CHAPTER XI

HISTORY OF THEORIES OF HEREDITY AND INHERITANCE

"Like leaves on trees the race of man is found,
Now green in youth, now withering on the ground;
Another race the following spring supplies,
They fall successive and successive rise."

ILIAD (*Pope's Translation*).

[The same may be said of the succession of theories of heredity, but, in both cases, there is a persistent living tree, to whose growth all the leaves contribute.]

§ 1. *What is required of Theories of Heredity and Inheritance.*

§ 2. *The Old Theories of Heredity.*

§ 3. *Theories of Pangenesis.*

§ 4. *Theory of Genetic or Germinal Continuity.*

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§ 1. *What is required of Theories of Heredity and Inheritance*

THE main object of a theory of heredity is to express in as simple terms as possible the nature of the genetic relation which binds generations together, and to interpret the facts of inheritance in terms of this relation.

The Uniqueness of the Germ-Cells.—The first and chief problem is to account for the material basis of heredity—*i.e.* in all ordinary cases, for the germ-cells. What is their origin and history? what relation have they to the parental body which bears them, from which they are liberated? what relation have they to the germ-cells of the body into which they develop? Or, more generally, in what way are they peculiar? how do they differ from ordinary cells? to what do they owe their unique reproductive power? In short, what enables them to develop into organisms like the parent-organisms? To these questions it is possible to give a satisfactory answer.

The Architecture of Inheritance.—The second problem is of a different nature, and much more difficult. In some way, every one must admit, the germ-cells or gametes are potential organisms. Without any aid except that afforded by an appropriate environment, they can develop into complete organisms. In some way, the organism, the inheritance, lies *in posse* in the germ-cells. Can we form any image of this? Can we construct any hypothetical scheme of the manner in which the inheritance is organised within the germ-cells? Chemists frame hypothetical conceptions regarding the structure of chemical molecules, and judge of the validity of these by their usefulness in formulating the changes which the molecules undergo in certain conditions; physicists make similar mental pictures—imaginary models—of the constitution of atoms and so on. Can biologists do the same in regard to the material basis of inheritance?

This is the fundamental problem of inheritance, and it can only be approached indirectly. The organisation can never be seen or verified; all the complexities in germ-cells which microscopic analysis reveals are not more than the rough outlines of the real edifice—the edifice which the scientific imagination must build. But the speculative construction is not left to irresponsible fancy; it must be such that it corresponds to and enables us to formulate the visible and measurable facts of inheritance, and the processes of development. It must be harmonious with the large generalisations of inheritance, such as Mendel's law or Galton's law; it must also be harmonious with every peculiar phenomenon, such as resemblance to a remote ancestor.

Theory of Development.—A careful study of the history of the germ-cells enables us to form *a general theory of heredity*, enables us to understand how the germ-cells have their peculiar reproducing power.

A consideration of the facts of inheritance, both general and special, enables us to form *a general theory of inheritance—i.e.* a speculative thought-model of what the architecture of the germinal material may or must be.

But it is also necessary to try to form some picture of what occurs during development. The inheritance is in some way expressed, the potentialities are realised, the legacy is cashed—can we form any image of what occurs ? As before, our image may not be actually what occurs, but it must not contradict anything that occurs, and, more positively, it must help us to formulate what occurs. This is the business of *the theory of development.*

Other Theories are involved.—The result of development is always an organism more or less like the parent, but the completeness of hereditary resemblance is usually affected by the occurrence of variations, sometimes minute and quantitative, sometimes large and qualitative. It is evident, therefore, that theories of heredity, inheritance, and development must be supplemented by *a theory of variation.*

Nor is it possible to abstract the theory of heredity and inheritance from the theory of growth, reproduction, and sex; from the theory of environmental and functional influences which we sum up in the term "nurture"; from the theory of the correlation of psychical and corporeal life; and from the general theory of organic evolution in which all biological theories are combined.

