XI.

Remarks on Certain Problems of the Day.

1890.

From the 'Biologisches Centralblatt,' Bd. X., Nr. 1 and 2, pages 1 and 33: March, 1890.

XI.

REMARKS ON CERTAIN PROBLEMS OF THE DAY.

THE following essay was originally intended as an answer to the criticisms which Professor Vines [1] brought forward against certain of my views, shortly after the publication, in an English form, of a collected edition of those essays of mine which appeared in Germany during the years 1881–1889 [2]. This answer has been published in German because similar objections have been urged by German writers, and I further hope that this essay may perhaps serve to render clearer some of the problems with which it deals. Much might have been added on the points here referred to, but the occasion, and the nature of the essay itself, called for a certain amount of restriction, and enforced a concentrated treatment of the most important subjects.

Professor Vines commenced his article by a criticism of that attribute of immortality which I have claimed both for unicellular organisms and for the reproductive cells of multicellular beings. If I rightly understand the English professor, he does not contest the truth of this view, but he fails to find in my book a satisfactory explanation of the process by which the immortal organisms gave rise, in the course of their phyletic development, to mortal descendants. The first difficulty which presents itself is to understand how the mortal heteroplastides can have been evolved from the immortal monoplastides or homoplastides. The explanation of this process, given in my book, is the only one which seems applicable to the

[1] 'Nature,' Oct. 24, 1889, p. 621 et seqq.
[2] See Vol. I of the present Edition.

rigin of the more complex forms of organic life, namely, that, n accordance with the principle of division of labour, the cell-ody of the unicellular ancestor divided into two dissimilar alves, which differed from each other both in structure and unction. From a single cell which was capable of performing ll functions, a group of cells arose and shared the various inds of work between them. According to my theory, the rimitive division produced two kinds of cells, the mortal cells f the body proper (*soma*) and the immortal germ-cells. Un-loubtedly Professor Vines believes, as I do, in the principle of livision of labour, and in the rôle which this principle plays in he development of the organic world; but the division of a micellular being into somatic and reproductive cells appears to im impossible, and my explanation of the process as due to nequal cell-division does not satisfy him; he holds that 'it is bsurd to say that an immortal substance can be converted into mortal substance[1].'

At first sight indeed this may appear as a great difficulty; it s in reality, however, caused by a confusion between two dis-inct ideas, namely, immortality and eternity. The immortality f unicellular beings and of the reproductive cells of multicel-ular organisms is, I believe, a fact which does not admit of dis-ute. As soon as it is once made clear that the fission of a nonoplastid is in no way bound up with the death of either alf, there can be no further dispute about the unlimited per-istence of the individual. But this is very far from affirming hat such individuals are endowed with eternal life; on the ontrary, we always assume that the organic life on our earth nce had a beginning. The conception of eternity involves the ast as well as the future, for eternity is without beginning and vithout end; but it is obvious that such a conception does not oncern us here. Eternity is at best but an artificial idea; in eality it is no true idea at all, since we cannot conceive it; it is nly the negation of an idea, being in fact the negation of that vhich passes away. When we begin to discuss eternity, we ee that from the point of view of Natural Science, nothing is ternal except the ultimate particles of matter and their forces; or no one of the thousandfold phenomena and combinations inder which matter and force present themselves to us can

[1] 'Nature,' Oct. 1889, p. 623.

be eternal. The immortality of unicellular organisms and of germ-cells is, as I said years ago, not absolute, but potential; for they are not, like the gods of ancient Greece, compelled to live for ever. Thus we are told that Ares received a wound which would have proved fatal to any mortal, but although he roared as loud as ten thousand bulls, he could not die. The organisms in question can, and the majority of them do die, but a part of each lives on. But is it one and the same substance which continues to live? Does not life, here and everywhere else, depend on assimilation, that is on a constant change of material? What then is immortal? Apparently not a substance at all, but a certain form of motion. The protoplasm of unicellular beings possesses such an arrangement in its chemical and molecular structure, that the cycle of material which makes up life is ever repeating itself, and can always begin afresh so long as the external conditions remain favourable. In this respect it may be compared to the circulation of water on the earth. Water evaporates, is condensed into cloud, falls to the earth as rain, only once more to evaporate, and thus the cycle repeats itself. And just as there exists no inherent cause in the physical and chemical nature of water, which interrupts this circulation, so in the physical nature of the protoplasm of unicellular beings there is nothing which puts an end to the cycle of existence,—that is fission, growth by assimilation, and then fission again. It is this property which I have called immortality, and in organic nature it is the only real immortality to be met with. It is a purely biological conception, and must be distinguished from the immortality of non-living, that is of inorganic, matter.

