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TRANSLATIONS

OF

FOREIGN BIOLOGICAL MEMOIRS

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ESSAYS UPON HEREDITY

AND KINDRED

BIOLOGICAL PROBLEMS

BY

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AUTHORISED TRANSLATION

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Oxford

AT THE CLARENDON PRESS

1889

AUTHOR'S PREFACE.

The essays which now appear for the first time in the form of a single volume were not written upon any prearranged plan, but have been published separately at various intervals during the course of the last seven years. Although when writing the earlier essays I was not aware that the others would follow, the whole series is, nevertheless, closely connected together. The questions which each essay seeks to explain have all arisen gradually out of the subjects treated in the first. Reflecting upon the causes which regulate the duration of life in various forms, I was drawn on to the consideration of fresh questions which demanded further research. These considerations and the results of such research form the subject-matter of all the subsequent essays.

I am here making use of the word 'research' in a sense somewhat different from that in which it is generally employed in natural science; for it is commonly supposed to imply the making of new observations. Some of these essays, especially Nos. IV, V, and VI, essentially depend upon new discoveries. But in most of the remaining essays the researches are of a more abstract nature, and consist in bringing forward new points of view, founded upon a variety of well-known facts. I believe, however, that the history of science proves that advance is not only due to the discovery of new facts, but also to their correct interpretation: a true conception of natural processes can only be arrived at in this way. It is chiefly in this sense that the contents of these essays are to be looked upon as research.

The fact that they contain the record of research made it impossible to introduce any essential alterations in the translation, even in those points about which my opinion has since changed to some extent. I should to-day express some of the points in Essays I, IV, and V, somewhat differently; but had I made such alterations, the relation between the essays as a whole would have been rendered less clear, for each of the earlier ones formed the foundation of that which succeeded it. Even certain errors of interpretation are on this account left uncorrected. Thus, for instance, in Essay IV it is assumed that the two polar bodies expelled by sexual eggs are identical; for at that time there was no reason for doubting that they were physiologically equivalent. The discovery of the numerical law of the polar bodies described in Essay VI, led to what I believe to be a truer knowledge of them. In this way the causes of parthenogenesis, as developed in Essay V, received an important addition in the fact published in Essay VI, that only one polar body is expelled by parthenogenetic eggs. This fact alone explains why sexual eggs cannot as a rule develope without fertilization.

Hence the reader must not take the individual essays as the full and complete expression of my present opinion; but they must rather be looked upon as stages in research, as steps towards a more perfect knowledge.

I must therefore express the hope that the essays may be read in the same order as that in which they appeared, and in which they are arranged in the present volume. The reader will then follow the same road which I traversed in the development of the views here set forth; and even though he may be now and then led away from the direct route, perhaps such deviations may not be without interest.

I should wish to express my warm thanks to Mr. Poulton for the great trouble he has taken in editing the translation, which in many places presented exceptional difficulties. The greater part of the text I have looked through in proof, and I believe that it well expresses the sense of the original; although naturally I cannot presume to judge concerning the niceties of the English language. I am especially grateful to the three gentlemen who have brought these essays before an English public, because I believe that many English naturalists, even when thoroughly conversant with the German tongue, might possibly misinterpret many points in the original; for the difficulty of the questions treated of greatly increases the difficulty of the language.

If the readers of this book only feel half as much pleasure in its perusal as I experienced in writing it, I shall be more than satisfied.

AUGUST WEISMANN.

FREIBURG I. BREISGAU,
January, 1889.

EDITORS' PREFACE.

The attention of English biologists and men of science was first called to Professor Weismann's essays by an article entitled 'Death' in 'The Nineteenth Century' for May, 1885, by Mr. A. E. Shipley. Since then the interest in the author's arguments and conclusions has become very general; having been especially increased by Professor Moseley's two articles in 'Nature' (Vol. XXXIII, p. 154, and Vol. XXXIV, p. 629), and by the discussion upon 'The Transmission of Acquired Characters,' introduced by Professor Lankester at the meeting of the British Association at Manchester in 1887,—a discussion in which Professor Weismann himself took part. The deep interest which has everywhere been expressed in a subject which concerns the very foundations of evolution, has encouraged the Editors to hope that a volume containing a collection of all Professor Weismann's essays upon heredity and kindred problems would supply a real want. At the present time, when scientific periodicals contain frequent references to these essays, and when the various issues which have been raised by them are discussed on every occasion at which biologists come together, it is above all things necessary to know exactly what the author himself has said. And there are many signs that discussion has already suffered for want of this knowledge.

