V.

THE SIGNIFICANCE OF SEXUAL REPRODUCTION IN THE THEORY OF NATURAL SELECTION.

1886.

SIGNIFICANCE OF SEXUAL REPRODUCTION, ETC.

PREFACE.

The greater part of the present essay was delivered at the first general meeting of the Association of German Naturalists, at Strassburg, on September 18th, 1885, and is printed in the Proceedings of the fifty-eighth meeting of that Society.

The form of a lecture has been retained in the present publication, but its contents have been extended in many ways. Besides many small and a few large additions to the text, I have added six appendices in order to treat of certain subjects more fully than was possible in the lecture itself, in which I was often obliged to be content with mere hints and suggestions. This appears to be all the more necessary because it is impossible to suppose that many views and ideas upon which the lecture was based would be well known to all readers, although they have been described in my former papers. It was above all necessary to deal with the class of acquired characters, which, as it seems to me, is easily confounded, especially by the medical profession, with the much broader class of new characters generally. Only those new characters can be called 'acquired' which owe their origin to external influences, and the term 'acquired' must be denied to those which depend upon the mysterious relationship between the different hereditary tendencies which meet in the fertilized ovum. These latter are not 'acquired' but inherited, although the ancestors did not possess them as such, but only as it were the elements of which they are composed. Such new characters as these do not at present admit of an exact analysis: we have to be satisfied with the undoubted fact of their occurrence. The transmission or non-transmission of acquired characters must be of the highest importance for a theory of heredity, and therefore for the true appreciation of the causes which lead to the transformation of species. Any one who believes, as I do, that acquired characters are not transmitted, will be compelled to assume that the process of natural selection has had a far larger share in the transformation of species than has been as yet accorded to it; for if such characters are not transmitted, the modifying influence of external circumstances in many cases remains restricted to the individual, and cannot have any part in producing transformation. We shall also be compelled to abandon the ideas as to the origin of individual variability which have been hitherto accepted, and shall be obliged to look for a new source of this phenomenon, upon which the processes of selection entirely depend.

In the following pages I have attempted to suggest such a source.

A. W.

FREIBURG I. BR.,
November 22, 1885.

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APPENDICES.

V.

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During the quarter of a century which has elapsed since Biology began to occupy itself again with general problems, at least one main fact has been made clear by the united labours of numerous men of science, viz. the fact that the Theory of Descent, the idea of development in the organic world, is the only conception as to the origin of the latter, which is scientifically tenable. It is not only that, in the light of this theory, numerous facts receive for the first time a meaning and significance; it is not only that, under its influence, all the ascertained facts can be harmoniously grouped together; but in some departments it has already yielded the highest results which can be expected from any theory, it has rendered possible the prediction of facts, not indeed with the absolute certainty of calculation, but still with a high degree of probability. It has been predicted that man, who, in the adult state, only possesses twelve pairs of ribs, would be found to have thirteen or fourteen in the embryonic state: it has been predicted that, at this early period in his existence, he would possess the insignificant remnant of a very small bone in the wrist, the so-called *os centrale*, which must have existed in the adult condition of his extremely remote ancestors. Both predictions have been fulfilled, just as the planet Neptune was discovered after its existence had been predicted from the disturbances induced in the orbit of Uranus.

That existing species have not arisen independently, but have been derived from other and mostly extinct species, and that on the whole this development has taken place in the direction of greater complexity, may be maintained with the same degree of certainty as that with which astronomy asserts that the earth moves round the sun; for a conclusion may be arrived at as safely by other methods as by mathematical calculation.

If I make this assertion so unhesitatingly, I do not make it in the belief that I am bringing forward anything new nor because

I think that any opposition will be encountered, but simply because I wish to begin by pointing out the firm ground on which we stand, before considering the numerous problems which still remain unsolved. Such problems appear as soon as we pass from the facts of the case to their explanation; as soon as we pass from the statement 'The organic world has arisen by development,' to the question 'But how has this been effected, by the action of what forces, by what means, and under what circumstances?'

In attempting to answer these questions we are very far from dealing with certainties; and opinions are still conflicting. But the answer lies in the domain of future investigation, that unknown country which we have to explore.

It is true that this country is not entirely unknown, and if I am not mistaken, Charles Darwin, who in our time has been the first to revive the long-dormant theory of descent, has already given a sketch, which may well serve as a basis for the complete map of the domain; although perhaps many details will be added, and many others taken away. In the principle of natural selection, Darwin has indicated the route by which we must enter this unknown land.

But this opinion is not universal, and only recently Carl Nägeli[1], the famous botanist, has expressed decided doubts as to the general applicability of the principle of natural selection. According to Nägeli, the co-operation of the external conditions of life with the known forces of the organism, viz. heredity and variability, are insufficient to explain the regular course of development pursued by the organic world. He considers that natural selection is at best an auxiliary principle, which accepts or rejects existing characters, but which is unable to create anything new: he believes that the causes of transformation reside within the organism alone. Nägeli further assumes that organisms contain forces which cause periodical transformation of the species, and he imagines that the organic world, as a whole, has arisen in a manner similar to that in which a single individual arises.

Just as a seed produces a certain plant because it possesses a certain constitution, and just as, in this process, certain conditions must be favourable (light, warmth, moisture, &c.) in order that development may take place, although they do not determine the

[1] C. Nägeli, 'Mechanisch-physiologische Theorie der Abstammungslehre.' München u. Leipzig, 1884.

kind or the manner of development; so, in precisely the same way, the tree of the whole organic world has grown up from the first and lowest forms of life on our planet, under a necessity arising from within, and on the whole independently of external influences. According to Nägeli, the cause which compels every form of living substance to change, from time to time, in the course of its secular growth, and which moulds it afresh into new species, must lie within the organic substance itself, and must depend upon its molecular structure.

It is with sincere admiration and real pleasure that we read the exposition in which Nägeli gives, as it were, the result of all his researches which bear upon the great question of the development of the organic world. But although we derive true enjoyment from the contemplation of the elaborate and ingeniously wrought-out theoretical conception,—which like a beautiful building or a work of art is complete in itself,—and although we must be convinced that its rise has depended upon the progress of knowledge, and that by its means we shall eventually reach a fuller knowledge; it is nevertheless true that we cannot accept the author's fundamental hypothesis. I at least believe that I am not alone in this respect, and that but few zoologists will be found who can adopt the hypothesis which forms the foundation of Nägeli's theory.

It is not my intention at present to justify my own widely different views, but the subject of this lecture compels me to briefly explain my position in relation to Nägeli, and to give some of the reasons why I cannot accept his theory of an active force of transformation arising and working within the organism; and I must also explain the reasons which induce me to adhere to the theory of natural selection.

The supposition of such a phyletic force of transformation (see Appendix I, p. 298) possesses, in my opinion, the greatest defect that any theory can have,—it does not explain the phenomena. I do not mean to imply that it is incapable of rendering certain subordinate phenomena intelligible, but that it leaves a larger number of facts entirely unexplained. It does not afford any explanation of the purposefulness seen in organisms: and this is just the main problem which the organic world offers for our solution. That species are, from time to time, transformed into new ones might perhaps be understood by means of an internal transforming force, but that they are so changed as to become better adapted to the new conditions under which they have to live, is left entirely unintelligible by this theory. For we certainly cannot accept as an explanation Nägeli's statement that organisms possess the power of being transformed in an adaptive manner simply by the action of an external stimulus (see Appendix II, p. 300).

In addition to this fundamental defect, we must also note that there are absolutely no proofs in support of the foundation of this theory, viz. of the existence of an internal transforming force.

Nägeli has very ingeniously worked out his conception of idioplasm, and this conception is certainly an important acquisition and one that will last, although without the special meaning given to it by its author. But is this special meaning anything more than pure hypothesis? Can we say more than this of the ingenious description of the minute molecular structure of the hypothetical basis of life? Could not idioplasm be built up in a manner entirely different from that which Nägeli supposes? And can conclusions drawn from its supposed structure be brought forward to prove anything? The only proof that idioplasm must necessarily change, in the course of time, as the result of its own structure, is to be found in the fact that Nägeli has so constructed it; and no one will doubt that the structure of idioplasm might have been so conceived as to render any transformation from within itself entirely impossible.

But even if it is theoretically possible to imagine that idioplasm possesses such a structure that it changes in a certain manner, as the result of mere growth, we should not be justified in thus assuming the existence of a new and totally unknown principle until it had been proved that known forces are insufficient for the explanation of the observed phenomena.

Can any one assert that this proof has been forthcoming? It has been again and again pointed out that the phyletic development of the vegetable kingdom proceeds with regularity and according to law, as we see in the preponderance and constancy of so-called purely 'morphological' characters in plants. The formation of natural groups in the animal and vegetable kingdoms compels us to admit that organic evolution has frequently proceeded for longer or shorter periods along certain developmental lines. But we are not on this account compelled to adopt the supposition of unknown internal forces which have determined such lines of development.

Many years ago I attempted to prove[1] that the constitution or physical nature of an organism must exercise a restricting influence upon its capacity for variation. A given species cannot change into any other species, which may be thought of. A beetle could not be transformed into a vertebrate animal: it could not even become a grasshopper or a butterfly; but it could change into a new species of beetle, although only at first into a species of the same genus. Every new species must have been directly continuous with the old one from which it arose, and this fact alone implies that phyletic development must necessarily follow certain lines.