If then this real immortality is simply a cyclical movement conditional on certain physical properties of protoplasm, why should it be inconceivable that this property, under certain circumstances, should alter to some extent, so that the phases of metabolic activity should not exactly repeat themselves, but after a certain number of cycles should come to an end, resulting in death? All living matter varies, and why is it inconceivable that variations of protoplasm should arise which, while fulfilling better certain functions advantageous to the individual, should be associated with a metabolism that does not exactly repeat itself a metabolism that sooner or later comes to a stand-still? To my mind the descent of the immortal to the condition of mortality, is less to be marvelled at than the fact that monoplastids and germ-cells have remained immortal. The slightest change in the properties of living matter might involve such a descent, and certain essential peculiarities in the composition of this substance must be most rigidly maintained, in order that the metabolic cycle may sweep on with perfect smoothness, and raise no obstacle against its own persistence. Even if we know nothing further of these essential peculiarities of structure, we may at least maintain that the rigorous and unceasing operation of natural selection is necessary to maintain them. Any deviation from this standard ends in death. I believe that I have shown that organs which have ceased to be useful become rudimentary, and ultimately disappear owing to the principle of panmixia alone,—not because of the direct effect of disuse, but because natural selection no longer maintains them at their former level. What is true of organs is also true of their functions; for function is but the expression of certain peculiarities of structure, whether we can directly perceive the connection or not. If then the immortality of unicellular beings rests on the fact that the structural arrangement of their substance is so accurately adjusted that the metabolic cycle always comes back to the same point,—why should, or rather, how could this property of the protoplasm, which is the cause of immortality, be retained when it ceased to be necessary? And clearly it is no longer of use in the somatic cells of heteroplastids. From the moment that natural selection relaxed its hold upon this property of the protoplasm, the power of panmixia began to be felt, and ultimately led to its disappearance. Prof. Vines will probably ask how this process can be conceived. I answer, quite simply. Let us suppose that certain individuals appeared among the monoplastids with such variation of the chemical or molecular characters, that the continuous recurrence of their metabolic cycle came to an end, so that natural death became a necessity. These individuals could never give rise to a persistent variety. But if individuals with a similar variation in their somatic cells arose among the heteroplastids, no detriment would be felt by the species: the body-cells would indeed die, but the undying germ-cells would secure the continuance of the species. By means of the distinction between somatic and germ-cells, natural selection was enabled to direct its attention, to speak metaphorically, to the immortality of the germ-cells, and to an entirely different range of properties among the somatic cells, such as the capacity for movement, irritability, increased powers of assimilation, &c. &c. We do not yet know whether an increase in these properties is directly connected with a change of constitution involving the loss of immortality, but it is not impossible that this may be the case; and, if so, the somatic cells would have ceased to be immortal more quickly than if panmixia were the only agency at work.

I have adduced in my fourth essay[1] the cases of the Volvocinean genera, *Volvox* and *Pandorina*, as examples of the differentiation of the lowest heteroplastids from the homoplastids. All the cells of *Pandorina* are similar and perform similar functions. *Volvox*, on the other hand, consists of somatic and germ-cells, and it is here that we should expect the introduction of natural death. Dr. Klein's recent observations[2] show that this, as a matter of fact, takes place: as soon as the germ-cells are matured, and have left the body of the Alga, the flagellate somatic cells begin to shrink, and in one or two days are all dead. This is all the more interesting because the somatic cells fulfil nutritive functions for the aggregate. It is true that they are not alone in performing the office of assimilation, for the germ-cells also contain chlorophyll; but the immense size which the latter attain in *Volvox* can only be explained on the supposition that they receive nutriment from the somatic cells. These cells are so constituted that they assimilate, but when once the spherical colony has attained its definite size they have ceased to grow. By means of a fine protoplasmic network the body-cells pass on to the germ-cells all the nutriment they acquire from the decomposition of carbon dioxide and water, and when the reproductive cells are mature they die. In this case adaptation for supplying nutriment to the germ-cells may have hastened the introduction of death among the somatic cells, inasmuch as some structure may

[1] See Vol. I, p. 163.

[2] Ludwig Klein, 'Morphologische und Biologische Studien über die Gattung Volvox.' Pringsheim's Jahrbücher für wissenschaftliche Botanik, Bd. XX. 1889.

have arisen in the latter which rendered possible more energetic assimilation, but which was accompanied by an expenditure of nutriment, and which, after the lapse of a certain time, involved the complete cessation of assimilation, and consequently the death of the organism.

The conception of a change in the protoplasm which involves *the loss of immortality is to my mind no more improbable or* more difficult than the commonly received view of the differentiation of somatic cells which gradually takes place in their phylogeny, by which they are enabled to assume various natures, i. e. absorptive, secretory, muscular, nervous, &c. An unchangeable immortal protoplasm does not exist, only an immortal 'form of activity' in organic matter.

Thus my former statement, that unicellular organisms and the reproductive cells of higher forms do not suffer natural death, is maintained in its entirety; and I know of no better way to give expression to this idea than to say that such structures possess immortality, that is real, true immortality, not the phantastic, visionary immortality of the old Greek gods. If then death from internal causes has no existence for the organisms and structures in question, we can nevertheless maintain with absolute certainty that every one of them will come to an end, not indeed by the operation of forces from within, but because the external conditions which are necessary for the constant renewal of vital activity must at some future time themselves cease to be. The physicist predicts that the circulation of water on the earth will at some time inevitably cease, not because of any change in the nature of water, but because external conditions will render impossible this kind of movement of its particles.

Professor Vines then attacks my views on embryogeny. He finds it 'not a little remarkable that Professor Weismann should not have offered any suggestion as to the conception which he has formed of the mode in which the conversion of germ-plasm into somatoplasm can take place, considering that this assumption is the key to his whole position [1].' He finds in this the same difficulty as in the phyletic development of multicellular from unicellular organisms. He concludes his objection with the words, 'There is really no other criticism to be made on an

[1] 'Nature,' Oct. 1889, p. 623.

unsupported assumption such as this, than to say that it involves a contradiction in terms[1].' By this Professor Vines means that the eternal cannot, from its very nature, pass into the mortal, as it must do, if the perishable soma is derived from undying germ-cells. It is obvious that this objection rests upon the same confusion between immortality and eternity which has been already rendered clear. I do not wish to reproach Professor Vines with regard to this confusion; some years ago I encountered the same objection, and did not at once see where the answer lay. We have hitherto been without a scientific conception of immortality: we must understand by this term—not life without beginning or end—but life which, when it has once originated, continues without limit, accompanied or unaccompanied by modification (viz. specific changes in unicellular organisms, or in the germ-plasm of multicellular forms). This immortality is a movement of organic material, which always recurs in a cycle, and is associated with no force that tends to arrest its progress, just as the motion of planets is associated with nothing which tends to arrest their movement, although it had a beginning and must at some future time, by the operation of external causes, come to an end.