But while we recognise that abstraction of particular problems is merely a device to facilitate clear thinking, and by no means without the counterbalancing dangers which all abstraction involves, we propose in this chapter to restrict our attention to the theories of heredity and inheritance, and to give a general historical retrospect.

It cannot be said that this historical retrospect leads us to any complete and satisfactory interpretation of all the puzzling facts which are covered by the word "heredity," but it will indicate some of the main attempts which have been made, and which of these are most promising. We must still recognise the justice of Herbert Spencer's words :

"A positive explanation of heredity is not to be expected in the present state of biology. We can look for nothing beyond a simplification of the problem, and a reduction of it to the same category with certain other problems which also admit of hypothetical solution only. If an hypothesis which certain other wide-spread phenomena have already thrust upon us can be shown to render the phenomena of heredity more intelligible than they at present seem, we shall have reason to entertain it." *

§ 2. *The Old Theories of Heredity*

There have been many attempts at theories of heredity and inheritance, but it is not profitable to say much about the earlier ones, most of which were theological or metaphysical rather than scientific. It will be seen, however, that shrewd enough ideas are sometimes hidden in the old theories, whose phraseology no longer appeals to the scientific mind.

(*a*) **Theological Theories.**—In olden times the idea was prevalent that the germ of a new human life was at conception possessed by a spirit, which thereafter became responsible for development. As it is not so very long ago (1760 or later) that even digestion was explained as the work of a spirit, it need not surprise us that development was relegated to a similar unverifiable efficiency. Sometimes the spirit was, so to speak, of second-hand origin, having previously belonged to some ancestor or to some animal. The idea of successive reincarnations has had many expressions in the West as well as in the East.

* Herbert Spencer, *Principles of Biology*, vol. i. (1st ed. 1863).

So far as the idea persists in the minds of civilised men, it is so much purified and sublimed that, if it does not appeal to the student of science as what he would call true, it is at least such that he cannot wisely call it false. For we believe in mosaic or ancestral inheritance, and though we know that this has a definite material basis, we have no warrant for denying that this has also its metakinetic or spiritual aspect. In any case, there is more than a metaphor in such phrases as "the hand of the past," or "the beast in the man."

(*b*) **"Metaphysical" Theories.**—For a time, especially in the latter half of the eighteenth century, it was the custom to appeal to *vires formativæ*, "hereditary tendencies," and "principles of heredity," by aid of which the germ was supposed to grow into the likeness of its parents. It was in part the old story of explaining the working of the clock by "the principle of horologity," and in part a pedantic way of saying "We don't know."

Nor need we sneer at our predecessors in this respect, for the tendency to resort to verbal explanations is hardly to be driven from even the scientific mind except by severe intellectual asceticism. And in so far as it expresses a respectful ignorance, a consciousness of the complexity of the problem, an awareness that we have still to use x (the power of life) in our biological equations, such "metaphysical" mist is perhaps preferable to the frost of a materialism which blasts the buds of wonder and gives an illusory clearness to the vision.

Although William Harvey (1578–1657), working "in the harness of Aristotle," maintained that "all animals are in some sort produced from eggs," he at the same time believed in spontaneous generation as firmly as his master did. Although he maintained that the living creature begins in an apparently simple *primordium* in which "no part of the future offspring exists *de facto*, but all parts inhere *in potentia*," he was quite unable to suggest or give any scientific account of the *primordium* and its powers of development. He was forced to fall back on a metaphysical conception of inheritance and development. "Not only is there a soul or vital principle present in the vegetative part, but even before this there is inherent mind, foresight, and understanding, which, from the very commencement to the being and perfect formation of the chick, dispose and order and take up all things requisite, moulding them in the new being, with consummate art, into the form and likeness of its parents."

(*c*) **"Preformationist" Theories.**—During the seventeenth and eighteenth centuries, and even within the limits of the nineteenth, a theory of inheritance and development prevailed, according to which the germ (either the ovum or the sperm), contained a miniature organism, pre-formed though invisible, which only required to be unfolded ("evolved") in order to become the future animal.