I can fully understand how it is that a botanist has more inclination than a zoologist to take refuge in internal developmental forces. The relation of form to function, the adaptation of the organism to the internal and external conditions of life, is less prominent in plants than in animals; and it is even true that a large amount of observation and ingenuity is often necessary in order to make out any adaptation at all. The temptation to accept the view that everything depends upon internal directing causes is therefore all the greater. Nägeli indeed looks at the subject from the opposite point of view, and considers that the true underlying cause of transformation is in animals obscured by adaptation, but is more apparent in plants[2]. Sufficient justification for this opinion cannot, however, be furnished by the fact that in plants many characters have not been as yet explained by adaptation. We should do well to remember the extent to which the number of so-called 'morphological' characters in plants has been lessened during the last twenty years. What a flood of light was thrown upon the forms and colours of flowers, so often curious and apparently arbitrary, when Sprengel's long-neglected discovery was extended and duly appreciated as the result of Darwin's investigations, and when the subject was further advanced by Hermann Müller's admirable researches! Even the venation of leaves, which was formerly considered to be entirely without significance, has been shown to possess a high biological value

[1] 'Ueber die Berechtigung der Darwin'schen Theorie.' Leipzig, 1868, p. 27.

[2] l. c., Preface, p. vi.

by the ingenious investigations of J. Sachs (see Appendix III, p. 308). We have not yet reached the limits of investigation, and no reason can be assigned for the belief that we shall not some day receive an explanation of characters which are now unintelligible[1].

It is obvious that the zoologist cannot lay too much stress upon the intimate connexion between form and function, a connexion which extends to the minutest details: it is almost impossible to insist too much upon the perfect manner in which adaptation to certain conditions of life is carried out in the animal body. In the animal body we find nothing without a meaning, nothing which might be otherwise; each organ, even each cell or part of a cell is, as it were, tuned for the special part it has to perform in relation to the surroundings.

It is true that we are as yet unable to explain the adaptive character of every structure in any single species, but whenever we succeed in making out the significance of a structure, it always proves to be a fresh example of adaptation. Any one who has attempted to study the structure of a species in detail, and to account for the relation of its parts to the functions of the whole, will be altogether inclined to believe with me that everything depends upon adaptation. There is no part of the body of an individual or of any of its ancestors, not even the minutest and most insignificant part, which has arisen in any other way than under the influence of the conditions of life; and the parts of the body conform to these conditions, as the channel of a river is shaped by the stream which flows over it.

These are indeed only convictions, not real proofs; for we are not yet sufficiently intimately acquainted with any species to be able to recognize the nature and meaning of all the details of its structure, in all their relations: and we are still less able to trace the ancestral history in each case, and to make out the origin of those structures of which the presence in the descendants depends primarily upon heredity. But already a fair advance towards the attainment of inductive proof has been made; for the number of adaptations which have been established is now very large and

[1] Since the above was written many other morphological peculiarities of plants have been rightly explained as adaptations. Compare, for instance, the investigations of Stahl on the means by which plants protect themselves against the attacks of snails and slugs (Jena, 1888).—A. W., 1888.

is increasing every day. If, however, we anticipate the results of future researches, and admit that an organism only consists of adaptations, based upon an ancestral constitution, it is obvious that nothing remains to be explained by a phyletic force, even though the latter be presented to us in the refined form of Nägeli's self-changing idioplasm.

It will perhaps be useful to illustrate my views by a familiar example. I choose the well-known group of the whales. These animals are placental mammals, which, probably in secondary times, arose from terrestrial Mammalia, by adaptation to an aquatic life.

Everything that is characteristic of these animals and distinguishes them from other mammals depends upon this adaptation. Their fore-limbs have been transformed into rigid paddles, only movable at the shoulder-joint; upon the back and the tail there are ridges with a form somewhat similar to the dorsal and caudal fins of fishes. The organ of hearing is without any external ear and without an air-containing external auditory meatus. The aerial vibrations do not pass, as in other mammals, from the external auditory passage to the tympanic cavity and thus to the nerve-terminations of the inner ear; but they reach the tympanic cavity by direct transmission through the bones of the skull, which possess a special structure and contain abundant air-cavities. This arrangement is obviously adapted for hearing in water. The nostrils also exhibit peculiarities, for they do not open near the mouth, but upon the forehead, so that the animal can breathe, even in a rough sea, as soon as it comes to the surface. In order to facilitate rapid movement in water, the whole body has become extended in length, and spindle-shaped, like the body of a fish. The hind limbs are absent in no other mammals, the fish-like *Sirenia* being alone excepted. In the whales, as in the *Sirenia*, these appendages have become useless, owing to the powerfully developed tail-fin; they are now rudimentary and consist of some small bones and muscles deeply buried in the body of the animal, which nevertheless, in certain species, still exhibit the original structure of the hind-limb. The hairy covering of other mammals has also disappeared, its place having been taken by a thick layer of fat beneath the skin, which affords a much better protection against cold. This fatty layer was also necessary in order to diminish the specific gravity of the animal, and to thus render it equal to that of sea-water. In the structure of the skull there are also a number of peculiarities, all of which are directly or indirectly connected with the conditions under which these animals live. In the whalebone whales, the enormous size of the face, the immense jaws, and wide mouth are very striking. Can it be suggested that this very characteristic appearance is entirely due to the guidance of some internal transforming force, or to some spontaneous modification of the idioplasm? Any such suggestion cannot be accepted, for it is easy to show that all these structural features depend upon adaptation to a peculiar mode of feeding. Functional teeth are absent, but rudimentary ones exist in the embryo as relics of an ancestral condition in which these organs were fully developed. Large plates of whalebone with finely divided ends are suspended vertically from the roof of the mouth. These whales feed upon small organisms, about an inch in length, which swim or float upon the water in countless numbers; and in order that they may subsist upon such minute animals, it is necessary to obtain them in immense numbers. This is achieved by means of the huge mouth which takes in a vast quantity of water at a single mouthful. The water then filters away through the plates of whalebone, while the organisms which form the whale's food remain stranded in the mouth. Is it necessary to add that the internal organs—so far as we understand the details of their functions, and so far as their structure differs from that of the corresponding organs in other Mammalia—have also been directly or indirectly modified by adaptation to an aquatic life? Thus all whales possess a very peculiar arrangement of the nasal passages and larynx, enabling them to breathe and swallow at the same time: the lungs are of enormous length, and thus cause the animal to assume a horizontal position in the water without the exercise of muscular effort: in consequence of this latter modification, the diaphragm extends in a nearly horizontal direction: there are moreover certain arrangements in the vascular system which enable the animal to remain under water for a considerable time, and so on.

And now, in reference to this special example, I will repeat the question which I have asked before:—'If everything that is characteristic of a group of animals depends upon adaptation, what remains to be explained by the operation of an internal developmental force?' What remains of a whale when we have taken away its adaptive characters? We are compelled to reply that nothing remains except the general plan of mammalian organization, which existed previously in the mammalian ancestors of the *Cetacea*. But if everything which stamps these animals as whales has arisen by adaptation, it follows that the internal developmental force cannot have had any share in the origin of this group.

And yet this very force is said to be the main factor in the transformation of species, and Nägeli unhesitatingly asserts that both the animal and vegetable kingdoms would have become very much as they now are, if there had been no adaptation to new conditions, and no such thing as competition in the struggle for existence[1].

But even if we admit that such an assumption affords some explanation, instead of being the renunciation of all attempts at explanation; if we admit that an organism, the characteristic peculiarities of which entirely depend upon adaptation, has been formed by an internal developmental force; we should still be unable to explain how it happens that such an organism, suited to certain conditions of life, and unable to exist under other conditions, appeared at that very place on the earth's surface, and at that very time in the earth's history, which offered the conditions appropriate for its existence. As I have previously argued, the believers in an internal developmental force are compelled to invent an auxiliary hypothesis, a kind of 'pre-established harmony' which explains how it is that changes in the organic world advance step by step, parallel with changes in the crust of the earth and in other conditions of life; just as, according to Leibnitz, body and soul, although independent of each other, proceed along parallel courses, like two chronometers which keep perfect time. And even this supposition would not be sufficient, because the place must be taken into account as well as the time: thus the whales could not have existed if they had first appeared upon dry land. We know of countless instances in which a species is exclusively and precisely adapted to a certain localized area, and could not thrive anywhere else. We have only to remember the cases of mimicry in which one insect gains protection by resembling another, the cases of

[1] l. c., pp. 117, 286.

protective resemblance to the bark or the leaves of a certain species of plant, or the numerous marvellous adaptations of parasitic animals to certain parts of certain species of hosts.

A mimetic species cannot have appeared at any place other than that in which it exists: it cannot have arisen through an internal developmental force. But if single species, or even whole orders like the *Cetacea*, have arisen independently of any such force, then we may safely assert that the existence of the supposed force is neither required by reason nor necessity.

Hence, abstaining from the invocation of unknown forces, we are justified in carrying on Darwin's attempt to explain the transformation of organisms by the action of known forces and known phenomena. I say 'carry on the attempt,' because I do not believe that our knowledge in this direction has ended with Darwin, and it seems to me that we have already arrived at ideas which are incompatible with certain important points in his general theory, and which therefore necessitate some modification of the latter.

The theory of natural selection explains the rise of new species by supposing that changes occur, from time to time, in those conditions of life to which an organism must adapt itself if it is to continue in existence. Thus a selective process is set up which ensures that only those out of the existing variations are preserved, which correspond in the highest degree to the changed conditions of life. By continued selection in the same direction the deviations from the type, although at first very insignificant, are accumulated and increased until they become specific differences.

I should wish to assert more definitely than Darwin has done, that alterations in the conditions of life, together with changes in the organism itself, must have advanced very gradually and by the smallest steps, in such a way that, at each period in the whole process of transformation, the species has remained sufficiently adapted to the surrounding conditions. An abrupt transformation of a species is inconceivable, because it would render the species incapable of existence. If the whole organization of an animal depends upon adaptation, if the animal body is, as it were, an extremely complex combination of new and old adaptations, it would be a highly remarkable coincidence if, after any sudden alteration occurring simultaneously in many parts of the body, all these parts were changed in such a manner that they again formed a whole which exactly corresponded to the altered external conditions. Those who assume the existence of such a sudden transformation overlook the fact that everything in the animal body is exactly calculated to maintain the existence of the species, and that it is just sufficient for this purpose; and they forget that the minutest change in the least important organ may be enough to render the species incapable of existence.