Further on, Professor Vines says, 'I understand Professor Weismann to *imply that his theory of heredity is not*—*like*, *for* instance, Darwin's theory of pangenesis—"a provisional or purely formal solution[2]" of the question, but one which is applicable to every detail of embryogeny, as well as to the more general phenomena of heredity and variation[3].' I have indeed, in contradistinction to my own attempt to give a *theoretical basis to heredity*, spoken of Darwin's pangenesis as a purely formal solution of the question; and perhaps I may be allowed to give a short explanation of the expression, for I fear that, not only Professor Vines, but many other readers of my essays may have misunderstood me. On the one hand I am afraid that they may have found in my words a tacit objection to Darwin's pangenesis, an objection which I did not at all intend, and, on the other, that I was inclined to overstate the value of my own theory.

There are, I think, two kinds of theory which may be con-

[1] 'Nature,' Oct. 1889, p. 623. [2] See Vol. I, p. 168.
[3] 'Nature,' Oct. 1889, p. 623.

veniently distinguished as *ideal* and *real*. Practically it is found that they are seldom sharply discriminated; often both kinds occur combined in one and the same theory: nevertheless they should be clearly distinguished. The *ideal* theory seeks to explain phenomena by any arbitrarily chosen principle, quite apart from the question whether the principle has any actual existence or not[1]. The ideal theory only seeks to show that there are hypotheses on which the phenomena in question are explicable. Real theories however are not content with plausible hypotheses, but endeavour to include only those which possess some degree of probability: they attempt to give not merely a formal solution, but, if possible, the correct one. Sir William Thomson has attempted to explain the dispersion of rays of light, by imagining the existence of molecules which are composed of concentric hollow spheres, arranged one inside the other and connected together by springs. But this distinguished physicist never for a moment believed in the existence of real molecules, provided with springs; he wished to show that existing conceptions were capable of rendering intelligible the phenomena of dispersion. Obviously Darwin's pangenesis was conceived in this spirit, and was therefore called by him 'provisional'; although in later life he may have come to attach real worth to the theory. I consider the gemmules to be a deliberate invention, like Sir William Thomson's molecules provided with springs, which have no claim to reality: the gemmules merely serve to show the sort of suppositions we must make in order to understand the phenomena of heredity.

Ideal theories are by no means useless. They are the first and often the indispensable steps which we must take on our way to the understanding of complex phenomena. They form the foundation upon which real theories can gradually be raised. Above all, they supply the impulse to re-examine again and again the phenomena they attempt to explain. I should probably never have been led to deny the inheritance of acquired characters, if Darwin's pangenesis had not shown me that the belief in such transmission involved an assumption so

[1] The two philosophers Herbart and Lotze have named these two types of theory '*fiction*' and '*hypothesis*': the former term agrees with *ideal* in expressing the consciousness of unreality.

difficult to realize as that of the giving off, circulation, and accumulation of gemmules.

I do not even now assert that Darwin's pangenesis may not possibly contain a nucleus of truth. De Vries, in his recent exceedingly interesting work[1], has shown that the ideal (impossible) pangenesis of Darwin may be modified into a real (possible) theory, by making a few, although very profound, modifications. He accepts my contention that acquired or somatogenetic changes cannot be inherited, and thus dismisses precisely that part of pangenesis, which, in my opinion, lies outside the limits of possibility, namely the throwing off, circulation and collection of the gemmules. The future will decide whether the assumption of modified gemmules furnishes a better explanation of the facts of heredity than my hypothesis.

But under any circumstances, I do not in any way presume to consider that the whole problem of heredity is solved. I have undertaken investigations on some of the more important points raised by the problem, and consequently have been led to formulate certain fundamental principles in order to explain some of the phenomena of heredity; but no one knows more thoroughly than I do how far we still are from definitely and completely understanding, not only every detail of embryology, but the more general phenomena also. My endeavour has been to substitute a 'real' theory for the 'ideal' theory which has existed hitherto; and I therefore took pains in thinking out conceptions which should, as far as possible, correspond with the results of actual observations. There is undoubtedly a material basis of heredity in the egg, which can with equal certainty be transmitted from nucleus to nucleus, and it may be modified, or may remain unchanged in the process. Furthermore, the supposition that this substance is able to impress a specific character on the cell involves nothing that appears to be impossible or non-existent. So far from this being the case, we are even now able to prove that the character is thus actually stamped upon the cell, although we cannot understand the way in which the process happens. Finally, my view that germ-plasm in an inactive condition potentially contains certain tendencies of the somatic cells which are ultimately derived from it, stands upon a firm basis, for we know that ancestral

[1] Hugo de Vries, 'Intrazelluläre Pangenesis,' Jena, 1889.

characters can be inherited in a latent state, and we also know that the process of inheritance is associated with a certain substance, the idioplasm of the germ-cell. Such idioplasm must therefore be in an inactive state during the period of latency.

If it can be demonstrated that such principles suffice to explain the phenomena of heredity, we have made an essential advance beyond the ideal theory of pangenesis, which is built up on suppositions which do not correspond with realities. Perhaps the path which I have struck out may by degrees lead to a satisfactory solution of the numerous questions connected with heredity; perhaps further investigation may show that we are on the wrong track and must abandon it; what the future of the question may be no one can foretell. My thoughts upon heredity are not final, but rather serve as a starting-point for further thought; they constitute no complete theory of heredity which claims to have satisfied all sides of this most complex subject; they are rather 'researches' which, if fortune favours, will, sooner or later, directly or indirectly, lead to the formation of a real theory. I have expressly stated this in the Preface to the English Edition of my collected essays.

In the same place I have emphasized the fact that my book did not originate as a whole, but is made up of a series of researches, each of which, I hope, marks some advance, each of which is built up on the foundation provided by the previous one. It contains to some extent the history of the development of my views as they have gradually shaped themselves in the course of nearly ten years' work. It is therefore unreasonable to extract ideas from the earlier essays and to make use of them against the later views. All the essays have been left unchanged, and 'certain errors of interpretation . . . . . . left uncorrected[1],' because otherwise the intimate connection which exists between the essays could not have been distinctly traced.