A translation of Essays I and II was commenced by Mr. A. E. Shipley during his residence at Freiburg in the winter of 1884. His work was greatly aided by the kind assistance of Dr. van Rees of Amsterdam, to whom we desire to express our most sincere thanks. The translation was laid aside until the summer of 1888, when Mr. Shipley was invited to co-operate with the other editors in the preparation of the present volume; the Clarendon Press having consented to publish the complete series of essays as one of their Foreign Biological Memoirs.

We think it probable that this work may interest many who are not trained biologists, but who approach the subject from its philosophical or social aspects. Such readers would do well to first study Essays I, II, VII, and VIII, inasmuch as some preparation for the more technical treatment pursued in the other essays will thus be gained.

The notes signed A. W. and dated, were added by the author during the progress of the translation. The notes included in square brackets were added by the Editors; the authorship being indicated by initials in all cases.

In conclusion, it is our pleasant duty to thank those who have kindly helped us by reading the proof-sheets and making valuable suggestions. Our warmest thanks are due to Mrs. Arthur Lyttelton, Mr. W. Hatchett Jackson, Deputy Linacre Professor in the University of Oxford, Mr. J. S. Haldane, and Professor R. Meldola. Important suggestions were also made by Professor E. Ray Lankester, Mr. Francis Galton, and Dr. A. R. Wallace. Professor W. N. Parker also greatly helped us by looking over the proof-sheets with Professor Weismann.

E. B. P.
S. S.
A. E. S.

Oxford, *February, 1889*.

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Abstracts of Professor Weismann's Essays on Heredity and Kindred Problems, already Published in this Country.

I. A short abstract in 'Nature,' Vol. XXXVII, pp. 541-542, by P. C. Mitchell.
II. A short abstract in 'Nature,' Vol. XXXVIII, pp. 156-157, by P. C. Mitchell.
III. A short article on the subject of this Essay in 'The Nineteenth Century' for May, 1885, by A. E. Shipley.
IV. Abstract in 'Nature,' Vol. XXXIII, pp. 154-157, by Professor Moseley.
V. Abstract in 'Nature,' Vol. XXXIV, pp. 629-632, by Professor Moseley.
VI. Abstract in 'Nature,' Vol. XXXVI, pp. 607-609, by Professor Weismann.
VII, VIII. The Essays being of so recent a date no abstract has yet appeared in this country.

A criticism of Professor Weismann's theories will be found in 'The Physiology of Plants,' by Professor Vines, Lecture XXIII, pp. 660 et seqq.

I.

THE DURATION OF LIFE.

1881.

1

THE DURATION OF LIFE.

PREFACE.

The following paper was read at the meeting of the Association of German Naturalists at Salzburg, on September 21st, 1881; and it is here printed in essentially the same form. A somewhat longer discussion of a few points has been now intercalated; these were necessarily omitted from the lecture itself for the sake of brevity, and are, therefore, not contained in the account printed in the Proceedings of the fifty-fourth meeting of the Association.

Further additions would not have been admissible without an essential change of form, and therefore I have not put into the text a note which ought otherwise to have been there, and which is now to be found in the Appendix, as Note 8. It fills up a gap which was left in the text, for the above-mentioned reason, by attempting to give an explanation of the normal death of cells of tissues—an explanation which is required if we are to maintain that unicellular organisms are so constituted as to be potentially immortal.