It may perhaps be objected that the case is different in plants, as is proved by the American weeds which have spread all over Europe, or the European plants which have become naturalized in Australia. Reference might also be made to the plants which inhabited the plains during the glacial epoch, and which at its close migrated to the Alpine mountains and to the far north, and which have remained unaltered under the apparently diverse conditions of life to which they have been subjected for so long a time. Similar instances may also be found among animals. The rabbit, which was brought by sailors to the Atlantic island of Porto Santo, has bred abundantly and remains unchanged in this locality; the European frogs, which were introduced into Madeira, have increased immensely and have become almost a plague; and the European sparrow now thrives in Australia quite as well as with us. But these instances do not prove that adaptation to external conditions of life is not of primary importance; they do not prove that an organism which is adapted to a certain environment will, when unmodified, remain capable of existence amid new surroundings. They only prove that the above-mentioned species found in those countries the same conditions of life as at home, or at least that they met with conditions to which their organization could be subjected without the necessity for modification. Not every new environment includes such changed conditions as will be effective in modifying every species of plant or animal. The rabbit of Porto Santo certainly feeds on herbs different from those which form the food of its relations in Europe, but such a change does not mean an effective alteration in the conditions under which this species lives, for the herbs in both localities are equally well suited to the needs of the animal.

But if we suppose that the wild rabbit, occurring in Europe, were to suddenly lose but a trifle of its wariness, its keen sight, its fine sense of hearing or of smell, or were to suddenly acquire a colour different from that which it now possesses, it would become incapable of existence as a species, and would soon die out. The same result would probably occur if any of its internal organs, such as the lungs or the liver, were suddenly modified. Perhaps single individuals would still remain capable of existence under these circumstances, but the whole species would suffer a certain decline from the maximum development of its powers of resistance, and would thus become extinct. The sudden transformation of a species appears to me to be inconceivable from a physiological point of view, at any rate in animals.

Hence the transformation of a species can only take place by the smallest steps, and must depend upon the accumulation of those differences which characterise individuals, or, as we call them, 'individual differences.' There is no doubt that these differences are always present, and thus, at first sight, it appears to be simply a matter of course that they will afford the material by means of which natural selection produces new forms of life. But the case is not so simple as it appeared to be until recently; that is if I am right in believing that in all animals and plants which are reproduced by true germs, only those characters which were potentially present in the germ of the parent can be transmitted to the succeeding generation.

I believe that heredity depends upon the fact that a small portion of the effective substance of the germ, the germ-plasm, remains unchanged during the development of the ovum into an organism, and that this part of the germ-plasm serves as a foundation from which the germ-cells of the new organism are produced[1]. There is therefore continuity of the germ-plasm from one generation to another. One might represent the germ-plasm by the metaphor of a long creeping root-stock from which plants arise at intervals, these latter representing the individuals of successive generations.

Hence it follows that the transmission of acquired characters is an impossibility, for if the germ-plasm is not formed anew in each individual but is derived from that which preceded it, its structure, and above all its molecular constitution, cannot depend upon the individual in which it happens to occur, but such an individual

[1] Compare the second and fourth of the preceding Essays, 'On Heredity' and 'The Continuity of the Germ-plasm as the Foundation of a Theory of Heredity.'

only forms, as it were, the nutritive soil at the expense of which the germ-plasm grows, while the latter possessed its characteristic structure from the beginning, viz. before the commencement of growth. But the tendencies of heredity, of which the germ-plasm is the bearer, depend upon this very molecular structure, and hence only those characters can be transmitted through successive generations which have been previously inherited, viz. those characters which were potentially contained in the structure of the germ-plasm. It also follows that those other characters which have been acquired by the influence of special external conditions, during the life-time of the parent, cannot be transmitted at all.

The opposite view has, up to the present time, been maintained, and it has been assumed, as a matter of course, that acquired characters can be transmitted; furthermore, extremely complicated and artificial theories have been constructed in order to explain how it may be possible for changes produced by the action of external influences, in the course of a life-time, to be communicated to the germ and thus to become hereditary. But no single fact is known which really proves that acquired characters can be transmitted, for the ascertained facts which seem to point to the transmission of artificially produced diseases cannot be considered as a proof; and as long as such proof is wanting we have no right to make this supposition, unless compelled to do so by the impossibility of suggesting a mode in which the transformation of species can take place without its aid. (See Appendix IV, p. 310.)

It is obvious that the unconscious conviction that we need the aid of acquired characters has hitherto securely maintained the assumed axiom of the transmission of such features. It was believed that we could not do without such an axiom in order to explain the transformation of species; and this was believed not only by those who hold that the direct action of external influences plays an important part in the process, but also by those who hold that the operation of natural selection is the main factor.

Individual variability forms the most important foundation of the theory of natural selection: without it the latter could not exist, for this alone can furnish the minute differences by the accumulation of which new forms are said to arise in the course of generations. But how can such hereditary individual characters exist if the changes wrought by the action of external influences, during the life of an individual, cannot be transmitted? We are clearly compelled to find some other source of hereditary individual differences, or the theory of natural selection would collapse, as it certainly would if hereditary individual variations did not exist. If, on the other hand, acquired differences are transmitted, this would prove that there must be something wrong in the theory of the continuity of the germ-plasm, as above described, and in the non-transmission of acquired characters which results from this theory. But I believe that it is possible to suggest that the origin of hereditary individual characters takes place in a manner quite different from any which has been as yet brought forward. To explain this origin is the task which I am about to undertake in the following pages.

The origin of individual variability has been hitherto represented somewhat as follows. The phenomena of heredity lead to the conclusion that each organism is capable of producing germs, from which, theoretically at least, exact copies of the parent may arise. In reality this is never the case, because each organism possesses the power of reacting on the different external influences with which it is brought into contact, a power without which it could neither develope nor exist. Each organism reacting in a different way must be to some extent changed. Favourable nutrition makes such an organism strong and large; unfavourable nutrition renders it small and weak, and what is true of the whole organism may also be said of its parts. Now it is obvious that even the children of the same mother meet with influences different in kind and degree, from the very beginning of their existence, so that they must necessarily become unlike, even if we suppose them to have been derived from absolutely identical germs, with precisely the same hereditary tendencies.

In this manner individual differences are believed to have been introduced. But if acquired characters are not transmitted the whole chain of argument collapses, for none of those changes which are caused by the conditions of nutrition acting upon single parts of the whole organism, including the results of training and of the use or disuse of single organs,—none of these changes can furnish hereditary differences, nor can they be transmitted to succeeding generations. They are, as it were, only transient characters as far as the species is concerned.

The children of accomplished pianists do not inherit the art of playing the piano; they have to learn it in the same laborious manner as that by which their parents acquired it; they do not inherit anything except that which their parents also possessed when children, viz. manual dexterity and a good ear. Furthermore, language is not transmitted to our children, although it has been practised not only by ourselves but by an almost endless line of ancestors. Only recently, facts have again been worked up and brought together, which show that children of highly civilized nations have no trace of a language when they have grown up in a wild condition and in complete isolation [1]. The power of speech is an acquired or transient character: it is not inherited, and cannot be transmitted: it disappears with the organism which manifests it. Not only do similar phenomena occur in the vegetable kingdom, but they present themselves in an especially striking manner.

When Nägeli [2] introduced Alpine plants, taken from their natural habitat, into the botanical garden at Munich, many of the species were so greatly altered that they could hardly be recognized: for instance, the small Alpine hawk-weeds became large and thickly branching, and they blossomed freely. But if such plants, or even their descendants, were removed to a poor gravelly soil the new characters entirely disappeared, and the plants were re-transformed into the original Alpine form. The re-transformation was always complete, even when the species had been cultivated in rich garden soil for several generations.

Similar experiments with identical results were made twenty years ago by Alexis Jordan [3], who chiefly made use of *Draba verna* in his researches. These experiments furnish very strong proofs, because they were originally undertaken without the bias which may be given by a theory. Jordan only intended to decide experimentally whether the numerous forms of the plant, as it occurs wild in different habitats, are mere varieties or true species. He found that the different forms do not pass into one another, and

[1] Compare Rauber, 'Homo sapiens ferus oder die Zustände der Verwilderten.' Leipzig, 1885.

[2] 'Sitzungsberichte der baierischen Akademie der Wissenschaften,' vom 18 Nov. 1865. Compare also his 'Mechanisch-physiologische Theorie der Abstammungslehre,' p. 102, etc.

[3] Jordan, 'Remarques sur le fait de l'existence en société des espèces végétales affines.' Lyon, 1873.

are in all cases re-transformed after they have been altered by cultivation in a soil different from that in which they usually grow, and he therefore assumed that they were true species. All these experiments therefore confirm the conclusion that external influences may alter the individual, but that the changes produced are not transmitted to the germs, and are never hereditary.

Nägeli indeed asserts that innate individual differences do not exist in plants. The differences which we find, for instance, between two beeches or oaks, are always, according to him, modifications produced by the influence of varying local conditions. But it is obvious that Nägeli goes too far in this respect, although it may be conceded that innate individual differences in plants are much more difficult to distinguish from those which are acquired, than in animals.

There is no doubt about the occurrence of innate and hereditary individual characters in animals, and we may find an especially interesting illustration in the case of man. The human eye can with practice appreciate the most minute differences between individual men, and especially differences of feature. Every one knows that peculiarities of feature persist in certain families through a long series of generations. I need hardly remind the reader of the broad forehead of the Julii, the projecting chin of the Hapsburgs, or the curved nose of the Bourbons. Hence every one can see that hereditary individual characters do unquestionably exist in man. The same conclusion may be affirmed with equal certainty for all our domestic animals, and I do not see any reason why there should be any doubt about its application to other animals and to plants.