The objections which Professor Vines urges against my theory of the Continuity of the Germ-plasm entirely depend, in my opinion, on an unintentional confusion of my ideas; for he applies the views of the second essay to the ideas in some of the later ones, with which they do not harmonize. I will attempt to explain this in few words: in my second essay[2] (1883)

[1] See Author's Preface to First Edition, Vol. I, p. iv.
[2] See Vol. I, p. 67.

I contrasted the body (*soma*) with the germ-cells and explained heredity by the supposition of a material basis residing in the germ-cells ; i. e. the germ-plasm, which is continuously passed on from one generation to another. When the essay was being written, I was not aware that this germ-plasm existed only in the nucleus of the egg-cell, and I was therefore able to contrast the entire substance of which the egg-cell consists, or the germ-plasm, with the substance which composes the body-cells, hence called somatoplasm. In the fourth essay[1] (1885) I expressed my conviction, which agreed with that shortly before expressed by Strasburger and O. Hertwig, that the substance of the egg-nucleus, or, more precisely, the chromatin of the nuclear loops, formed the material basis of heredity, the body of the cell being only nutritive and capable of being moulded by forces emanating from the nucleus, but in no way formative. Together with the two above-mentioned writers, I transferred the conception of idioplasm—introduced at that time by Nägeli, although defined by him in an essentially different manner,—to the material basis of heredity in the egg-nucleus, and submitted that not only in the ovum but in every cell the chromatin of the nuclear thread was the idioplasm which dominated the whole cell, and impressed its own specific character upon the originally indifferent cell-body. From this time I no longer spoke of the cells of the body as simply somatic protoplasm (somatoplasm), but in each cell I distinguished, first, between the idioplasm, or substance which gives to the nucleus its power of predisposition, and the body of the cell or cytoplasm ; and, secondly, I distinguished between the idioplasm of the egg-nucleus and that of the nucleus of somatic cells. The idioplasm of the germ- or sperm-cell alone was called germ-plasm (idioplasm of reproductive cells), while the idioplasm of the somatic cells was called somatic idioplasm. Embryogeny, in my opinion, depends only on changes in the idioplasm of the egg-nucleus, i. e. changes in the germ-plasm. In my fourth essay there is a description of the manner in which the idioplasm of the egg-nucleus divides, in many species, at the first segmentation, each half undergoing certain regular modifications of nuclear substance, so that neither daughter-cell possesses the collective hereditary tendencies of the species, but one

[1] See Vol. I, p. 163.

contains those of the ectoderm, and the other those of the endoderm. The later stages of embryogeny depend on a continuance of such regular modifications of idioplasm. Each fresh division sorts out fresh predispositions, previously mixed in the nucleus of the mother-cell, until at length the full number of embryonic cells have come into existence, each with an idioplasm in its nucleus which stamps the specific histological character upon the cell.

I fail to understand why this idea presents such remarkable difficulties to Professor Vines. In most species the separation of the sexual cells takes place late in the embryogeny. Now in order to maintain the continuity of germ-plasm from one generation to another, I have supposed that, at the first division of the ovum, not all the germ-plasm (i. e. idioplasm of the first ontogenetic stage) becomes changed into idioplasm of the second stage, but that a minute portion of it persists unchanged included in one or other of the daughter-cells, where it remains inactive, intermingled with the nuclear idioplasm; I have further assumed that in this condition it is transmitted through a longer or shorter series of cell-generations until at length it reaches certain cells on which it impresses the characters of germ-cells, and in these it resumes its activity. This view is not entirely devoid of support; for it is in some degree confirmed by actual observations, especially by those on the remarkable wanderings through which the germ-cells of Hydroids pass, after starting from their original place of formation [1].

But let us leave the consideration of the degree of probability which my theory may possess, and consider only its logical accuracy. Professor Vines says, 'The fate of the germ-plasm of the fertilized ovum is, according to Professor Weismann, to be converted in part into the somatoplasm (!) of the embryo, and in part to be stored up in the germ-cells of the embryo. This being so, how are we to conceive that the germ-plasm of the ovum can impress upon the somatoplasm (!) of the developing embryo, the hereditary character of which it (the germ-plasm) is the bearer? This function cannot be discharged by that portion of the germ-plasm of the ovum which has be-

[1] Weismann, 'Die Entstehung der Sexualzellen bei den Hydromedusen,' Jena, 1883.

come converted into the somatoplasm (!) of the embryo, *for the simple reason that it has ceased to be germ-plasm*, and must therefore have lost the properties characteristic of that substance. Neither can it be discharged by that portion of the germ-plasm of the ovum which is aggregated in the germ-cells of the embryo, for under these circumstances it is withdrawn from all direct relation with the developing somatic cells. The question remains without an answer [1].'

I believe, however, that the answer is to be found above. I know nothing of the 'somatoplasm' of Professor Vines: my germ-plasm, or idioplasm of the 1st ontogenetic stage, is not modified into the 'somatoplasm' of Professor Vines, but into idioplasm of the 2nd ontogenetic stage, and then into that of the 3rd, 4th, 5th, and so on up to the 100th and 1000th stage; and each stage of idioplasm confers its own specific character upon the cell in the nucleus of which it lies.

Professor Vines also criticises my views as to the idioplastic nature of the nuclear substance (the chromatin granules in the nuclear loops, &c.). He maintains that it is as easy to speak of the continuity of the cell-body as the continuity of the nuclear substance, and that hereditary peculiarities can be as well transmitted to the offspring by the former as by the latter.

I can quite understand why a botanist should take this view, and indeed, in bringing it forward, Professor Vines does not stand alone. Waldeyer [2] maintained, in 1888, that established facts did not justify us in regarding the nuclear loops as possessing an idioplastic nature. Among other zoologists, Whitman [3] has pronounced very decidedly against the idioplastic nature of the nucleus, and in their recent work, Geddes and Thomson [4] have done the same.