Moreover, the egg of a fowl contained not only a micro-organism or miniature model of the chick, but likewise, in increasing minuteness, similar models of future generations. Thus the rash theorists pointed out that Mother Eve must have included 1,543,657—or, according to another computation, 200,000 million—homunculi; and, what was still more rash, they *figured* the miniature homunculus which lay within the sperm. The "ovists," who held that the ovum contained the miniature, did battle with the "animalculists," who supported the claims of the sperm; but both schools agreed in the general idea, that microcosm lay within microcosm, germ within germ, like the leaves within a bud awaiting successive unfolding, or like an infinite juggler's-box, to the "evolution" of which there was no end.

A thoroughgoing representative of the preformationist school was Charles Bonnet (1720–93), who discovered the parthenogenesis of green-flies, and made many important observations on polyps and worms, but after the failure of his eyesight became more exclusively a speculative thinker. He pondered over generation and development, and ended by almost denying them both. He assumed "as a fundamental principle, that nothing is generated, and that what we call generation is but the simple development of what pre-existed under an invisible form, and more or less different from that which becomes manifest to our senses." In the same way, the renowned physiologist, Albrecht von Haller, said "Es gibt kein Werden" ("There is no becoming"); and it became the fashion to declare that all development was an illusion—only an unfolding or *evolutio*. In contrast to Harvey's conclusion, "The first concrement of the future body grows, gradually divides, and is distinguished into parts; not all at once, but some produced after the others, each emerging in its order," Haller wrote, "No part of the body is made from another; all are created at once."

To the main conception of preformation and unfolding, two subsidiary hypotheses were added: (i) that of *emboîtement*, according to which the germ contains the preformation not of one organism only, but of successive generations; and (ii), that germs occurred scattered throughout the organism, capable of developing into buds, of replacing lost parts, and so forth—neither of them ideas to be laughed at, though their particular expression was necessarily erroneous.

The long-lived theory, variously termed the "preformation theory," the "theory of evolutio," the "mystical hypothesis," the theory of "emboîtement" or "Einschachtelung," or "die Skatulationstheorie," seemed to get its deathblow from Wolff's demonstration (1759) of "epigenesis," or the gradual development of obvious complexity from an apparently simple rudiment. We say "seemed," because the theory, as theories will, persisted long after the deathblow was given. Moreover, though Wolff demonstrated in the chick that gradual becoming which we call development, he had no way of accounting for the uniqueness of the germ-cells, and had to fall back on the postulate of a *vis corporis essentialis*.

Every one allows that the concrete expressions of the preformationist doctrine were crude and false. No microscope, however powerful, will show a miniature model of the future organism lying within either egg or sperm. But, as Huxley pointed out, the preformationists were obviously right in insisting that the future organism must indeed be materially implicit within the germ; and they were also right in supposing that the germ involved the rudiment not only of the organism into which it grew, but of the next generation as well. But the preformationists themselves had not and could not have any understanding of the two elements of truth which we can now read into their theories, and which are at present expressed in modern rehabilitations, (i) in the "evolutionist" conception of inheritance and development, and (ii) in the conception of germinal continuity. It is a mistake to think that either of these is in any direct way affiliated to the preformationist doctrine.

The preformationists stocked the germ with some sort of preformed model, quite unverifiable as they thought of it, and thus made development easy by reducing it to mere unfolding; but they could not account for the preformation.

Yet their antagonists were equally unsatisfactory, for as one of the most scholarly of embryologists, Prof. C. O. Whitman, has said, "Aristotle, Harvey, Wolff, and Blumenbach all traversed the same problem, and landed in the same pitfall. They all faced the question of preformation, and discovering no natural way by which the germ could come ready-made, they insisted that the germ must start anew every time and from the pit of material homogeneity, acquiring everything under the guidance of hyperphysical agencies, assisted by the accident of external conditions."