But now the question arises,—How can we explain the presence of such characters consistently with a belief in the continuity of the germ-plasm, a theory which implies the rejection of the supposition that acquired characters can become hereditary? How can the individuals of any species come to possess various characters which are undoubtedly hereditary, if all changes which are due to the influence of external conditions are transient and disappear with the individual in which they arose? Why is it that individuals are distinguished by innate characters, as well as by those which I have previously called transient, and how can deep-seated hereditary characters arise at all, if they are not produced by the external influences to which the individual is exposed?

In the first place it may be argued that external influences may not only act on the mature individual, or during its development, but that they may also act at a still earlier period upon the germ-cell from which it arises. It may be imagined that such influences of different kinds might produce corresponding minute alterations in the molecular structure of the germ-plasm, and as the latter is, according to our supposition, transmitted from one generation to another, it follows that such changes would be hereditary.

Without altogether denying that such influences may directly modify the germ-cells, I nevertheless believe that they have no share in the production of hereditary *individual* characters.

The germ-plasm or idioplasm of the germ-cell (if this latter term be preferred) certainly possesses an exceedingly complex minute structure, but it is nevertheless a substance of extreme stability, for it absorbs nourishment and grows enormously without the least change in its complex molecular structure. With Nägeli we may indeed safely affirm so much, although we are unable to acquire any direct knowledge as to the constitution of germ-plasm. When we know that many species have persisted unchanged for thousands of years, we have before us the proof that their germ-plasm has preserved exactly the same molecular structure during the whole period. I may remind the reader that many of the embalmed bodies of the sacred Egyptian animals must be four thousand years old, and that the species are identical with those now existing in the same locality. Now, since the quantity of germ-plasm contained in a single germ-cell must be very minute, and since only a very small fraction can remain unchanged when the germ-cell developes into an organism, it follows that an enormous growth of this small fraction must take place in every individual, for it must be remembered that each individual produces thousands of germ-cells. It is therefore not too much to say that, during a period of four thousand years, the growth of the germ-plasm in the Egyptian ibis or crocodile must have been quite stupendous. But in the animals and plants which inhabit the Alps and the far north, we have instances of species which have remained unchanged for a much longer period, viz. for the time which has elapsed between the close of the glacial epoch and the present day. In such organisms the growth of the germ-plasm must therefore have been still greater.

If nevertheless the molecular structure of the germ-plasm has remained precisely the same, this substance cannot be readily modifiable, and there is very little chance of the smallest changes being produced in its molecular structure, by the operation of those minute transient variations in nutrition to which the germ-cells, together with every other part of the organism, are exposed. The rate of growth of the germ-plasm will certainly vary, but its structure is unlikely to be affected for the above-mentioned reasons, and also because the influences are mostly changeable, and occur sometimes in one and sometimes in another direction.

Hereditary individual differences must therefore be derived from some other source.

I believe that such a source is to be looked for in the form of reproduction by which the great majority of existing organisms are propagated: viz. in sexual, or, as Häckel calls it, amphigonic reproduction.

It is well known that this process consists in the coalescence of two distinct germ-cells, or perhaps only of their nuclei. These germ-cells contain the germ-substance, the germ-plasm, and this again, owing to its specific molecular structure, is the bearer of the hereditary tendencies of the organism from which the germ-cell has been derived. Thus in amphigonic reproduction two groups of hereditary tendencies are as it were combined. I regard this combination as the cause of hereditary individual characters, and I believe that the production of such characters is the true significance of amphigonic reproduction. The object of this process is to create those individual differences which form the material out of which natural selection produces new species.

At first sight this conclusion appears to be very startling and almost incredible, because we are on the contrary inclined to believe that the continued combination of existing differences, which is implied by the very existence of amphigonic reproduction, cannot lead to their intensification, but rather to their diminution and gradual obliteration. Indeed the opinion has already been expressed that deviations from the specific type are rapidly destroyed by the operation of sexual reproduction. Such an opinion may be true with regard to specific characters, because the deviations from a specific type occur in such rare cases that they cannot hold their ground against the large number of normal individuals. But the case is different with those minute differences which are characteristic of individuals, because every individual possesses them, although of a different kind and degree. The extinction of such differences could only take place if a few individuals constituted a whole species; but the number of individuals which together represent a species is not only very large but generally incalculable. Cross-breeding between all individuals is impossible, and hence the obliteration of individual differences is also impossible.

In order to explain the effects of sexual reproduction, we will first of all consider what happens in monogonic or unisexual reproduction, which actually occurs in parthenogenetic organisms. Let us imagine an individual producing germ-cells, each of which may by itself develope into a new individual. If we then suppose a species to be made up of individuals which are absolutely identical, it follows that their descendants must also remain identical through any number of generations, if we neglect the transient non-transmissible peculiarities caused by differences of food and other external conditions.

Although the individuals of such a species might be actually different, they would be potentially identical: in the mature state they might differ, but they must have been identical in origin. The germs of all of them must contain exactly the same hereditary tendencies, and if it were possible for their development to take place under exactly the same conditions, identical individuals would be produced.

Let us now assume that the individuals of such a species, reproducing itself by the monogonic process and therefore without cross-breeding, differ, not only in transient but also in hereditary characters. If this were the case, each individual would produce descendants possessing the same hereditary differences which were characteristic of itself; and thus from each individual a series of generations would emanate, the single individuals of which would be potentially identical with each other and with their first ancestor. Hence the same individual differences would be repeated again and again, in each succeeding generation, and even if all the descendants lived to reproduce themselves, there would be at last just as many groups of potentially identical individuals as there were single individuals at the beginning.

Similar cases actually occur in many species in which sexual reproduction has been entirely replaced by the parthenogenetic method, as in many species of *Cynips* and in certain lower Crustacea. But all these differ from our hypothetical case in one important respect; it is always impossible for all the descendants to reach maturity and reproduce themselves. The vast majority of the descendants generally perish at an early stage, and only about as many remain to continue the species as reached maturity in the preceding generation.

We have now to consider whether such a species can be subject to the operation of natural selection. Let us take the case of an insect living among green leaves, and possessing a green colour as a protection against discovery by its enemies. We will assume that the hereditary individual differences consist of various shades of green. Let us further suppose that the sudden extinction of its food-plant compelled this species to seek another plant with a somewhat different shade of green. It is clear that such an insect would not be completely adapted to the new environment. It would therefore be compelled, metaphorically speaking, to endeavour to bring its colour into closer harmony with that of the new food-plant, or else the increased chances of detection given to its enemies would lead to its slow but certain extinction.

It is obvious that such a species would be altogether unable to produce the required adaptation, for *ex hypothesi*, its hereditary variations remain the same, one generation after another. If therefore the required shade of green was not previously present, as one of the original individual differences, it could not be produced at any time. If, however, we suppose that such a colour existed previously in certain individuals, it follows that those with other shades of green would be gradually exterminated, while the former would alone survive. But this process would not be an adaptation in the sense used in the theory of natural selection. It would indeed be a process of selection, but it could form no more than the beginning of that process which we call natural selection. If the latter could only bring existing characters into prominence, it would not be worth much consideration, for it could never produce a new species. A species never includes, from the beginning, individuals which deviate from the specific type as widely as the individuals of the most nearly allied species deviate from it. And it would be still less possible to explain, on such a principle, the origin of the whole organic world; for, if so, all existing species would have been included as variations of the first species. Natural selection must be able to do infinitely more than this, if it is to be of any importance as a principle of development. It must be able to accumulate minute existing differences in the required direction, and thus to create new characters. In our example it ought to be able, after preserving those individuals with a colour nearest to the required shade, to lead their descendants onward through successive stages towards a complete harmony of colour.

But such a result is quite unattainable with the asexual method of reproduction: in other words, natural selection, in the true meaning of the term, viz. a process which could produce new characters in the manner above described, is an impossibility in a species propagated by asexual reproduction.

If it could be shown that a purely parthenogenetic species had become transformed into a new one, such an observation would prove the existence of some force of transformation other than selective processes, for the new species could not have been produced by these latter. As already explained, the only selection which would be possible for such a species, would lead to the survival of one group of individuals and to the extinction of all others. Thus in our example that group of individuals would alone survive, the ancestors of which originally possessed the appropriate colour. But if one group alone survived, it follows that all hereditary individual differences would have disappeared from the species, for the members of such a single group are identical with one another and with their original ancestors. We thus reach the conclusion that monogonic reproduction can never cause hereditary individual variability, but that, on the other hand, it is very likely to lead to its entire suppression.

But the case is very different with sexual reproduction. When once individual differences have begun to appear in a species propagated by this process, uniformity among its individuals can never again be reached. So far from this being the case, the differences must even be increased in the course of generations, not indeed in intensity, but in number, for new combinations of the individual characters will continually arise.

Again, assuming the existence of a number of individuals which differ from one another by a few hereditary individual characters, *it follows that no individual of the second generation can be identical with any other.* They must all differ, not only actually but also potentially, for their differences exist at the very beginning of development, and do not solely depend upon the accidental conditions under which they live. Moreover, no one of the descendants can be identical with any of the ancestors, for each of the former unites within itself the hereditary tendencies of two parents, and its organism is therefore, as it were, a compromise between two developmental tendencies. Similarly in the third generation, the hereditary tendencies of two individuals of the second generation enter into combination. But since the germ-plasm of the latter *is not simple, but composed of two individually distinct kinds of* germ-plasm, it follows that an individual of the third generation is a compromise between four different hereditary tendencies. In the fourth generation, eight; in the fifth, sixteen; in the sixth, thirty-two different hereditary tendencies must come together, and each of them will make itself more or less felt in some part of the future organism. Thus by the sixth generation a large number of varied combinations of ancestral individual characters will appear, combinations which have never existed before and which can never exist again.