The facts which suggested to my mind that the nuclear loops are the material basis of heredity,—in fact the idioplasm,—are enumerated in my fourth essay [5]. They were chiefly the observations of Van Beneden on the process of fertilization in the

[1] 'Nature,' Oct. 1889, p. 623.

[2] Waldeyer, 'Ueber Karyokinese und ihre Beziehung zu den Befruchtungsorganen,' Archiv für Mikr. Anatomie, Bd. XXXII. 1888.

[3] Whitman, 'The Seat of formative and regenerative Energy,' Boston, 1888.

[4] Geddes and Thomson, 'The Evolution of Sex,' London, 1889.

[5] See Vol. I, p. 163.

egg of *Ascaris megalocephala*, the observations of Strasburger on the fertilization of the egg-cell in phanerogams by means of the nucleus alone, and the experiments of Nussbaum and Gruber on the artificial division of Infusoria. To these may be added certain other considerations of essential importance, viz. the occurrence of karyokinesis, and the fact that the formation of polar bodies by the ova of animals can be rendered intelligible only on the assumption that the idioplasm resides in the nucleus. The formation of polar bodies involves the division of the nuclear substance of the egg into two halves similar in quantity, but the cell-body itself is divided into two entirely dissimilar portions, the relative sizes of which differ in different species. The essential part of this expulsion of polar bodies from the ovum, must lie in the division of the nuclear substance, and not in the division of the cell. These facts and considerations, in conjunction with others, completely convinced me that the nuclear substance is the sole carrier of hereditary tendencies: the view which I expressed ten years earlier (1873), of the physiological equality (Homodynamy) of the nuclei of both male and female germ-cells, became to my mind a certainty, and I then advanced the theory of fertilization which is to be found in my fourth essay. No one, as far as I know, with the single exception of Strasburger, has expressed similar views on the essential nature of fertilization, at any rate with regard to the homodynamy of the sexual nuclei. The distinguished observer E. van Beneden, to whom we owe so much of our knowledge of the processes of fertilization, has maintained his belief in the old view which looks upon fertilization as the union of two elements which are essentially opposed to each other. He is unable to free himself from the dominant idea, so firmly embedded in the biological mind, that sexual difference is something fundamental, and an essential principle of life itself. To him, the fertilized ovum is a 'hermaphrodite' being, which unites in itself both male and female entities,—an idea which has commended itself to many authorities, but an idea of which the logical outcome forces us to regard all the cells of the body as hermaphrodite. Van Beneden was at the same time swayed by the opinion, which is shared by so many workers in other lands, that fertilization is a process of rejuvenescence, without which terrestrial life could not continue. Many observers still cling to this view, and Maupas[1] has recently claimed to have found a proof of its soundness by showing that it is essential for Infusoria to conjugate (sexual reproduction) from time to time.

This contention forms a striking example of the difficulty with which even scientifically trained minds can shake off deeply rooted convictions. Although it must be clear to every one that unicellular organisms are immortal, although Maupas has himself produced superabundant proofs that the reproduction of Infusoria by fission can go on without ceasing, and although he maintains that 'les cycles évolutifs des Ciliés peuvent se succéder à l'infini' (p. 437), nevertheless the power of the old tradition of the necessity of death is so strong in him that he is incapable of recognizing this simple fact. Rather than adopt the views propounded by others, he prefers to accept the hypothesis that unicellular organisms are really mortal and are subject to natural death, but that this is kept in abeyance and postponed by the influence of conjugation.

If we ask, whence comes this idea of the necessity of death, we receive the answer,—from our experience of man and the higher animals and plants. If we further ask, why has it hitherto been entirely overlooked that among these organisms certain parts of the body (the reproductive cells) are endowed with immortality, the answer is,—because we have only recently come to know and completely appreciate the facts of reproduction, and therefore have only just arrived at a correct estimate of them, and are now for the first time able to recognize in our reproductive cells, the undying parts of our individuality.

For how long then will reproduction be regarded as a dynamical process, as a stimulus, as 'the spark in the powder cask,' or in biological language the vitalizing of the egg? This conception is directly derived from the old vital force of earlier times, and it is the unrecognized reflection of this latter idea which influences many writers, and which, proteus-like, continually appearing in new forms, evokes the belief in a necessity for the rekindling of life.

If we lay aside preconceived notions and simply review the

[1] E. Maupas, 'Le rajeunissement karyogamique chez les Ciliés,' Arch. Zool. expér. et générale, 2 sér., Tom. vii. Nr. 1, 2, et 3, 1889.