It was, indeed, a deadlock until concrete investigation disclosed the origin of the germ-cells with their heritage of organisation, until the actual nature of the genetic linkage between successive generations was disclosed.

§ 3. *Theories of Pangenesis*

Passing from theological, metaphysical, and mystical interpretations, we come to a whole series of theories, which are in varying degrees scientific, and may be fairly enough described by the general designation *pangenetic*. They all have this in common, that they seek to explain the uniqueness of the germ-cell by regarding it as a centre of contributions from different parts of the organism.

Early Forms.—We need not delay over the earlier and vaguer forms of this supposition. At such different epochs as are suggested by the names of Democritus and Hippocrates, Paracelsus and Maupertuis, incipient theories of pangenesis—prophecies of Darwin's—were suggested. Thus, Democritus maintained that the "seed" of animals was elaborated by contributions from all parts of the body, and that the constituent parts reproduced in development the organs and parts from which they had originated. Two millennia later, Buffon, of whose speculation Darwin appears at first to have been unaware, again conceived of the germs as mingled extracts from all parts of the body, or as collections of samples from the various organs. If such were indeed the case, Buffon and his predecessors saw no further difficulty, for each contributed sample produced in the development of the embryo a structure like its parental origin. Bonnet (1776) was another who suggested the possibility of molecules passing from the organs of the body to build up the germ.

Spencer's Theory of Physiological Units.—In 1861, the physiologist Brücke emphasised the usefulness of assuming the existence of biological units (*Elementarorganismen*) ranking between the molecule and the cell. In July, 1863, Herbert Spencer adopted a somewhat similar hypothesis of "physiological units," lower in degree than the visible cell-units, but more complex than the chemical molecules. As there is much in his argument which seems useful to-day, we give a brief summary (see *Principles of Biology* (1st ed.), vol. i. p. 181 *et seq.*).

In the growth of an embryo from apparent simplicity to obvious complexity, in the regeneration of lost parts, in the regrowth of a whole by a part, the living substance arranges itself in definite form as some not-living substances do when crystallising out of a solution. In restating the fact, Spencer supposes that certain units composing the living substance possess "polarity," like the chemical units in crystallisation, meaning by "polarity" the unexplained power of definite arrangement. The units cannot be the chemical molecules of albumen and the like, for these do not show the particular kind of differentiation seen in growth; nor can the units be the cells, for the differentiation in question may be seen within the limits of a single cell.

"There seems no alternative but to suppose that the chemical units combine into units immensely more complex than themselves, complex as they are; and that in each organism, the physiological units produced by this further compounding of highly compound atoms have a more or less distinctive character. We must conclude that, in each case, some slight difference of composition in these units, leading to some slight difference in their mutual play of forces, produces a difference in the form which the aggregate of them assumes."

After the judicious sentences quoted on page 398, Spencer goes on to say: "The applicability of any method of interpretation to two different but allied classes of facts is evidence of its truth. The power which organisms display of reproducing lost parts, we saw to be inexplicable except on the assumption that the units of which any organism is built have an innate tendency to arrange themselves into the shape of that organism. We inferred that these units must be the possessors of special polarities, resulting from their special structures; and that by the mutual play of their polarities they are compelled to take the form of the species to which they belong." This is illustrated by reference to the way in which pieces of a Begonia-leaf will reproduce the whole plant. "The assumption to which we seem driven by the *ensemble* of the evidence, is that sperm-cells and germ-cells [better, egg-cells] are essentially nothing more than vehicles, in which are contained small groups of the physiological units in a fit state for obeying their proclivity towards the structural arrangement of the species they belong to." If the likeness of offspring to parents is thus determined, it becomes manifest, *a priori*, that besides the transmission of generic and specific peculiarities, there will be a transmission of those individual peculiarities which, arising without assignable causes, are classed as "spontaneous." So far, in our quotations, there is no distinct suggestion of the central idea of pangenesis nor of the transmissibility of modifications.