We do not know the number of generations over which the specific hereditary tendencies of the *first generation can make* themselves felt. Many facts seem to indicate however that the number is large, and it is at all events greater than six. When we remember that, in the tenth generation, a single germ contains 1024 different germ-plasms, with their inherent hereditary tendencies, it is quite clear that continued sexual reproduction can never lead to the re-appearance of exactly the same combination, but that new ones must always arise.

New combinations are all the more probable because the different idioplasms composing the germ-plasm in the germ-cells of any individual are present in different degrees of intensity at different times of its life; in other words, the intensity of the component idioplasms is a function of time. This conclusion follows from the fact that children of the same parents are never exactly identical. In one child the characters of the father may predominate, in another those of the mother, in another again those of either grand-parent or great-grand-parent.

We are thus led to the conclusion that even in a few sexually produced generations a large number of well-marked individuals must arise: and this would even be true of generations springing from our hypothetical species, assumed to be without ancestors, and characterised by few individual differences. But of course organisms which reproduce themselves sexually are never without ancestors, and if these latter were also propagated by the sexual method, it follows that each generation of every sexual species is in the stage which we have previously assumed for the tenth or some much later generation of the hypothetical species. In other words, each individual contains a maximum of hereditary tendencies and an infinite variety of possible individual characters (see Appendix VI, p. 326).

In this manner we can explain the origin of hereditary individual variability as it is known in man and the higher animals, and as it is required for the theory which explains the transformation of species by means of natural selection.

Before proceeding further, I must attempt to answer a question which obviously suggests itself. For the sake of argument, I have assumed the existence of a first generation, of which the individuals were already characterised by individual differences. Can we find any explanation of these latter, or are we compelled to take them for granted, without any attempt to enquire into their origin? If we abandon this enquiry, we can never achieve a complete solution of the problems of heredity and variability. We have, it is true, shown that hereditary differences, when they have once appeared, would, through sexual reproduction, undergo development into the diverse forms which actually exist; but this conclusion affords us no explanation of the source whence such differences have been derived. If the external conditions acting directly upon an organism can only produce transient (viz. non-hereditary) differences in the latter, and if, on the other hand, the external influences which act upon the germ-cell can only produce a change in its molecular structure after operating over very long periods, it seems that we have exhausted all the possible sources of hereditary differences without reaching any satisfactory explanation.

I believe, however, that an explanation can be given. The origin of hereditary individual variability cannot indeed be found in the higher organisms—the Metazoa and Metaphyta; but it is to be sought for in the lowest—the unicellular organisms. In these latter the distinction between body-cell and germ-cell does not exist. Such organisms are reproduced by division, and if therefore any one of them becomes changed in the course of its life by some external influence, and thus receives an individual character, the method of reproduction ensures that the acquired peculiarity will be transmitted to its descendants. If, for instance, a Protozoon, by constantly struggling against the mechanical influence of currents in water, were to gain a somewhat denser and more resistent protoplasm, or were to acquire the power of adhering more strongly than the other individuals of its species, the peculiarity in question would be directly continued on into its two descendants, for the latter are at first nothing more than the two halves of the former. It therefore follows that every modification which appears in the course of its life, every individual character, however it may have arisen, must necessarily be directly transmitted to the two offspring of a unicellular organism.

The pianist, whom I have already used as an illustration, may by practice develope the muscles of his fingers so as to ensure the highest dexterity and power; but such an effect would be entirely transient, for it depends upon a modification in local nutrition which would be unable to cause any change in the molecular structure of the germ-cells, and could not therefore produce any effect upon the offspring. And even if we admit that some change might be caused in the germ-cells, the chances would be infinity to nothing against the production of the appropriate effect, viz. such a change as would lead to the development in the child of the acquired characters of the parent.

In the lowest unicellular organisms, however, the case is entirely different. Here parent and offspring are still, in a certain sense, one and the same thing: the child is a part, and usually half, of the parent. If therefore the individuals of a unicellular species are acted upon by any of the various external influences, it is inevitable that hereditary individual differences will arise in them; and as a matter of fact it is indisputable that changes are thus produced in these organisms, and that the resulting characters are transmitted. It has been directly observed that individual differences do occur in unicellular organisms,—differences in size, colour, form, and the number or arrangement of cilia. It must be admitted that we have not hitherto paid sufficient attention to this point, and moreover our best microscopes are only very rough means of observation when we come to deal with such minute organisms. Nevertheless we cannot doubt that the individuals of the same species are not absolutely identical.

We are thus driven to the conclusion that the ultimate origin of hereditary individual differences lies in the direct action of external influences upon the organism. Hereditary variability cannot however arise in this way at every stage of organic development, as biologists have hitherto been inclined to believe. It can only arise in the lowest unicellular organisms; and when once individual difference had been attained by these, it necessarily passed over into the higher organisms when they first appeared. Sexual reproduction coming into existence at the same time, the hereditary differences were increased and multiplied, and arranged in ever-changing combinations.

Sexual reproduction can also increase the differences between individuals, because constant cross-breeding must necessarily and repeatedly lead to a combination of forces which tend in the same direction, and which may determine the constitution of any part of the body. If, for instance, the same part of the body is strongly developed in both parents, the experience of breeders tells us that the part in question is likely to be even more strongly developed in the offspring; and that weakly developed parts will in the same manner tend to become still weaker. Amphigonic reproduction therefore ensures that every character which is subject to individual fluctuation must appear in many individuals with a strengthened degree of development, in many others with a development which is less than normal, while in a still larger number of individuals the average development will be reached. Such differences afford the material by means of which natural selection is able to increase or weaken each character according to the needs of the species. By the removal of the less well-adapted individuals, natural selection increases the chance of beneficial cross-breeding in the subsequent generations.

Every one must admit that, if a species came into existence having only a small number of individual differences which appeared in the different parts of different individuals, the number of differences would increase with each sexually produced generation, until all the parts in which the variations occurred had received a peculiar character in all individuals.

Moreover sexual reproduction not only adds to the number of existing differences, but it also brings them into new combinations, and this latter consequence is as important as the former.

The former consequence can hardly make itself felt in any existing species, because in them every part already possesses its peculiar character in all individuals. The second consequence is, however, more important, viz. the production of new combinations of individual characters by sexual reproduction; for, as Darwin has already pointed out, we must imagine that not only are single characters changed in the process of breeding, but that probably several, and perhaps very many characters, are simultaneously modified. No two species, however nearly allied, differ from each other in but a single character. Even our eyesight, which has by no means reached the highest pitch of development, can always detect several, and often very many points of difference; and if we possessed the powers necessary for making an absolutely accurate comparison, we should probably find that everything is different in two nearly allied species.

It is true that a great number of these differences depend upon correlation, but others must depend upon simultaneous primary changes.

A large butterfly (*Kallima paralecta*), found in the East Indian forests, has often been described in its position of rest as almost exactly resembling a withered leaf; the resemblance in colour being aided by the markings which imitate the venation of a leaf. These markings are composed of two parts, the upper of which is on the fore-wings, while the lower one is on the hind wings. The butterfly when at rest must therefore keep the wings in such a position that the two parts of each marking exactly correspond, for otherwise the character would be valueless; and as a matter of fact the wings are held in the appropriate position, although the butterfly is of course unconscious of what it is doing. Hence a mechanism must exist in the insect's brain which compels it to assume this attitude, and it is clear that the mechanism cannot have been developed before the peculiar manner of holding the wings became advantageous to the butterfly, viz. before the similarity to a leaf had made its first appearance. Conversely, this latter resemblance could not develope before the butterfly had gained the habit of holding its wings in the appropriate position. Both characters must therefore have come into existence simultaneously, and must have undergone increase side by side: the marking progressing from an imperfect to a very close similarity, while the position of the wings gradually approached the attitude which was exactly appropriate. The development of certain minute structural elements of the central nervous system, and the appropriate distribution of colouring matter on the wings, must have taken place simultaneously, and only those individuals have been selected to continue the species which possessed the favourable variations in both these directions.

It is, however, obvious that sexual reproduction will readily afford such combinations of required characters, for by its means the most diverse features are continually united in the same individual, and this seems to me to be one of its most important results.

I do not know what meaning can be attributed to sexual reproduction other than the creation of hereditary individual characters to form the material upon which natural selection may work. Sexual reproduction is so universal in all classes of multicellular organisms, and nature deviates so rarely from it, that it must necessarily be of pre-eminent importance. If it be true that new species are produced by processes of selection, it follows that the development of the whole organic world depends on these processes, and the part that amphigony has to play in nature, by rendering selection possible among multicellular organisms, is not only important, but of the very highest imaginable importance.

But when I maintain that the meaning of sexual reproduction is to render possible the transformation of the higher organisms by means of natural selection, such a statement is not equivalent to the assertion that sexual reproduction originally came into existence in order to achieve this end. The effects which are now produced by sexual reproduction did not constitute the causes which led to its first appearance. Sexual reproduction came into existence before it could lead to hereditary individual variability. Its first appearance must therefore have had some other cause; but the nature of this cause can hardly be determined with any degree of certainty or precision from the facts with which we are at present acquainted. The general solution of the problem will, however, be found to lie in the conjugation of unicellular organisms, which forms the precursor of true sexual reproduction. The coalescence of two unicellular individuals which represents the simplest and therefore probably the most primitive form of conjugation, must have some directly beneficial effect upon the species in which it occurs.