facts of the case, we see, on the one side, unicellular animals which continually increase by division, and, on the other, multicellular animals which are differentiated into somatic and germ-cells,—animals in which the body dies, while the reproductive cells possess the same power of unlimited increase by division that is possessed by unicellular beings. But what leads us to consider that the capacity for continuous reproduction is rendered possible by the fusion of the essential material of one organism with that of another, such as we see in both conjugation and fertilization? Nothing but the unconscious tradition of the inevitability of death. Maupas thinks that he has proved the existence of natural death among the Infusoria, since he has shown by his investigations,—excellent as far as observation is concerned,—that, from time to time, conjugation must make its appearance, or the colony would die out; but he forgets that as a matter of fact under natural conditions, the possibility of conjugation is granted, and that thus the so-called natural death does not appear more often in nature than in the case of those metazoan ova which fail to meet with a spermatozoon. The Infusorian which has not conjugated gradually disappears, like the animal egg which remains unfertilized; and the so-called 'senile degeneration' (Maupas) of the former exactly corresponds to the gradual decomposition and dissolution of the latter, a process which was described long ago, in a species of *Moina*, in one of my memoirs on the Daphnids. Conjugation, no less than fertilization, is undoubtedly a process of vast importance; but I believe that its significance lies in the maintenance and continual intermingling of individual variations, or it may be that some other advantage is conferred which acts for the preservation of the species. In any case nature attaches great importance to it, and seeks to ensure it, for each species, to the greatest possible extent. For this purpose she has made provision that the periodical recurrence of the process should affect as many individuals as possible. If however, in spite of every provision, unfavourable circumstances should bring it about that certain individuals have no part in the process of conjugation, is it to be wondered at that nature should care nothing for their preservation? Or, to speak less figuratively, we must not be surprised to see that means are taken to prevent the unlimited increase of those individuals which are less favourably placed for the continuation of the species. How, in fact, can this be otherwise, since, in Infusoria, the unlimited continuance of life is bound up with conjugation, just as in the ova or spermatozoa of higher organisms, it is dependant on fertilization. It might be objected that the cases are different, inasmuch as the germ-cells which fail to be fertilized perish for lack of nourishment, while the Infusoria which fail to conjugate experience no such difficulty: when therefore they come to an end after a certain number of generations, their death must be due to the working of other causes. But in the above-mentioned Daphnid *Moina rectirostris* when copulation has not taken place the unfertilized egg is not laid at all. It retains the very position in the ovary which it would occupy during development, and it is placed under the most favourable conditions of nutrition. For some time it retains its vitality, but if still unfertilized, it ultimately dies and undergoes dissolution, being finally completely reabsorbed by the surrounding epithelial cells of the ovary. The egg is so constituted that it remains alive for a certain time awaiting fertilization, and then, in spite of the most favourable conditions of nutrition, it perishes. If copulation be delayed in the nearly allied *Moina paradoxa*, the unfertilized eggs are laid and die at once, so that their material is lost to the animal. It is obvious that the arrangement in *Moina rectirostris* is a special adaptation enabling the organism to utilize the material of the large eggs which, unless fertilized, are incapable of further development. We do not know what kind of an arrangement it is which involves the death of the egg although surrounded by such favourable conditions of nutrition, any more than we know what causes the fate of the unconjugated Infusorian : the facts however show that some arrangement must exist to produce such results. The continued life of an egg requiring fertilization, is dependant on fertilization ; that of an Infusorian needing conjugation, on conjugation.

The experiments of Maupas seem to show that Infusoria are adapted for fertilization, that periodical conjugation is one of the conditions of their life, like food and oxygen. But it is a fallacy, only explicable on the ground of deep-rooted prejudice, to argue from this that they are really mortal, and that their actual immortality depends on the magic of conjugation. One might just as well maintain that food is the cause of Infusorian immortality, inasmuch as death ensues when food is withheld. I believe that the essential, fundamental, and original peculiarity of living matter was the power to assimilate and to grow without limit. On this depends the existence of the whole organic world: it is a primary power, not a secondary one, and cannot have been conjured up afterwards in the organism by any refined artifice, call it conjugation, fertilization, or anything else. It must have been present from the very beginning of life on the earth. How otherwise could life have persisted up to the first appearance of conjugation or fertilization? For there can be scarcely any doubt that neither of these processes is found in the lowest organisms at present known to us. I therefore think that the loss of this fundamental power of unlimited growth must be regarded as a secondary adaptation, called forth by certain special circumstances which rendered it necessary for achieving the combination of different individual hereditary tendencies. When, therefore, certain writers speak of these processes of conjugation and fertilization as a rejuvenescence, in the sense of a renewal of vital energy, I can only believe that they are upholding a long-vanquished and mystical principle. It is quite otherwise if we speak of the conjugation of Infusoria as a rejuvenescence in the sense of a dissolution and re-formation of many parts: this is a process which may depend throughout on well-known natural forces, and which makes its appearance not only in conjugation but in division also. I have no objection to raise against this kind of rejuvenescence; in fact the continual repetition of such regeneration among these undying organisms, exposed, as they are, to constant wear and tear, becomes a necessary assumption.

In my fourth essay, the idea of fertilization being regarded as a process of rejuvenescence, in the sense of a renewal of vital force, is opposed, and the converse view is clearly enunciated. To condense my argument into a sentence,—we ought not to speak, as formerly, of the two conjugating nuclei of the germ-cells as male and female, but as *paternal* and *maternal*; they are not opposed to each other, but are essentially alike, differing only as one individual differs from another of the same species. Fertilization is no process of rejuvenescence, it is nothing more than a mingling of the hereditary tendencies of two individuals.

These tendencies are exclusively contained in the nuclear loops; the cell-bodies of the spermatozoon and ovum are in this respect indifferent, and serve only as the nutritive material which is formed and transformed in a definite way by the dominating idioplasm of the nucleus, as clay is moulded by the hand of a sculptor. That the egg and the spermatozoon differ so greatly in appearance and function, *and that they mutually* attract each other, depend on secondary adaptations, which ensure that they shall find each other, that their idioplasm or nuclear substance shall come into contact, while, at the same time, a certain amount of nutriment shall be provided for the embryogeny, &c. &c. And just as the differentiation of cells into male and female reproductive elements is secondary, so is that of male and female individuals: all the numerous differences in form and function which characterize sex among the higher animals, all the so-called 'secondary sexual characters,' *affecting even the highest mental qualities of mankind*, are nothing but adaptations to bring about the union of the hereditary tendencies of two individuals.

These are briefly the ideas on fertilization which I indicated in the year 1873, and which I published in a detailed and definite form in 1885, after the discoveries of Van Beneden on the morphological processes which take place during the fertilization of the egg of *Ascaris*[1]. Towards the end of the essay I used these words, 'If it were possible to introduce the female pronucleus of an egg into another egg of the same species, immediately after the transformation of the nucleus of the latter into the female pronucleus, it is very probable that the two nuclei would conjugate just as if a fertilizing sperm-nucleus had penetrated. *If this were so, the direct proof that* egg-nucleus and sperm-nucleus are identical would be furnished. Unfortunately the practical difficulties are so great *that it* is hardly possible that the experiment can ever be made; but such want of experimental proof is partially compensated for by the fact, ascertained by Berthold, that in certain Algæ (*Ectocarpus* and *Scytosiphon*) there is not only a female, but also a male parthenogenesis; for he shows that in these species the male germ-cells may sometimes develop into plants, which however are very weakly[2].'