The other parts of the Appendix contain, partly further expansions, partly proofs of the views brought forward in the text, and above all a compilation of all the observations which are known to me upon the duration of life in several groups of animals. I am indebted to several eminent specialists for the communication of many data, which are among the most exact that I have been able to obtain. Thus Dr. Hagen of Cambridge (U.S.A.) was kind enough to send me an account of his observations upon insects of different orders: Mr. W. H. Edwards of West Virginia, and Dr. Speyer of Rhoden—their experience with butterflies. Dr. Adler of Schleswig sent me data upon the duration of life in *Cynipidae*, which have a special value, as they are accompanied by very exact observations upon the conditions of life in these animals; hence in 4
this case we can directly examine the factors upon which, as I believe, the duration of life is chiefly based. Sir John Lubbock in England, and Dr. August Forel of Zürich, have had the kindness to send me an account of their observations upon ants, and S. Clessin of Ochsenfurth his researches upon our native land and fresh-water Mollusca.

In publishing these valuable communications, together with all facts which I have been able to collect from literature upon the subject of the duration of life, and the little which I have myself observed upon this subject, I hope to provide a stimulus for further observation in this field, which has been hitherto much neglected. The views which I have brought forward in this paper are based on a comparatively small number of facts, at least as far as the duration of life in various species is concerned. The larger the number of accurate data which are supplied, and the more exactly the duration of life and its conditions are ascertained, the more securely will it be possible to establish our views upon the causes which determine the duration of life.

A. W.

NAPLES, *Dec. 6, 1881*.

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I.

THE DURATION OF LIFE.

With your permission, I will bring before you to-day some thoughts upon the subject of the duration of life. I can scarcely do better than begin with the simple but significant words of Johannes Müller: ‘Organic bodies are perishable; while life maintains the appearance of immortality in the constant succession of similar individuals, the individuals themselves pass away.’

Omitting, for the time being, any discussion as to the precise accuracy of this statement, it is at any rate obvious that the life of an individual has its natural limit, at least among those animals and plants which are met with in every-day life. But it is equally obvious that the limits are very differently placed in the various species of animals and plants. These differences are so manifest that they have given rise to popular sayings. Thus Jacob Grimm mentions an old German saying, ‘A wren lives three years, a dog three times as long as a wren, a horse three times as long as a dog, and a man three times as long as a horse, that is eighty-one years. A donkey attains three times the age of a man, a wild goose three times that of a donkey, a crow three times that of a wild goose, a deer three times that of a crow, and an oak three times the age of a deer.’

If this be true a deer would live 6000 years, and an oak nearly 20,000 years. The saying is certainly not founded upon exact observation, but it becomes true if looked upon as a general statement that the duration of life is very different in different organisms.

The question now arises as to the causes of these great differences. How is it that individuals are endowed with the power of living long in such very various degrees?

One is at first tempted to seek the answer by an appeal to the differences in morphological and chemical structure which separate species from one another. In fact all attempts to throw light upon the subject which have been made up to the present time lie in this direction. 6

All these explanations are nevertheless insufficient. In a certain sense it is true that the causes of the duration of life must be contained in the organism itself, and cannot be found in any of its external conditions or circumstances. But structure and chemical composition—in short the physiological constitution of the body in the ordinary sense of the words—are not the only factors which determine duration of life. This conclusion forces itself upon our attention as soon as the attempt is made to explain existing facts by these factors alone: there must be some other additional cause contained in the organism as an unknown and invisible part of its constitution, a cause which determines the duration of life.

The size of the organism must in the first place be taken into consideration. Of all organisms in the world, large trees have the longest lives. The Adansonias of the Cape Verd Islands are said to live for 6000 years. The largest animals also attain the greatest age. Thus there is no doubt that whales live for some hundreds of years. Elephants live 200 years, and it would not be difficult to construct a descending series of animals in which the duration of life diminishes in almost exact proportion to the decrease in the size of the body. Thus a horse lives forty years, a blackbird eighteen, a mouse six, and many insects only a few days or weeks.

If however the facts are examined a little more closely it will be observed that the great age (200 years) reached by an elephant is also attained by many smaller animals, such as the pike and carp. The horse lives forty years, but so does a cat or a toad; and a sea anemone has been known to live for over fifty years. The duration of life in a pig (about twenty years) is the same as that in a crayfish, although the latter does not nearly attain the hundredth part of the weight of a pig.

It is therefore evident that length of life cannot be determined by the size of the body alone. There is, however, some relation between these two attributes. A large animal lives longer than a small one because it is larger; it would not be able to become even comparatively large unless endowed with a comparatively long duration of life.