But Spencer goes on to say: "That changes of structure caused by changes of action must also be transmitted, however obscurely, from one generation to another, appears to be a deduction from first principles—or if not a specific deduction, still, a general implication. . . . The units and the aggregate must act and react on each other. The forces exercised by each unit on the aggregate, and by the aggregate on each unit, must ever tend towards a balance. If nothing prevents, the units will mould the aggregate into a form in equilibrium with their pre-existing polarities. If, contrariwise, the aggregate is made by incident actions to take a new form, its forces must tend to re-mould the units into harmony with this new form; and to say that the physiological units are in any degree so remoulded as to bring their polar forces towards equilibrium with the forces of the modified aggregate, is to say that when separated in the shape of reproductive centres, these units will tend to build themselves up into an aggregate modified in the same direction" (p. 256). That is to say, representative physiological units of the body congregate in vehicles which we call ova and spermatozoa, carrying with them, on their journey to form a new generation, some definite and representative results of the modifications acquired by the parental body.

The physiological units may be compared to a band of travellers who found a settlement, who build houses and arrange many matters according to their "character," "tendency," "individuality," "polarity"—phrase it as one will. In course of time their constructed aggregate is modified by circumstances, by incident forces of war, want, weather, and the like, and the characters of the units are also modified; subsequently, some of them gather into "reproductive centres," which establish new aggregates, largely after the likeness of the first, and yet modified by the experiences endured.

On *a priori* grounds, this view seems not without plausibility, but Spencer's theory had to yield before the *fact* of germinal continuity.

Darwin's Theory of Pangenesis.—The best-known theory of this class is, of course, the "provisional hypothesis of pangenesis" suggested by Darwin in his *Variation of Animals and Plants under Domestication* (1868). The chief suggestions of this theory are well known to be as follows:

(1) Every cell of the body, not too highly differentiated, throws off characteristic gemmules;
(2) These multiply by fission, retaining their characteristics;
(3) They become specially concentrated in the reproductive elements in both sexes;
(4) In development the gemmules unite with others like themselves, and grow into cells like those from which they were originally given off, or they may remain latent during development even through several generations.

We do not know whether Mr. Darwin had seriously considered Mr. Herbert Spencer's hypothesis of "physiological units," but, as Prof. Ray Lankester points out, the hypotheses might be called complementary. "The persistence of the same material gemmule and the vast increase in the number of gemmules, and consequently of material bulk, make a *material* theory difficult. Modified force-centres, becoming further modified in each generation, such as Mr. Spencer's physiological units, might be made to fit in with Mr. Darwin's hypothesis in other respects" (Ray Lankester, 1870, p. 32). "In fact, in place of the theory of emission from the constituent cells of an organism of material gemmules which circulate through the system and affect every living cell, and accumulate in sperm-cells and germ-cells, we may substitute the theory of transmission of force, the two theories standing to one another in the same relation as the emission and undulatory theories of light."

But we fear that this suggestion has only prophetic value, for we are not yet in biology in a position to utilise ideas of "modified force-centres" or "transmission of force." We must creep along with the slippery clue "metabolism" in our fingers!

One impression, however, we must emphasise—namely, that for the time Darwin's "*provisional* hypothesis of pangenesis" had all the merits of a warrantable scientific hypothesis, and had the marks of that insight of genius which the illustrious author was wont to deny in his humble conviction that "it's dogged as does it."

"Mr. Darwin wished to picture to himself, and to enable others to picture to themselves, a process which would account for (that is, hold together and explain) not merely the simpler facts of hereditary transmission, but those very curious though abundant cases in which a character is transmitted in a latent form, and at last reappears after many generations, such cases being known as 'atavism,' or 'reversion'; and again, those cases of latent transmission in which characteristics special to the male are transmitted to the male offspring through the female parent without being manifest in her; and yet again, the appearance at a particular period of life of characters inherited and remaining latent in the young organism." *

* E. Ray Lankester, 1890, p. 279; *Nature*, July 15th, 1876.