[1] See Vol. I, Essay iv, p. 163. [2] See Vol. I, pp. 252, 253.

Since then I have made the attempt to fertilize the ovum of a frog with the nucleus of another; the experiment did not succeed, and we could scarcely expect it to do so, considering the very considerable amount of injury caused by transferring a nucleus into another egg.

Boveri [1] has been more fortunate; for he succeeded in finding an object which permitted the converse of my experiment. Adopting the method of R. Hertwig, he separated, by shaking, the nucleus from the ovum of an *Echinus*, and succeeded in rearing such denucleated eggs by the introduction of spermatozoa. A regular segmentation nucleus was formed from the spermatozoon which penetrated the egg, embryogeny followed its usual course, and the egg gave rise to a perfect but rather small larva, which swam freely about in the water, and lived until the seventh day.

This experiment is by itself sufficient to prove that the views on fertilization adopted by Strasburger and myself are correct, viz. that the nucleus of the spermatozoon can play the part of the nucleus of the egg, and *vice versa*, and that the older view to which Professor Vines [2] adheres, must be given up.

An interesting and important modification of Boveri's experiment, affords further support to the results obtained by him, and confirms—if indeed confirmation be necessary—the view which looks upon the nuclear substance as idioplasm, as maintained by O. Hertwig, Strasburger, and myself [3].

If the eggs of *Echinus microtuberculatus*, artificially deprived of their nuclei, be fertilized, not with the spermatozoa of their own species, but with those of another, *Sphaerechinus granularis*, *larvae are developed with the true characters of the last species only*, that is to say, nothing is inherited from the mother but everything from the father. The nuclear substance is the sole bearer of hereditary tendencies and by it the cell is governed.

I have explained the first polar body of the metazoan egg as the carrier of ovogenetic idioplasm which must be removed

[1] Boveri, 'Ein geschlechtlich erzeugter Organismus ohne mütterliche Eigenschaften.' Gesellsch. f. Morph. u. Physiol. München, 16 Juli, 1883.

[2] S. H. Vines, 'Lectures on the Physiology of Plants.' Cambridge, 1886, pp. 638-681.

[3] Cf. Kölliker, 'Die Bedeutung der Zellenkerne für die Vorgänge der Vererbung.' Z. f. W. Z. Bd. 42, 1885.

in order that the germ-plasm may become dominant. It is possible that this explanation may be incorrect. The latest observations on the conjugation of Infusoria, as recorded in the excellent works of Maupas and R. Hertwig, are opposed to my explanation, although the idea upon which it was formed is justified. Since it is the nuclear substance which gives to the cell its specific character, the egg-cell must before fertilization be dominated by an idioplasm distinct from that of the sperm-cell, for they are, up to this point, of different form and function. As soon however as fertilization is accomplished they both contain the same idioplasm, namely germ-plasm. Hence the earlier dominant idioplasm must be different from the later.

This fundamental idea upon which my interpretation of the first polar body was founded appears to be sound. One might perhaps imagine that the idioplasm of the egg was originally different from that of the spermatozoon, but that both possessed the power of changing into germ-plasm. But this would leave wholly unexplained the fact that parthenogenetic eggs extrude one polar body. Both facts become clear, if ova and spermatozoa are dominated until they reach maturity by different histogenetic idioplasmata, with which a small amount of germ-plasm is mingled, and if when the former are removed, the germ-plasm governs both cells. This process is in no way extraordinary and unparalleled; for entirely analogous divisions of the idioplasm into halves of unequal quality, must take place hundreds of times in every embryogeny. However, I willingly admit that on this question the last word has not yet been spoken, and would merely add that my theory of heredity is not concerned thereby. As regards my theory, the significance of the second polar body, and not that of the first, is decisive. Even if it be demonstrated that my interpretation of the first polar body is erroneous, this would not interfere with the conception of the second as halving the number of ancestral germ-plasmata. I should then look upon the first division as merely leading up to the second, as a first step necessary for the reduction of the ancestral plasmata, although the reason for its necessity is not at present quite clear to us.

The occurrence of regular changes in the idioplasm during ontogeny, which I have urged, and which has been attacked by so many writers, particularly by Kölliker[1], now appears to be justified. If the nucleus of a spermatozoon is capable of conveying to the body of an ovum which has lost its nucleus, the hereditary tendencies contained in itself, and of producing an organism with paternal characters only,—then we can scarcely conceive of ontogeny except as a series of regular changes of the idioplasm, advancing from cell-division to cell-division, and giving its special character to the body of every cell at every stage of growth, not only in respect to form, but also to function, and especially with regard to the rhythm of cell-division.