Apart from all other reasons, no one could imagine that the gigantic body of an elephant could be built up like that of a mouse in three weeks, or in a single day like that of the larva of certain flies. The gestation of an elephant lasts for nearly two years, and maturity is only reached after a lapse of about twenty-four years. 7

Furthermore, to ensure the preservation of the species, a longer time is required by a large animal than by a small one, when both have reached maturity. Thus Leuckart and later Herbert Spencer have pointed out that the absorbing surface of an animal only increases as the square of its length, while its size increases as the cube; and it therefore follows that the larger an animal becomes, the greater will be the difficulty experienced in assimilating any nourishment over and above that which it requires for its own needs, and therefore the more slowly will it reproduce itself.

But although it may be stated generally that the duration of the period of growth and length of life are longest in the largest animals, it is nevertheless impossible to maintain that there is any fixed relation between the two; and Flourens was mistaken when he considered that the length of life was always equivalent to five times the duration of the period of growth. Such a conclusion might be accepted in the case of man if we set his period of growth at twenty years and his length of life at a hundred; but it cannot be accepted for the majority of other Mammalia. Thus the horse lives from forty to fifty years, and the latter age is at least as frequently reached among horses as a hundred years among men; but the horse becomes mature in four years, and the length of its life is thus ten or twelve times as long as its period of growth.

The second factor which influences the duration of life is purely physiological: it is the rate at which the animal lives, the rapidity with which assimilation and the other vital processes take place. Upon this point Lotze remarks in his Microcosmus—'Active and restless mobility destroys the organized body: the swift-footed animals hunted by man, as also dogs, and even apes, are inferior in length of life to man and the larger beasts of prey, which satisfy their needs by a few vigorous efforts.' 'The inertness of the Amphibia is, on the other hand, accompanied by relatively great length of life.'

There is certainly some truth in these observations, and yet it would be a great mistake to assume that activity necessarily implies a short life. The most active birds have very long lives, as will be shown later on: they live as long as and sometimes longer than the majority of Amphibia which reach the same size. The organism must not be looked upon as a heap of combustible material, which is completely reduced to ashes in a certain time the length of which is determined by size, and by the rate at which it burns; but it should be rather compared to a fire, to which fresh fuel can be continually added, and which, whether it burns quickly or slowly, can be kept burning as long as necessity demands. 8

The connection between activity and shortness of life cannot be explained by supposing that a more rapid consumption of the body occurs, but it is explicable because the increased rate at which the vital processes take place permit the more rapid achievement of the aim and purpose of life, viz. the attainment of maturity and the reproduction of the species.

When I speak of the aim and purpose of life, I am only using figures of speech, and I do not mean to imply that nature is in any way working consciously.

When I was speaking of the relation between duration of life and the size of the body, I might have added another factor which also exerts some influence, viz. the complexity of the structure. Two organisms of the same size, but belonging to different grades of organization, will require different periods of time for their development. Certain animals of a very lowly organization, such as the Rhizopoda, may attain a diameter of ·5 mm. and may thus become larger than many insects' eggs. Yet under favourable circumstances an Amoeba can divide into two animals in ten minutes, while no insect's egg can develope into the young animal in a less period than twenty-four hours. Time is required for the development of the immense number of cells which must in the latter case arise from the single egg-cell.

Hence we may say that the peculiar constitution of an animal does in part determine the length of time which must elapse before reproduction begins. The period before reproduction is however only part of the whole life of an animal, which of course extends over the total period during which the animal exists.

Hitherto it has always been assumed that the duration of this total period is solely determined by the constitution of the animal's body. But the assumption is erroneous. The strength of the 9
spring which drives the wheel of life does not solely depend upon the size of the wheel itself or upon the material of which it is made; and, leaving the metaphor, duration of life is not exclusively determined by the size of the animal, the complexity of its structure, and the rate of its metabolism. The facts are plainly and clearly opposed to such a supposition.