Jäger's Theory.—The next theory—Jäger's—is difficult to summarise, partly because of its technical character, partly because the author does not appear to be quite consistent in his statement of it at different times. The main points, under the present section, are as follows:

(1) Each organ and tissue contains, along with the molecules of its albumen, a specific "scent-stuff" (Duft- und Würzestoff).

(2) In hunger and similar experience the albumen liberates the "scent-stuff," which penetrates through the body as fatty acids, ethers, etc.

(3) These are specially attracted to the reproductive cells, which, when mature, are thus specialised by the reception of scent-stuff, and have in their protoplasm *vires formativæ* enough to reproduce a new organism like the parent.

It will be seen later on that this hypothesis of chemical pangenesis *is not the most important contribution made by* Jäger to the theory of heredity.

Galton's Modified Theory of Pangenesis.—From experiments on the transfusion of blood, Mr. Francis Galton was led to conclude that "the doctrine of pangenesis, pure and simple, is incorrect." But he did more than urge serious objections against Darwin's theory; he formulated one of his own, to which, with the exception of Prof. Herdman, subsequent investigators do not appear to have attached sufficient importance. The very important part of Galton's theory will be discussed in its proper place; it is not included in the series of pangenetic hypotheses. Galton is, in fact, one of the numerous biologists who have suggested the continuity of the germinal protoplasm. He is included at this stage, however, because he admitted as a subsidiary hypothesis a limited amount of pangenesis. To account for those cases which suggest that characters acquired by the individual parent are "faintly heritable," Galton supposed that "each cell may throw off a few germs that find their way into the circulation, and have thereby a chance of occasionally finding their way to the sexual elements and of becoming naturalised among them." This part of his theory is obviously a cautious admission of limited pangenesis to account for a number of puzzling cases.

Brooks' Theory.—In 1883, in his valuable work entitled *The Law of Heredity*, Prof. W. K. Brooks gave full expression to a modification of Darwin's view of pangenesis. The main positions, which are here relevant, may be summarised as follows, almost in the author's words :

(1) The male and female cells are specialised in different directions ; their union gives variability.

(2) The ovum is a cell which has gradually acquired a complicated organisation, and which contains material particles of some kind to correspond to each of the hereditary characteristics of the species.

(3) The ovum reproducing its like, as other cells, gives rise not only to the divergent cells of the organism, but also to cells like itself.

(4) Each cell of the body has the power to throw off minute germs. When, through a change in its environment, its functions are disturbed, and its conditions of life become unfavourable, it throws off small particles which are the germs or gemmules of this particular cell.

(5) These germs may be carried to all parts of the body. They may penetrate to an ovarian ovum or to a bud, but the male cell has gradually acquired, as its especial and distinctive function, a peculiar power to gather and store up germs.

(6) In fertilisation each gemmule unites with that particle of the ovum which is destined to give rise in the offspring to the cell which corresponds to the one which produced the gemmule, or else it unites with a closely related

particle, destined to give rise to a closely related cell. Such a cell will be a hybrid, tending to vary.

(7) As the ovarian ova of the offspring share, by direct inheritance, all the properties of the fertilised ovum, the organisms to which they give rise will tend to vary in the same way.

(8) A cell which has thus varied will continue to throw off gemmules, and thus to transmit variability to the corresponding part in the bodies of successive generations of descendants until a favourable variation is seized upon by natural selection.

(9) As the ovum which produced this selected organism will transmit the same variation to its ovarian ova by direct inheritance, the characteristic will be established as specific, and transmitted henceforth without gemmules.

The above theory, being important, has been stated at some length. Apart from the suggestion of variation as due to sexual intermingling, with which Weismann has made us more familiar—apart, too, from the suggestion of germinal continuity, the credit of which Brooks shares—there are several important points to be emphasised in the modification proposed. It is in *unwonted and abnormal* conditions that the cells of the body throw off gemmules. The *male* elements are the special centres of their accumulation ; the female it is that keeps up the *general* resemblance between offspring and parent.