Various assumptions may be made as to the nature of these beneficial effects, and it will be useful to consider in detail some of those suggestions which have been brought forward. Eminent biologists, such as Victor Hensen [1] and Edouard van Beneden [2], believe that conjugation, and indeed sexual reproduction generally, must be considered as 'a rejuvenescence of life.' Bütschli also accepts this view, at any rate as regards conjugation. These authorities imagine that the wonderful phenomena of life, of which the underlying cause is still an unsolved problem, cannot be continued indefinitely by the action of forces arising from within itself, that the clock-work would be stopped after a longer or shorter time, that the reproduction of purely asexual organisms would cease, just as the life of the individual finally comes to an end, or as a spinning wheel comes to rest in consequence of friction, and requires a renewed impetus if its motion is to continue. In order that reproduction may continue without interruption, these writers believe that a rejuvenescence of the living substance is necessary, that the clock-work of reproduction must be wound up afresh; and they recognize such a rejuvenescence in sexual reproduction and in conjugation, or in other words in the fusion of two cells, whether in the form of germ-cells or of two unicellular organisms.

Edouard van Beneden expresses this idea in the following words:—'Il semble que la faculté que possèdent les cellules, de se multiplier par division soit limitée: il arrive un moment où elles ne sont plus capables de se diviser ultérieurement, à moins qu'elles ne subissent le phénomène du rajeunissement par le fait de la fécondation.

[1] S. Hermann's 'Handbuch der Physiologie,' Theil II; 'Physiologie der Zeugung,' by V. Hensen.

[2] E. van Beneden, 'Recherches sur la maturation de l'œuf, la fécondation et la division cellulaire.' Gand u. Leipzig, 1883, pp. 404 et seq.

Chez les animaux et les plantes les seules cellules capables d'être rajeunies sont les œufs; les seules capables de rajeunir sont les *spermatocytes. Toutes les autres parties de l'individu sont vouées* à la mort. La fécondation est la condition de la continuité de la vie. Par elle le générateur échappe à la mort' (l. c., p. 405). Victor Hensen thinks it possible that the germ and its products are prevented from dying by means of normal fertilization: he says that the law which states that every egg must be fertilized, was formulated before the discovery of parthenogenesis and cannot now be maintained, but that we are nevertheless compelled to assume that even the most completely parthenogenetic species requires fertilization after many generations (l. c., p. 236).

If the theory of rejuvenescence be thoroughly examined, it will be *found to be nothing more than the expression* of the fact that sexual reproduction persists without any ascertainable limit. From the fact of its general occurrence, the conclusion is, however, drawn that asexual reproduction could not persist indefinitely as the only mode of reproduction in any species of animal. But proofs in support of this opinion are wanting, and it is very probable that it would never have been advanced if it had been possible to explain the general occurrence of sexual reproduction in any other way,—if we had been able to ascribe any other significance to this pre-eminently important process.

But quite apart from the fact that it is impossible to bring forward any proofs, the theory of rejuvenescence seems to me to be unsatisfactory in other ways. The whole conception of rejuvenescence, although very ingenious, has something uncertain about it, and can hardly be brought into accordance with the usual conception of life as based upon physical and mechanical forces. How can any one imagine that an Infusorian, which by continued division had lost its power of reproduction, could regain this power by forming a new individual, after fusion with another Infusorian, which had similarly become incapable of division? Twice nothing cannot make one. If indeed we could assume that each animal contained half the power necessary for reproduction, then both together would certainly form an efficient whole; but it is hardly possible to apply the term rejuvenescence to a process which is simply an addition, such as would be attained under other circumstances by mere growth; neglecting, for the present, that factor which, in my opinion, is of the utmost importance in conjugation,—the fusion of two hereditary tendencies. If rejuvenescence possesses any significance at all, it must be this,—that by its means a force, which did not previously exist in the conjugating individuals, is called into activity. Such a force would, however, owe its existence to latent energy stored up in each single animal during the period of asexual reproduction, and such latent forces would necessarily be of different natures, and of such a constitution that their union at the moment of conjugation would give rise to the active force of reproduction.

The process might perhaps be compared to the flight of two rockets, which by the combustion of some explosive substance (such as nitro-glycerine) stored up within themselves are impelled in such a direction that they would meet at the end of their course, when all the nitro-glycerine had been completely exhausted. The movement would then come to an end, unless the explosive material could have been meanwhile renewed. Now suppose that such a renewal were achieved by the formation of nitric acid in one of the rockets and glycerine in the other, so that when they came into contact nitro-glycerine would be formed afresh equal in quantity and in distribution on both the rockets to that which was originally present. In this way the movement would be renewed again and again with the same velocity, and might continue for ever.

Rejuvenescence can be rendered intelligible in theory by some such metaphor, but considerable difficulties are encountered in the rigid application of the metaphor to the facts of the case. In the first place, how is it possible that the motive force can be exhausted by continual division, while one of its components is being formed afresh in the same body and during the same time? When thoroughly examined the loss of the power of division is seen to follow from the loss of the powers of assimilation, nutrition, and growth. How is it possible that such a power can be weakened and finally entirely lost while one of its components is accumulated?

I believe that, instead of accepting such daring assumptions, it is better to be satisfied with the simple conception of living matter possessing as attributes the powers of unlimited assimilation and capacity for reproduction. With such a theory the mere form of reproduction, whether sexual or asexual, will have no influence upon the duration of the capacity: for force and matter undergo simultaneous increase, and are inseparably connected in this as in all other instances. This theory does not, however, exclude the possible occurrence of circumstances under which such an association is no longer necessary.

I could only consent to adopt the hypothesis of rejuvenescence, if it were rendered absolutely certain that reproduction by division could never under any circumstances persist indefinitely. But this cannot be proved with any greater certainty than the converse proposition, and hence, as far as direct proof is concerned, the facts are equally uncertain on both sides. The hypothesis of rejuvenescence is, however, opposed by the fact of parthenogenesis; for if fertilization possesses in any way the meaning of rejuvenescence, and depends upon the union of two different forms of force and of matter, which thus produce the power of reproduction, it follows that we cannot understand how it happens that the same power of reproduction may be sometimes produced from one form of matter, alone and unaided. Logically speaking, parthenogenesis should be as impossible as that either nitric acid or glycerine should separately produce the effect of nitro-glycerine. The supposition has indeed been made that in the case of parthenogenesis, one fertilization is sufficient for a whole series of generations, but this supposition is not only incapable of proof, but it is contradicted by the fact that certain eggs which may develope parthenogenetically are also capable of fertilization. If, in this case, the power of reproduction were sufficient for development, how is it that the egg is also capable of fertilization; and if the power were insufficient, how is it that the egg can develope parthenogenetically? And yet one and the same egg (in the bee) can develope into a new individual, with or without fertilization. We cannot escape this dilemma by making the further assumption, which is also incapable of proof, that a smaller amount of reproductive force is required for the development of a male individual than for the development of a female. It is true that the unfertilized eggs of the bee produce male individuals, while the fertilized ones develope into females, but in certain other species the converse association holds good, while in others, again, fertilization bears no relation to the sex of the offspring.

Although the mere fact that parthenogenesis occurs at all is, in my opinion, sufficient to disprove the theory of rejuvenescence, it is well to remember that parthenogenesis is now the only method of reproduction in many species (although we do not know the period of time over which these conditions have extended), and is nevertheless unattended by any perceptible decrease in fertility.

From all these considerations we may draw the conclusion that the process of rejuvenescence, as described above, cannot be accepted either as the existing or the original meaning of conjugation, and the question naturally arises as to what other significance this latter process can have possessed at its first beginning.

Rolph[1] has expressed the opinion that conjugation is a form of nutrition, so that the two conjugating individuals, as it were, devour each other. Cienkowsky[2] also regards conjugation as merely accelerated' assimilation. There is, however, not only an essential difference but a direct contrast between the processes of conjugation and nutrition. With regard to Cienkowsky's view, Hensen[3] has well said that 'coalescence in itself cannot be an accelerated nutrition, because even if we admit that both individuals are in want of nourishment, it is impossible that the need can be supplied by this process, unless one of them perishes and is really devoured.' In order that an animal may serve as the food of another, it must perish and must be brought into a fluid form, and finally it must be assimilated. In the case before us, however, two protoplasmic bodies are placed side by side and coalesce, without either of them passing into the liquid state. Two idioplasms unite, together with all the hereditary tendencies contained in them; but although it is certain that nutrition in the proper sense of the word cannot take place, because neither of the animals receives an addition of liquid food by the coalescence, yet the consequence of this process must be in one respect similar to that of nutrition and growth:—the mass of the body and the quantity of the forces contained in it undergo simultaneous increase. It is not inconceivable that effects are by this means rendered possible, which under the peculiar circumstances leading to conjugation, could not have been otherwise produced.

I believe that this is at any rate the direction in which we shall have to seek for the first meaning of conjugation, and for its

[1] Rolph, 'Biologische Probleme.' Leipzig, 1882.

[2] Cienkowsky, 'Arch. f. mikr. Anat.,' ix. p. 47. 1873.

[3] Hensen, 'Physiologie der Zeugung,' p. 139.

phyletic origin. This first result and meaning of conjugation may be provisionally expressed in the following formula:—conjugation originally signified a strengthening of the organism in relation to reproduction, which happened when from some external cause, such as want of oxygen, warmth, or food, the growth of the individual to the extent necessary for reproduction could not take place.

This explanation must not be regarded as equivalent to that afforded by the theory of rejuvenescence; for the latter process is said to be necessary for the continuance of reproduction, and ought therefore to occur periodically quite independently of external circumstances; while according to my theory, conjugation at first only occurred under unfavourable conditions, and assisted the species to overcome such difficulties.

But whatever the original meaning of conjugation may have been, it seems to have become already subordinated in the higher Protozoa, as is indicated by the changes in the course taken by this process. The higher Protozoa when conjugating do not as a rule coalesce completely and permanently[1] in the manner followed by the lower Protozoa, and it seems to me possible, or even probable, that in the former the process has already gained the full significance of sexual reproduction, and is to be looked upon as a source of variability.