How, for instance, can we explain from this point of view the fact that the queen-ant and the workers live for many years, while the males live for a few weeks at most? The sexes are not distinguished by any great difference in size or complexity of body, or in the rate of metabolism. In all these three particulars they must be looked upon as precisely the same, and yet there is this immense difference between the lengths of their lives.

I shall return later on to this and other similar cases, and for the present I assume it to be proved that physiological considerations alone cannot determine the duration of life. It is not these which alone determine the strength of the spring which moves the machinery of life; we know that springs of different strengths may be fixed in machines of the same kind and quality. This metaphor is however imperfect, because we cannot imagine the existence of any special force in an organism which determines the duration of its life; but it is nevertheless useful because it emphasises the fact that the duration of life is forced upon the organism by causes outside itself, just as the spring is fixed in its place by forces outside the machine, and not only fixed in its place, but chosen of a certain strength so that it will run down after a certain time.

To put it briefly, I consider that duration of life is really dependent upon adaptation to external conditions, that its length, whether longer or shorter, is governed by the needs of the species, and that it is determined by precisely the same mechanical process of regulation as that by which the structure and functions of an organism are adapted to its environment.

Assuming for the moment that these conclusions are valid, let us ask how the duration of life of any given species can have been determined by their means. In the first place, in regulating duration of life, the advantage to the species, and not to the individual, is alone of any importance. This must be obvious to any one who has once thoroughly thought out the process of natural selection. It is of no importance to the species whether the individual lives longer or 10
shorter, but it is of importance that the individual should be enabled to do its work towards the maintenance of the species. This work is reproduction, or the formation of a sufficient number of new individuals to compensate the species for those which die. As soon as the individual has performed its share in this work of compensation, it ceases to be of any value to the species, it has fulfilled its duty and may die. But the individual may be of advantage to the species for a longer period if it not only produces offspring, but tends them for a longer or shorter time, either by protecting, feeding, or instructing them. This last duty is not only

undertaken by man, but also by animals, although to a smaller extent; for instance, birds teach their young to fly, and so on.

We should therefore expect to find that, as a rule, life does not greatly outlast the period of reproduction except in those species which tend their young; and as a matter of fact we find that this is the case.

All mammals and birds outlive the period of reproduction, but this never occurs among insects except in those species which tend their young. Furthermore, the life of all the lower animals ceases also with the end of the reproductive period, as far as we can judge.

Duration of life is not however determined in this way, but only the point at which its termination occurs relatively to the cessation of reproduction. The duration itself depends first upon the length of time which is required for the animal to reach maturity—that is, the duration of its youth, and, secondly, upon the length of the period of fertility—that is the time which is necessary for the individual to produce a sufficient number of descendants to ensure the perpetuation of the species. It is precisely this latter point which is determined by external conditions.

There is no species of animal which is not exposed to destruction through various accidental agencies—by hunger or cold, by drought or flood, by epidemics, or by enemies, whether beasts of prey or parasites. We also know that these causes of death are only apparently accidental, or at least that they can only be called accidental as far as a single individual is concerned. As a matter of fact a far greater number of individuals perish through the operation [11] of these agencies than by natural death. There are thousands of species of which the existence depends upon the destruction of other species; as, for example, the various kinds of fish which feed on the countless minute Crustacea inhabiting our lakes.

It is easy to see that an individual is, *ceteris paribus*, more exposed to accidental death when the natural term of its life becomes longer; and therefore the longer the time required by an individual for the production of a sufficient number of descendants to ensure the existence of the species, the greater will be the number of individuals which perish accidentally before they have fulfilled this important duty. Hence it follows, first, that the number of descendants produced by any individual must be greater as the duration of its reproductive period becomes longer; and, secondly, the surprising result that nature does not tend to secure the longest possible life to the adult individual, but, on the contrary, tends to shorten the period of reproductive activity as far as possible, and with this the duration of life; but these conclusions only refer to the animal and not to the vegetable world.

All this sounds very paradoxical, but the facts show that it is true. At first sight numerous instances of remarkably long life seem to refute the argument, but the contradictions are only apparent and disappear on closer investigation.