It is not proposed to enter into criticism of pangenetic theories. The best criticism is found in that abandonment of special hypotheses which more recent advances have rendered possible. It has often been urged that the hypothesis of pangenesis involves not one but many suppositions—that it is just as difficult to understand why a gemmule should reproduce a cell like its own origin as to understand the entire problem, and so on. Detailed criticism will be found in the works of Galton, Ribot, Brooks, Herdman, Plarre, and others. It is enough for us to emphasise the comparative gratuitousness of any special theory whatever, a paradox which is explained in the succeeding section.

Apart from the fact that the pangenetic hypothesis is not in harmony with the results of experiments (*e.g.* on the transfusion of blood), or with what we know of the physiology of cells, it may be pointed out that the facts of inheritance are not such as might be expected if pangenesis were an actual occurrence. If it were, we should look for a frequent recurrence of, or for some specific hereditary influence from, exogenous morbid conditions, especially those associated with marked structural changes—for instance, injuries to the brain and spinal cord, cirrhosis of liver and kidney, cirrhotic induration of the lungs from dust inhalation. In fact, after a short series of generations the number of healthy subjects would be reduced to a minimum (Ziegler, 1886, p. 19).

§ 4. *Theory of Genetic or Germinal Continuity*

Owen.—As far back as 1849, Owen pointed out in his paper on parthenogenesis that in the developing germ it was possible to distinguish between cells which became much changed to form the body, and cells which remained little changed and formed the reproductive organs. This was probably the earliest distinct suggestion of the modern theory of germinal continuity.

Haeckel.—In 1866, in his classic *Generelle Morphologie*, Haeckel emphasised the simple and yet fundamental fact of the material continuity of offspring and parent. In an historical note upon the distinction between the "personal" and "germinal" parts of an organism, Rauber states that the distinction was proposed by Haeckel in 1874, and by himself in 1879.

Jäger.—Jäger stated the doctrine of germinal continuity very clearly and concisely at an early date: "Through a great series of generations the germinal protoplasm retains its specific properties, dividing in every reproduction into an ontogenetic portion, out of which the individual is built up, and a phylogenetic portion which is reserved to form the reproductive material of the mature offspring. This reservation of the phylogenetic material I described as *the continuity of the germ protoplasm*. . . . Encapsuled in the ontogenetic material, the phylogenetic protoplasm is sheltered from external influences, and retains its specific and embryonic characters."

Brooks.—Brooks notes that, in papers published in 1876 and 1877, he had also suggested the notion of germinal continuity, and the conception is clearly expressed in his work already quoted: "The ovum gives rise to the divergent cells of the organism, but also to cells like itself. The ovarian ova of the offspring are these latter cells, or their direct unmodified descendants. The ovarian ova of the offspring share by direct inheritance all the properties of the fertilised ovum."

Galton.—The important theory of Galton now requires notice. Two preliminary notes are requisite. Galton was extremely doubtful in regard to the genuine inheritance of acquired characters. It was to account for the possible faint inheritance of some of these that he still admitted, as a subsidiary hypothesis, a limited amount of pangenesis. In the second place, it is needful to notice at the outset Galton's term "stirp," which he uses to express the sum-total of the germs, gemmules, or organic units of some kind, which are to be found in the newly fertilised ovum.

(1) Only some of the germs within the stirp attain development in the cells of the "body." It is the dominant germs which so develop.

(2) The residual germs and their progeny form the sexual elements or buds. The part of the stirp developed into the "body" is almost sterile. The continuity is kept up by the undeveloped residual portion.

(3) The direct descent is not between body and body, but between stirp and stirp. "The stirp of the child may

be considered to have descended directly from a part of the stirps of each of its parents, but then the personal structure of the child is no more than an imperfect representation of his own stirp, and the personal structure of each of the parents is no more than an imperfect representation of each of their own stirps."

Here it will be seen that there is a definite expression of the notion that the germinal cells of the offspring are in very direct continuity with those of the parents. The antithesis between the "soma" and the chain of germ-cells is emphasised.