Whether this be so or not, I believe it is certain that sexual reproduction could not have been entirely abandoned at any period since the time when the Metazoa and Metaphyta first arose; for they derived this form of reproduction from their unicellular ancestors.

We know that organs and characters which have persisted through a long series of generations are transmitted with extreme tenacity, even when they have ceased to be of any direct use to their immediate possessors. The rudimentary organs in various animals, and not least in man, afford very strong proofs of the soundness of this conclusion. Another example has only recently been discovered in the sixth finger, which has been shown to exist in the human embryo[2], a part which has only been present in a rudimentary

[1] Coalescence takes place in the so-called bud-like conjugation of *Vorticellidae* and *Trichodinidae*, etc.

[2] Compare (1) Bardeleben, 'Zur Entwicklung der Fusswurzel,' Sitzungsber. d. Jen. Gesellschaft, Jahrg. 1885, Feb. 6; also 'Verhandl. d. Naturforscherversammlung zu Strassburg,' 1885, p. 203; (2) G. Baur, 'Zur Morphologie des Carpus und Tarsus der Wirbelthiere,' Zool. Anzeiger, 1885, pp. 326, 486.

form ever since the origin of the Amphibia[1]. Superfluous organs become rudimentary very slowly, and enormous periods must elapse before they completely disappear, while the older a character is, the more firmly it becomes rooted in the organism. What I have above called the physical constitution of a species is based upon these facts, and upon them depend the *tout ensemble* of inherited characters, which are adapted to one another and woven together into a harmonious whole. It is this specific nature of an organism which causes it to respond to external influences in a manner different from that followed by any other organism, which prevents it from changing in any way except along certain definite lines of variation, although these may be very numerous. Furthermore these facts ensure that characters cannot be taken at random from the constitution of a species and others substituted for them. Such a variation as a mammal wanting the firm axis of the backbone is an impossibility, not only because the backbone is necessary as a support to the body, but chiefly because this structure has been inherited from times immemorial, and has become so impressed upon the mammalian organization that any variation so great as to threaten its very existence cannot now take place. The view here set forth of the origin of hereditary variability by amphigonic reproduction, makes it clear that an organism is in a state of continual oscillation only upon the surface, so to speak, while the fundamental parts of its constitution, which have been inherited from extremely remote periods, remain unaffected.

Thus sexual reproduction itself did not cease after it had existed in the form of conjugation through innumerable generations of the vast numbers of species which have been included under the Protozoa; it did not cease even when its original physiological significance had lost its importance, either completely or in part. This process, however, had come to possess a new significance which ensured its continuance, in the enormous advantage conferred on a species by the power of adapting itself to new conditions of life, a power which could only be preserved by means of this method of reproduction. The formation of new species which among the lower Protozoa could be achieved without amphigony, could only be attained by means of this process in the Metazoa and Metaphyta. It was only

[1] In frogs the sixth toe exists in the hind legs as a rudimentary prehallux. Compare Born, Morpholog. Jahrbuch, Bd. I, 1876.

in this way that hereditary individual differences could arise and persist. It was impossible for amphigony to disappear, for each species in which it was preserved was necessarily superior to those which had lost it, and must have replaced them in the course of time; for the former alone could adapt itself to the ever-changing conditions of life, and the longer sexual reproduction endured, the more firmly was it necessarily impressed upon the constitution of the species, and the more difficult its disappearance became.

Sexual reproduction has nevertheless been lost in some cases, although only at first in certain generations. Thus in the *Aphidae* and in many lower Crustacea, generations with parthenogenetic reproduction alternate with others which reproduce themselves by the sexual method. But in most cases it is clear that this partial loss of amphigony conferred considerable advantages upon the species by giving increased capabilities for the maintenance of existence. By means of partial parthenogenesis a much more rapid increase in the number of individuals could be attained in a given time, and this fact is of the highest importance for the peculiar circumstances under which these species exist. A species of Crustacean which inhabits rapidly drying pools, and developes from winter-eggs which have remained dried up in the mud, has, as a rule, only a very short time in which to secure the existence of succeeding generations. The few sexual eggs which have escaped the attacks of numerous enemies develope immediately after the first shower of rain; the animals attain their full size in a few days and reproduce themselves as virgin females. Their descendants are propagated in the same manner, and thus in a short time almost incredible numbers of individuals are formed, until finally the sexual eggs are again produced. If now the pool dries up again, the existence of the colony is secured, for the number of animals which produce sexual eggs is very large, and the eggs themselves are of course far more numerous, so that in spite of the destructive agencies to which they are subjected, there will be every chance of the survival of a sufficient number to produce a new generation at a later period. Here, therefore, sexual reproduction has not been abandoned accidentally or from any internal cause, but as an adaptation to certain definite necessities imposed upon the organism by its surroundings.

It is, however, well known that there are certain instances in which sexual reproduction has been altogether lost, and in which parthenogenesis is the only form of propagation. In the animal kingdom, such a condition chiefly occurs in species of which the closely-allied forms exhibit the above-mentioned alternation between parthenogenesis and amphigony, viz. in many *Cynipidae* and *Aphidae*, and also in certain freshwater and marine Crustacea. We may imagine that these parthenogenetic species have arisen from forms with alternating methods of reproduction, by the disappearance of the sexual phase.

In any particular case, it may be difficult to point out the motive by which this change has been determined; but it is most probable that the same conditions which originally caused the intercalation of a parthenogenetic stage have been efficient in causing the gradual disappearance of the sexual stage. If a species of Crustacean, with the above-described alternating method of reproduction (heterogeny), were killed off by its enemies on a larger scale than before, it is obvious that the threatened extinction of the species could be checked by the attainment of a correspondingly greater degree of fertility. Such increased fertility might well be produced by pure parthenogenesis (see Appendix V, p. 323), by means of which the number of egg-producing individuals in all the previous sexual generations would be doubled.

In a certain sense, this would be the last and most extreme method by means of which a species might secure continued existence, for it is a method for which it would have to pay very dearly at a later period. If my theory as to the causes of hereditary individual variability be correct, it follows that all species with purely parthenogenetic reproduction are sure to die out; not, indeed, because of any failure in meeting the existing conditions of life, but because they are incapable of transforming themselves into new species, or, in fact, of adapting themselves to any new conditions. Such species can no longer be subject to the process of natural selection, because, with the disappearance of sexual reproduction, they have also lost the power of combining and increasing those hereditary individual characters which they possess.

All the facts with which we are acquainted confirm this conclusion, for whole groups of purely parthenogenetic species or genera are never met with, as would certainly be the case if parthenogenesis had been the only method of reproduction through a successional series of species. We always find it in isolated instances, and under conditions which compel the conclusion that it has become predominant in the species in question, and has not been transmitted from any preceding species.

There still remains a very different class of facts which, so far as we can judge, are in accordance with my theory as to the significance of sexual reproduction, and which may be quoted in its support. I refer to the condition of functionless organs in species with parthenogenetic reproduction.

Under the supposition that acquired characters cannot be transmitted—and this forms the foundation of the views here set forth—organs which are of no further use cannot become rudimentary in the direct and simple manner in which it has been hitherto imagined that degeneration takes place. It is true that an organ which does not perform any function exhibits a marked decrease of strength and perfection in the individual which possesses it, but such acquired degradation is not transmitted to its descendants, and we must therefore look for some other explanation of the firmly established fact that organs do become rudimentary through a series of generations. In seeking this explanation, we shall have to start from the supposition that new forms are not only created by natural selection, but are also preserved by its means. In order that any part of the body of an individual of any species may be kept at the maximum degree of development, it is necessary that all individuals possessing it in a less perfect form must be prevented from propagation—they must succumb in the struggle for existence. I will illustrate this by a special instance. In species which, like the birds of prey [1], depend for food upon the acuteness of their vision, all individuals with relatively weak eyesight must be exterminated, because they will fail in the competition for food. Such birds will perish before they have reproduced themselves, and their imperfect vision is not further transmitted. In this way the keen eyesight of birds of prey is kept up to its maximum.

But as soon as an organ becomes useless, the continued selection of individuals in which it is best developed must cease, and a process which I have termed *panmixia* takes place. When this

[1] I here make use of the same illustration which I employed in my first attempt to explain the effects of *panmixia*. Compare the second Essay 'On Heredity.'

process is in operation, not only those individuals with the best-developed organs have the chance of reproducing themselves, but also those individuals in which the organs are less well-developed. Hence follows a mixture of all possible degrees of perfection, which must in the course of time result in the deterioration of the average development of the organ. Thus a species which has retired into dark caverns must necessarily come to gradually possess less developed powers of vision; for defects in the structure of the eyes, which occur in consequence of individual variability, are not eliminated by natural selection, but may be transmitted and fixed in the descendants[1]. This result is all the more likely to happen, inasmuch as other organs which are of importance for the life of the species will gain what the functionless organ loses in size and nutrition. As at each stage of retrogressive transformation individual fluctuations always occur, a continued decline from the original degree of development will inevitably, although very slowly, take place, until the last remnant finally disappears. How inconceivably slowly this process goes on is shown by the numerous cases of rudimentary organs: by the above-mentioned embryonic sixth finger of man, or by the hind limbs of whales buried beneath the surface of the body, or by their embryonic tooth-germs. I believe that the very slowness with which functionless organs gradually disappear, agrees much better with my theory than with the one which has been hitherto held. The result of the disuse of an organ is considerable, even in the course of a single individual life, and if only a small fraction of such a result were transmitted to the descendants, the organ would be necessarily reduced to a minimum, in a hundred or at any rate in a thousand generations. But how many millions of generations may have elapsed since e.g. the teeth of the whalebone whales became useless, and were replaced by whalebone! We do not know the actual number of years, but we know that the whole material of the tertiary rocks has been derived from the older strata, deposited in the sea, elevated,

[[1] E. Ray Lankester has suggested (Encycl. Britann., art. 'Zoology,' pp. 818, 819) that the blindness of cave-dwelling and deep-sea animals is also due to the fact that 'those individuals with perfect eyes would follow the glimmer of light and eventually escape to the outer air or the shallower depths, leaving behind those with imperfect eyes to breed in the dark place. A natural selection would thus be effected.' Such a sifting process would certainly greatly quicken the rate of degeneration due to panmixia alone.—E. B. P.]

and has been itself largely removed by denudation, since that time.