Birds as a rule live to a surprisingly great age. Even the smallest of our native singing birds lives for ten years, while the nightingale and blackbird live from twelve to eighteen years. A pair of eider ducks were observed to make their nest in the same place for twenty years, and it is believed that these birds sometimes reach the age of nearly one hundred years. A cuckoo, which was recognised by a peculiar note in its call, was heard in the same forest for thirty-two consecutive years. Birds of prey, and birds which live in marshy districts, become much older, for they outlive more than one generation of men.

Schinz mentions a bearded vulture which was seen sitting on a rock upon a glacier near Grindelwald, and the oldest men in Grindelwald had, when boys, seen the same bird sitting on the same rock. A white-headed vulture in the Schönbrunn Zoological Gardens had been in captivity for 118 years, and many examples are known of eagles and falcons reaching an age of over 100 years. Finally, we must not forget Humboldt's[1] Atur parrot from the Orinoco, [12] concerning which the Indians said that it could not be understood because it spoke the language of an extinct tribe.

It is therefore necessary to ask how far we can show that such long lives are really the shortest which are possible under the circumstances.

Two factors must here be taken into consideration; first, that the young of birds are greatly exposed to destructive agencies; and, secondly, that the structure of a bird is adapted for flight and therefore excludes the possibility of any great degree of fertility.

Many birds, like the stormy petrel, the diver, guillemot, and other sea-birds, lay only a single egg, and breed (as is usually the case with birds) only once a year. Others, such as birds of prey, pigeons, and humming-birds, lay two eggs, and it is only those which fly badly, such as jungle fowls and pheasants, which produce a number of eggs (about twenty), and the young of these very species are especially exposed to those dangers which more or less affect the offspring of all birds. Even the eggs of our most powerful native bird of prey, the golden eagle, which all animals fear, and of which the eyrie, perched on a rocky height, is beyond the reach of any enemies, are very frequently destroyed by late frosts or snow in spring, and, at the end of the year in winter, the young birds encounter the fiercest of foes, viz. hunger. In the majority of birds, the egg, as soon as it is laid, becomes exposed to the attacks of enemies; martens and weasels, cats and owls, buzzards and crows are all on the look out for it. At a later period the same enemies destroy numbers of the helpless young, and in winter many succumb in the struggle against cold and hunger, or to the numerous dangers which attend migration over land and sea, dangers which decimate the young birds.

It is impossible directly to ascertain the exact number which are thus destroyed; but we can arrive at an estimate by an indirect method. If we agree with Darwin and Wallace in believing that in most species a certain degree of constancy is maintained in the number of individuals of successive generations, and that therefore the number of individuals within the same area remains tolerably uniform for a certain period of time; it follows that, if we know the fertility 13
and the average duration of life of a species, we can calculate the number of those which perish before reaching maturity. Unfortunately the average length of life is hardly known with certainty in the case of any species of bird. Let us however assume, for the sake of argument, that the individuals of a certain species live for ten years, and that they lay twenty eggs in each year; then of the 200 eggs which are laid during the ten years, which constitute the lifetime of an individual, 198 must be destroyed, and only two will reach maturity, if the number of individuals in the species is to remain constant. Or to take a concrete example; let us fix the duration of life in the golden eagle at 60 years, and its period of immaturity (of which the length is not exactly known) at ten years, and let us assume that it lays two eggs a year;—then a pair will produce 100 eggs in 50 years, and of these only two will develope into adult birds; and thus on an average a pair of eagles will only succeed in bringing a pair of young to maturity once in fifty years. And so far from being an exaggeration, this calculation rather under-estimates the proportion of mortality among the young; it is sufficient however to enforce the fact that the number of young destroyed must reach in birds a very high figure as compared with the number of those which survive [See Note 1].

If this argument holds, and at the same time the fertility from physical and other grounds cannot be increased, it follows that a relatively long life is the only means by which the maintenance of the species of birds can be secured. Hence a great length of life is proved to be an absolute necessity for birds.