Nussbaum.—The history must also include Nussbaum, who called emphatic attention to the very early differentiation and isolation of the sex-elements to be observed in some cases. The theory both of Jäger and of Nussbaum is that of a continuity of germinal *cells*. The theory of Weismann is more strictly that of the continuity of germinal *protoplasm*. The position of Jäger and Nussbaum may first be summarised more definitely:

(1) At an early stage in the embryo, the future reproductive cells of the organism are distinguishable from those which are forming the body.

(2) The latter develop in manifold variety, and lose almost all likeness to the mother germ.

(3) The former—the reproductive rudiments—are not implicated in the differentiation of the "soma," remain virtually unchanged, and continue the protoplasmic tradition unaltered.

(4) The sex-cells of the offspring being thus continuous with the parental sex-cells which gave rise to itself, they will in turn develop into similar products.

Now this fact of continuity of reproductive elements is obviously most satisfactory. If a fertilised egg-cell has certain characters, x, y, z, it develops into an organism in which these characters x, y, z are expressed; but, at the same time, the future reproductive cells are early set apart, retaining the characters x, y, z in all their entirety, to start a new organism again with the same capital. Balbiani, who was not influenced by theoretical considerations, observed in *Chironomus* that the future reproductive cells were isolated before even the blastoderm was completed ; that is to say, before almost any differentiation had occurred, a portion of the unspecialised ovum was insulated to continue the constancy of the species.

In this aspect the reproductive cells form a continuous chain, and the reproduction of like is as natural and necessary as it was in the Protozoa. No special theory is required. Similar conditions produce similar results. Unfortunately, however, a serious difficulty besets this easy theory. Such an early appearance and insulation of the reproductive cells, continuous with the very ovum itself, does indeed occur, and where it does the problem of heredity is simple. Early origin of special germ-cells, distinguished from those of the general " body," has been observed in some " worm-types " (leeches, *Sagitta*, threadworms, many Polyzoa) and in some Arthropods (*Moina* and *Cyclops* among crustaceans, not a few insects, Phalangidæ among spiders), while indications of the same early separation are not wanting in a number of other organisms. But it must be distinctly allowed that in most cases it is only after differentiation is relatively advanced that the future reproductive cells make their appearance. Thus we have to pass from the few cases as yet known of the continuity of the germinal *cells*, to the more general fact of the " continuity of the germ-plasma."

Weismann's Theory.—Weismann, like the previous investigators, had reached his conclusion independently. In the fact of continuity between the reproductive elements of generations, the solution of likeness must be found. But a direct chain of cellular continuity can only be said to exist in a few cases. The solution which is proposed for the majority of cases is as follows :

(1) " In each development a portion of the specific germinal

plasma (*Keimplasma*), which the parental ovum contains, is not used up in the formation of the offspring, but is reserved unchanged for the formation of the germinal cells of the following generation."

(2) What is actually continuous is the germ-plasm—" of definite chemical and special molecular constitution." A continuity of germinal cells is now rare; a continuity of intact germinal plasma is constant.

(3) This germ-plasm has its seat in the nucleus, is extremely complex in structure, but has nevertheless an extreme power of persistence and enormous powers of growth.

(4) "The germ-substance proper must be looked for in the chromatin of the nucleus of the germ-cell, and more precisely still in those ids or chromosomes which we conceive of as containing the primary constituents of a complete organism. Such ids in larger or smaller numbers make up the whole germ-plasm of a germ-cell, and each id in its turn consists of primary constituents or determinants, *i.e.* of vital units, each of which determines the origin and development of a particular part of the organism."

(5) "The splitting up of the substance of the ovum into a somatic part, which directs the development of the individual, and a propagative part, which reaches the germ-cells and there remains inactive, and later gives rise to the succeeding generation, constitutes *the theory of the continuity of the germ-plasm* which I first stated in a work which appeared in the year 1885" (1904, vol. i. p. 411).