considered the individual not as a unit in inheritance, but concentrated his attention upon the mode of inheritance of pairs of sharply contrasted characters. The method he adopted was that of hybridisation, and he kept accurate pedigree records showing the ancestry and the characterisation of each individual. He counted the number of individuals in each generation and the numbers of dissimilar kinds, and was able to give an exact mathematical statement of his results. His was the first attempt to reduce the phenomena of inheritance to a measurable basis, for he employed the exact quantitative methods that scientific discipline demands. The man, the method, and the material made discovery certain. He found that in the case of every one of the seven pairs of contrasted characters of the culinary pea with which he dealt, the mode of inheritance was the same. Out of his experimentation there emerged clearly the verifiable fact that when one or more pairs of alternative characters are involved in a breeding experiment, there is in the second hybrid generation an orderly reappearance of these characters in definite numerical proportions.

Mendelism is a scientific theory relating to the distributive mechanism of organic inheritance which, like most other hypotheses of this kind, postulates the existence of a number of individual particles of substance-factors—in the germplasm—each of which in its action influences the development of some particular character. It does not require that these particles shall be concerned solely with hereditary transmission. It demands that in respect of any particular character the individual must receive from its parents, one from each by way of the gamete, two factors, either similar or dissimilar according to whether or not in the respect of this character the parents were alike or different. It requires that when the individual in its turn elaborates its reproductive cells, into each ripe gamete there shall pass one or other, but not both, of these factors. The gamete can contain but a single set of factors; the zygote a double set, and of these one set shall have been received from each parent. Thus the zygote may be hybrid in respect

of a character or characters since one or more pairs of factors in its constitution may consist of dissimilar mates: the gamete, on the other hand, cannot be hybrid, since factorially it is constitutionally simplex. The theory postulates that the association of dissimilar factors in the zygote is not attended by any adulteration effect upon them.

The Mendelian method of character analysis, ardently pursued during the first decade of the twentieth century, made it perfectly clear that if there were actually such a thing as a material basis of organic inheritance, if the germplasm did exist in fact, then in the cell there must be some unit which is structurally continuous through all cell divisions from the first cleavage of the fertilised egg to the liberation of the ripe gametes by the resulting individual; that these units must be present in duplicate in the zygote; that they must segregate into single components at some point before the functional gametes are finally formed, and that in the zygote these units must be present in pairs.

As was to be expected, it was not long before results were obtained from breeding experimentation which demanded extension and modification of the theory as originally promulgated by Mendel. Mendel's second law of the independent segregation and recombination of factors, for example, was found by Bateson and Punnett not to apply invariably. In several instances this free assortment was found to be more or less absent, and characters in their transmission from generation to generation exhibited the tendency to remain together. In appropriate matings and in those cases in which such linkage was evidenced, linkage

proved to be incomplete and the percentage of recombination classes was found to be constant under controlled and stable conditions of experimentation and to be characteristic of a particular mating. With greater experience came the power to predict the percentage of such recombination classes in any experiment involving characters which exhibited this linkage relationship and such prophecy has been abundantly verified, and no exceptions so far have occurred to the rule. Upon this general result the hypothesis of the linear arrangement of factors within the germplasm is based.

As a result of this more recent experimentation, the factorial theory of organic inheritance has become modified and greater have become the demands which must be made upon the germplasm. It is now generally accepted that the hereditary characters are referable to paired elements in the germplasm which are held together in a definite number of linkage groups; that the members of each pair of elements separate when the germ-cells mature, in accordance with Mendel's first law, and in consequence each gamete comes to contain one set only; that the members of different linkage groups assort independently, in accordance with Mendel's second law; that an orderly interchange—crossing-over—takes place at times between the elements in corresponding linkage groups; and that the frequency of crossing-over furnishes evidence of the linear order of the elements with respect one to another. The germplasm in its nature and architecture is now required to be such as can accommodate the facts of linkage, of crossing-over, and of the linear order of factors.

(To be continued.)

Standards of Performance of Heat Engines.

THE discovery of the interchangeability of heat and mechanical work has been followed by progressive efforts to attain the maximum ratio for the efficiency of conversion of the former into the latter. It is significant of the limitations which attach to such conversion, and the remoteness of a complete solution, that after a century of progress we are still striving to express this efficiency as the ratio of a ratio. This reflection is suggested on perusal of the report recently issued by the Committee of Heat Engine Trials under the auspices of the Institution of Civil Engineers, one of the objects of which is to determine a suitable standard of performance, which shall have a known efficiency ratio, and to express the actual performance of an engine as a ratio thereof.

The limitations are well recognised. There are first of all those of a thermodynamic nature, which prescribe that within given limits of temperature the defect from perfect conversion cannot be less than the ratio of the minimum to the maximum absolute temperature; in other words, the maximum possible efficiency is given by $(1 - T_2/T_1)$; this is known as the Carnot efficiency, belonging to a perfect heat engine working on such a cycle that

heat reception takes place at, and only at, the maximum temperature T_1 , and heat rejection solely at the minimum temperature T_2 .

It might be thought at first that the quest for an intermediate ideal could end here and that this simple expression for the maximum efficiency thermodynamically possible would answer the requirements. But there are further limitations of a practical nature on account of which the Carnot efficiency ratio is still a long way removed from what can be obtained in practice, and it is preferred to soothe our baffled ambition by adopting a lower standard more in keeping with what can actually be realised.

The nearest approach to the Carnot cycle is made in the steam engine when using saturated steam. Here, except for the heating of the feed water up to boiler temperature, the whole of the heat reception takes place at a constant temperature, and, if we assume no losses by friction, radiation, etc., the whole of the heat rejection takes place at condenser temperature. This is known as the Rankine cycle. The only departure from the Carnot cycle is in the replacement of the compression stage by the simpler process of elevating