I have already mentioned that these animals demonstrate most clearly that physiological considerations do not by any means suffice to explain the duration of life. Although all vital processes take place with greater rapidity and the temperature of the blood is higher in birds than in mammals, yet the former greatly surpass the latter in length of life. Only in the largest Mammalia,—the whales and the elephants—is the duration of life equal to or perhaps greater than that of the longest lived birds. If we compare the relative weights of these animals, the Mammalia are everywhere at a disadvantage. Even such large animals as the horse and bear only attain an age of fifty years at the outside; the lion lives about thirty-five years, the wild 14
boar twenty-five, the sheep fifteen, the fox fourteen, the hare ten, the squirrel and the mouse

six years [See Note 2]; but the golden eagle, though it does not weigh more than from 9-12 pounds, and is thus intermediate as regards weight between the hare and the fox, attains nevertheless an age which is ten times as long. The explanation of this difference is to be found first in the much greater fertility of the smaller Mammalia, such as the rabbit or mouse, and secondly in the much lower mortality among the young of the larger Mammalia. The minimum duration of life necessary for the maintenance of the species is therefore much lower than it is among birds. Even here, however, we are not yet in possession of exact statistics indicating the number of young destroyed; but it is obvious that Mammalia possess over birds a great advantage in their intra-uterine development. In Mammalia the destruction of young only begins after birth, while in birds it begins during the development of the embryo. This distinction is in fact carried even further, for many mammals protect their young against enemies for a long time after birth.

It is unnecessary to go further into the details of these cases, or to consider whether and to what extent every class of the animal kingdom conforms to these principles. Thus to consider all or even most of the classes of the animal kingdom would be quite impossible at the present time, because our knowledge of the duration of life among animals is very incomplete. Biological problems have for a long time excited less interest than morphological ones. There is nothing or almost nothing to be found in existing zoological text books upon the duration of life in animals; and even monographs upon single classes, such as the Amphibia, reptiles, or even birds, contain very little on this subject. When we come to the lower animals, knowledge on this point is almost entirely wanting. I have not been able to find a single reference to the age in Echinodermata, and very little about that of worms, Crustacea, and Coelenterata [See Note 4]. The length of life in many molluscan species is very well known, because the age can be determined by markings on the shell [See Note 5]. But even in this group, any exact knowledge, such as would be available for our purpose, is still wanting concerning such necessary points as the degree of fertility, the relation to other animals, and many other factors. 15

Data the most exact in all respects are found among the insects [See Note 3], and to this class I will for a short time direct your special attention. We will first consider the duration of larval life. This varies very greatly, and chiefly depends upon the nature of the food, and the ease or difficulty with which it can be procured. The larvae of bees reach the pupal stage in five to six days; but it is well known that they are fed with substances of high nutritive value (honey and pollen), and that they require no great effort to obtain the food, which lies heaped up around them. The larval life in many *Ichneumonidae* is but little longer, being passed in a parasitic condition within other insects; abundance of accessible food is thus supplied by the tissues and juices of the host. Again, the larvae of the blow-fly become pupae in eight to ten days, although they move actively in boring their way under the skin and into the tissues of the dead animals upon which they live. The life of the leaf-eating caterpillars of butterflies and moths lasts for six weeks or longer, corresponding to the lower nutritive value of their food and the greater expenditure of muscular energy in obtaining it. Those caterpillars which live upon wood, such as *Cossus ligniperda*, have a larval life of two to three years, and the same is true of hymenopterous insects with similar habits, such as *Sirex*.

Furthermore, predaceous larvae require a long period for attaining their full size, for they can only obtain their prey at rare intervals and by the expenditure of considerable energy. Thus among the dragon-flies larval life lasts for a year, and among many may-flies even two or three years.

All these results can be easily understood from well-known physiological principles, and they indicate that the length of larval life is very elastic, and can be extended as circumstances demand; for otherwise carnivorous and wood-eating larvae could not have survived in the phyletic development of insects. Now it would be a great mistake to suppose that there is any reciprocal relation between duration of life in the larva and in the mature insect, or imago; or, to put it differently, to suppose that the total duration of life is the same in insects of the same size and activity, so that the time which is spent in the larval state is, as it were, deducted from the life of the imago, and *vice versa*. That this cannot be the case is shown by the fact already alluded to, that among bees and ants larval life is of the same length in males and females, while there is a difference of some years between the lengths of their lives as imagos. 16

The life of the imago is generally very short, and not only ends with the close of the period of reproduction, as was mentioned above, but this latter period is also itself extremely short [See Note 3].