Professor Vines raises a further objection against my views on the origin of variation. In the fifth essay[2] I looked for the significance of sexual reproduction in the fact that it alone could have called forth that multiplicity of form which is met with among the higher plants and animals, and that constantly varying combination of individual variations, which natural selection required for the creation of new species. I still hold to the view that the origin of sexual reproduction in reality depends on the assistance which it affords to the working of natural selection, and I am entirely convinced that the higher development of the organic world was only rendered possible by the introduction of sexual reproduction. On the other hand, I am inclined to believe that Professor Vines is right in his contention that sexual reproduction is not the only factor which maintains the variability of the Metazoa and Metaphyta. I might have pointed out in the English translation of my essays that my views on this point had somewhat altered since the appearance of the German originals. My lamented friend, Professor De Bary, too early lost to science, had already directed my attention to those fungi which propagate themselves parthenogenetically, and which Professor Vines justly cites against this part of my view; but I wished on the grounds mentioned above to make no alteration in the essays. At the time when I wrote the essay in question (1886), I was well aware that my views on the causes of individual variation were

[1] Kölliker, 'Das Karyoplasma und die Vererbung: eine Kritik der Weismann'schen Theorie von der Kontinuität des Keimplasmas.' Z. f. W. Z. Bd 44, p 228, 1886.
[2] See Vol. I, p. 257.

possibly incomplete, and in order to expose the correctness of my view to the widest available test, I carried out its logical consequences as thoroughly as possible, and laid down the principle that species which propagate parthenogenetically have no power to develop into new species. Furthermore, about the same time, I began a series of experiments to test the truth of this statement as to the capacity for variation possessed by parthenogenetic species; these have been continued up to the present time, and on some future occasion I hope to make them public.

But even if, as seems at present very probable, sexual reproduction is not the only origin of individual variability in the Metazoa, no one will deny that it is the chief means of increasing these variations and of continuing them in favourable proportions. In my opinion, the importance of the rôle which sexual reproduction plays in shaping the material for the process of selection is scarcely diminished, even if we concede that some amount of individual variability can be called forth by direct influences on the germ-plasm. Even Professor Vines considers it probable 'that the absence of sexuality in these plants (the parthenogenetic higher Fungi) may be just the reason why no higher forms have been evolved from them; for in this respect they present a striking contrast to the higher Algae in which sexuality is well marked[1].'

But when Professor Vines says 'there can be no doubt that sexual reproduction does very materially promote variation[2],' he does not intend to imply that this statement is self-evident; for it is well known to him that prominent investigators, like Strasburger[3], see in sexual reproduction the reverse action, 'that of preserving the constancy of specific characters.' I accept with pleasure his agreement with my view, confirming the chief result of my fifth essay, which may be expressed as follows:—Sexual reproduction has arisen by and for natural selection, as the only means by which the individual variations can be united and combined in every possible proportion.

Again, with respect to the problem of the inheritance of ac-

[1] 'Nature,' Oct. 1889, p. 626. [2] 'Nature,' Oct. 1889, p. 626.

[3] Strasburger, 'Neue Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen als Grundlage für eine Theorie der Zeugung.' Jena 1884, p. 140.

quired (somatogenic) characters, Professor Vines finds himself opposed to me; *for he regards such inheritance as possible.* I have denied this because it did not appear to me self-evident, as had been previously assumed by every one, but rather utterly unproven; and because I believe that completely unproved assumptions of such importance should not be made, when they need such a number of improbable hypotheses to make them intelligible. I have tested, as accurately as possible, all the available evidence for such inheritance and have found that they possess no value as proofs. There is no inheritance of mutilations, and, up to the present time, these form the only real basis for the assumption of the hereditary transmission of somatogenic variations. If, in my last essay [1], I did not directly deny all possibility of such inheritance, Professor Vines should interpret that in my favour and not to my discredit: it is not the business of an investigator to maintain that a proposition, which he sets forth in accordance with the present state of our knowledge, must be accepted as an infallible dogma. Professor Vines finds the 'statements of opinion so fluctuating that it is difficult to determine what his position exactly is,' but he could have easily arrived at my views, if he had judged them by the last essay, instead of promiscuously contrasting isolated passages from eight essays, which occupied eight years in their production. The last essay is especially concerned with 'the supposed transmission of mutilations,' and, at the end of it, my verdict on the state of the problem of the inheritance of acquired (somatogenic) characters, is set forth as follows, 'The true decision as to the Lamarckian principle [lies in] the explanation of the observed phenomena of transformation. If, as I believe, these phenomena can be explained without the Lamarckian principle, we have no right to assume a form of transmission of which we cannot prove the existence. Only if it could be shown that we cannot now or ever dispense with the principle should we be justified in accepting it [2].'

The distinguished botanist, De Vries, has shown that certain constituents of the cell-body, for example the chromatophores of Algæ, pass directly from the germ-cell of the mother into the daughter organism, whilst, as a rule, the male germ-cell contains no chromatophores. This appears to be a possible case of the

[1] See Vol. I, p. 431. [2] See Vol. I, p. 461.

inheritance of somatogenic variations. In these low plants the difference between somatic and reproductive cells is slight, and the body of the egg-cell does not require to undergo a complete change in its chemical and structural characters in order to develope into the body of the somatic cells of the daughter individual. But what has this to do with the question whether, for instance, the skill of a pianist's fingers, acquired through practice, can be transmitted to his descendants? How does the result of this practice reach the germ-cells? Here lies the real problem which those who maintain the inheritance of somatogenic characters must solve.

The above-mentioned observations of Boveri on the ova of Echinoderms deprived of their nuclei, prove that the body of the egg-cell contributes nothing to inheritance. If then the inheritance of somatogenic characters takes place, it can only be by means of the nuclear substance of the germ-cells, that is through the germ-plasm, and that not in its patent, but in its latent state.

To abandon the Lamarckian principle certainly does not facilitate the explanation of phenomena, but what we need is not a merely formal explanation of the origin of species, although it may be the most convenient, but an attempt to discover the real and genuine explanation. We must endeavour to explain the phenomena without this principle, and I believe I have made a beginning in this direction. I have lately investigated the phenomena in a case where one would not expect to be able to dispense with the principle of modification through use, viz. in the case of artistic endowment [1]. I propounded to myself the question whether the musical faculty in man could be conceived of as arising without the increase of the original faculty by use. And I arrived at the conclusion that not only was this principle unnecessary, but that use has actually taken no share in the evolution of the musical sense.

[1] 'Gedanken über Musik bei Thieren und beim Menschen.' Deutsche Rundschau, October, 1889. Translated as the tenth essay,—the second in the present volume.