Now if this theory as to the causes of deterioration in disused organs be correct, it follows that rudimentary organs can only occur in species with sexual reproduction, and that they cannot be formed in species which are exclusively reproduced by the parthenogenetic method: for, according to my theory, variability depends upon sexual reproduction, while the deterioration of an organ when disused, no less than its improvement when in use, depends upon variability. There are therefore two reasons which lead us to expect that organs which are no longer used will remain unreduced in species with asexual reproduction: first, because only a very slight degree of hereditary variability can be present, viz. such a degree as was transmitted from the time when sexual reproduction was first abandoned by the ancestors; and, secondly, because even these slight degrees of variability are not combined, or, in other words, because panmixia cannot occur.

And the facts seem to point in the direction required by the theory, for superfluous organs do not become rudimentary in parthenogenetic species. For example, as far as my experience goes, the *receptaculum seminis* does not deteriorate, although it is, of course, altogether functionless when parthenogenesis has become established. I do not attach much importance to the fact that the Psychids and Solenobias—(genera of Lepidoptera which Siebold and Leuckart have shown to include species with parthenogenetic reproduction)—still retain the complete female sexual apparatus, because colonies containing males still occasionally occur in these species. Although the majority of colonies are now purely female, the occasional appearance of males points to the fact that the unisexuality of the majority cannot have been of very long duration. The process of transformation of the species from a bisexual into a unisexual form, only composed of females, is obviously incomplete, and is still in process of development. The case is similar with several species of *Cynipidae*, which reproduce by the parthenogenetic method. In these cases the occurrence of a very small proportion of males is the general rule, and is not confined to single colonies. Thus Adler[1] counted 7 males and 664 females in the common *Cynips* of the rose.

[1] Adler, 'Zeitschrift f. wiss. Zool.,' Bd. XXXV, 1881.

In some Ostracodes, on the other hand, the males appear to be entirely wanting: at least, I have tried in vain for years to discover them in any locality or at any time of the year[1].

Cypris vidua and *Cypris reptans* are such species. Now, although the transformation of these formerly bisexual species into purely unisexual female species appears to be complete[2], yet the females still possess a large, pear-shaped *receptaculum seminis*, with its long spirally twisted duct, which is surrounded by a thick glandular layer. This is the more remarkable as the apparatus is very complicated in the Ostracodes, and retrogressive changes could be therefore easily detected. Furthermore among insects, in the genus *Chermes* the *receptaculum seminis* of the females has also remained unreduced, although the males appear to be entirely wanting, or at least have never been found, in spite of the united efforts of several acute observers[3]. The case is quite different in species which retain both sexual and parthenogenetic reproduction. Thus, the summer females of the *Aphidae* have lost the *receptaculum seminis*; and in these insects sexual reproduction has not ceased, but alternates regularly with parthenogenetic reproduction.

Certainly this proof of the truth of my theory as to the significance of sexual reproduction is far from settling the question: it only renders the theory highly probable. At present it is impossible to do more than this, because we do not yet possess a sufficient number of facts, for many of them could not have been sought for until after the theory had been suggested. We are here concerned with complicated phenomena, into which we cannot acquire an immediate insight, but can only attain it gradually.

But, nevertheless, I hope to have shown that the theory of

[1] Compare my paper, 'Parthenogenese bei den Ostracoden,' in 'Zool. Anzeiger,' 1880, p. 82. Purely negative evidence, unless on an immense scale, is quite rightly considered to be of no great value in most cases. But the condition of these animals renders the accumulation of such evidence unusually easy, because the presence of males in a colony of Ostracodes can be proved by a very simple indirect test. Thus if a colony contains any males the *receptacula seminis* of all mature females are filled with spermatozoa, and on the other hand we may be quite sure that males are absent, if after the examination of many mature females, no spermatozoa can be found in any of their *receptacula*.

[2] We cannot, however, be absolutely certain of this, for it is conceivable that males may still occur in colonies other than those examined.

[3] It has now been shown by Blochmann that males appear for a very short time towards the close of summer, as in the case of *Phylloxera*.—A.W., 1888.

natural selection is by no means incompatible with the theory of 'the continuity of the germ-plasm;' and, further, that if we accept this latter theory, sexual reproduction appears in an entirely new light: it has received a meaning, and has to a certain extent become intelligible.

The time in which men believed that science could be advanced by the mere collection of facts has long passed away: we know that it is not necessary to accumulate a vast number of miscellaneous facts, or to make as it were a catalogue of them; but we know that it is necessary to establish facts which, when grouped together in the light of a theory, will enable us to acquire a certain degree of insight into some natural phenomenon. In order to direct our attention to those new facts which are of immediate importance, it is absolutely necessary to seek the aid of some general theory for the arrangement and grouping of those which we already possess. This has been my object in the present paper.

But it may be perhaps objected that these phenomena are far too complicated to be attacked at the present time, and that we ought to wait quietly until the simpler phenomena have been resolved into their components. It may be asked whether the trouble and labour involved in the attempt to solve such questions as heredity or the transformation of species are not likely to be wasted and useless.

It is true that we sometimes meet with such opinions, but I believe that they are based upon a misunderstanding of the method which mankind has always followed in the investigation of nature, and which must therefore be founded upon the necessary relations existing between mankind and nature.

Science has often been compared to an edifice which has been solidly built by laying stone upon stone, until it has gradually risen to greater height and perfection. This comparison holds good up to a certain point, but it leads us to easily overlook the fact that this metaphorical building does not at any point rest upon the ground, and that, at least up to the present time, it has remained floating in the air. Not a single branch of science, not even Physics itself, has commenced building from below; all branches have begun to build at greater or less heights in the air, and have then built downwards: and even Physics has not yet reached the ground, for it is still very uncertain as to the nature of matter and force. In no single group of phenomena can we begin with the investigation of ultimate causes, because at this very point our means of reasoning stop short. We cannot begin with ultimate phenomena and gradually lead up to those which are more complicated: we cannot proceed synthetically and deductively, building up the phenomena from below; but we must as a rule proceed analytically and inductively, proceeding from above downwards.

No one will dispute these statements, but they are often forgotten, as is proved by the above-mentioned objection. If we were only permitted to attack the more complicated phenomena after gaining a complete insight into the simpler ones, then all scientists would be physicists and chemists, and not until Physics and Chemistry were done with should we be permitted to proceed to the investigation of organic nature. Under these circumstances we ought not to possess now any scientific theory of medicine; for the study of pathological physiology could not be commenced until normal physiology was completely known and understood. Yet how great a debt is owing by normal to pathological physiology! This is an example which enforces the conclusion that it is not only permissible, but in the highest degree advantageous, for the different spheres of phenomena to be attacked simultaneously.

Furthermore, if we had been compelled to proceed from the simple to the complex, what would have become of the Theory of Descent, the influence of which has advanced our knowledge of Biology to an altogether immeasurable extent?

But in this often repeated criticism that we are not yet ready to attack such complicated phenomena as heredity, is hidden still another fallacy, for it is implied that facts become less certain in proportion to the complexity of their causes. But is it less certain that the egg of an eagle developes into an eagle, or that the peculiarities of the father and mother are transmitted to the child, than that a stone falls to the ground when its support is taken away? Again, is it not possible to draw a perfectly distinct and certain conclusion as to the relative quantity of the material basis of heredity, present in the germ-cells of either parent, from the fact that the father and mother possess an equal or nearly equal share in heredity? But it is really unnecessary to argue in this way: why should we do more than re-affirm that such a method of procedure in scientific investigation is the only way by which we can gradually penetrate the hidden depths of natural phenomena?

No! Biology is not obliged to wait until Physics and Chemistry are completely finished; nor have we to wait for the investigation of the phenomena of heredity until the physiology of the cell is complete. Instead of comparing the progress of science to a building, I should prefer to compare it to a mining operation, undertaken in order to open up a freely branching lode. Such a lode must not be attacked from one point alone, but from many points simultaneously. From some of these we should quickly reach the deep-seated parts of the lode, from others we should only reach its superficial parts; but from every point some knowledge of the complex *tout ensemble* of the lode would be gained. And the more numerous the points of attack, the more complete would be the knowledge acquired, for valuable insight will be obtained in every place where the work is carried on with discretion and perseverance.

But discretion is indispensable for a fruitful result; or, leaving our metaphor, facts must be connected together by theories, if science is to advance. Just as theories are valueless without a firm basis of facts, so the mere collection of facts, without relation and without coherence, is utterly valueless. Science is impossible without hypotheses and theories: they are the plummets with which we test the depth of the ocean of unknown phenomena, and thus determine the future course to be pursued on our voyage of discovery. They do not give us absolute knowledge, but they afford us as much insight as it is possible for us to gain at the present time. To go on investigating without the guidance of theories, is like attempting to walk in a thick mist without a track and without a compass. We should get somewhere under these circumstances, but chance alone would determine whether we should reach a stony desert of unintelligible facts or a system of roads leading in some useful direction; and in most cases chance would decide against us.

In this sense I trust that the sign-post or compass which I offer may be accepted. Even though it should be its fate to be replaced by a better one at a later period, it will have fulfilled its object if it enables science to advance for even a short distance.