The larva of the cockchafer devours the roots of plants for a period of four years, but the mature insect with its more complex structure endures for a comparatively short time; for the beetle itself dies in about a month after completing its metamorphosis. And this is by no means an extreme case. Most butterflies have an even shorter life, and among the moths there are many species (as in the *Psychidae*) which only live for a few days, while others again, which reproduce by the parthenogenetic method, only live for twenty-four hours. The shortest life is found in the imagos of certain may-flies, which only live four to five hours. They emerge from the pupa-case towards the evening, and as soon as their wings have hardened, they begin to fly, and pair with one another. Then they hover over the water; their eggs are extruded all at once, and death follows almost immediately.

The short life of the imago in insects is easily explained by the principles set forth above. Insects belong to the number of those animals which, even in their mature state, are very liable to be destroyed by others which are dependent upon them for food; but they are at the same time among the most fertile of animals, and often produce an astonishing number of eggs in a very short time. And no better arrangement for the maintenance of the species under such circumstances can be imagined than that supplied by diminishing the duration of life, and simultaneously increasing the rapidity of reproduction.

This general tendency is developed to very different degrees according to conditions peculiar to each species. The shortening of the period of reproduction, and the duration of life to the greatest extent which is possible, depends upon a number of co-operating circumstances, which it is impossible to enumerate completely. Even the manner in which the eggs are laid 17
may have an important effect. If the larva of the may-fly lived upon some rare and widely distributed food-plant instead of at the bottom of streams, the imagos would be compelled to live longer, for they would be obliged—like many moths and butterflies—to lay their eggs singly or in small clusters, over a large area. This would require both time and strength, and they could not retain the rudimentary mouth which they now possess, for they would have to feed in order to acquire sufficient strength for long flights; and—whether they were carnivorous like dragon-flies, or honey-eating like butterflies—their feeding would itself cause a further expenditure of both time and strength, which would necessitate a still further increase in the duration of life. And as a matter of fact we find that dragon-flies and swift-flying hawk-moths often live for six or eight weeks and sometimes longer.

We must also remember that in many species the eggs are not mature immediately after the close of the pupal stage, but that they only gradually ripen during the life of the imago, and frequently, as in many beetles and butterflies, do not ripen simultaneously, but only a certain number at a time. This depends, first, upon the amount of reserve nutriment accumulated in the body of the insect during larval life; secondly, upon various but entirely different circumstances, such as the power of flight. Insects which fly swiftly and are continually on the wing, like hawk-moths and dragon-flies, cannot be burdened with a very large number of ripe eggs. In these cases the gradual ripening of the eggs becomes necessary, and involves an increase in the duration of life. In Lepidoptera, we see how the power of flight diminishes step by step as soon as other circumstances permit, and simultaneously how the eggs ripen more and more rapidly, while the length of life becomes shorter, until a minimum is reached. Only two stages in the process of transformation can be mentioned here.

The strongest flyers—the hawk-moths and butterflies—must be looked upon as the most specialised and highest types among the Lepidoptera. Not only do they possess organs for flight in their most perfect form, but also organs for feeding—the characteristic spiral proboscis or 'tongue.'

There are certain moths (among the Bombyces) of which the males fly as well as the hawk-moths, while the females are unable to use their large wings for flight, because the body is too 18 heavily weighted by a mass of eggs, all of which reach maturity at the same time. Such species, as for instance *Aglia tau*, are unable to distribute their eggs over a wide area, but are obliged to lay them all in a single spot. They can however do this without harm to the species, because their caterpillars live upon forest trees, which provide abundant food for a larger number of larvae than can be produced by the eggs of a single female. The eggs of *Aglia tau* are deposited directly after pairing, and shortly afterwards the insect dies at the foot of the tree among the moss-covered roots of which it has passed the winter in the pupal state. The female moth seldom lives for more than three or four days; but the males which fly swiftly in the forests, seeking for the less abundant females, live for a much longer period, certainly from eight to fourteen days[2].

The females of the *Psychidae* also deposit all their eggs in one place. The grasses and lichens upon which their caterpillars live grow close at hand upon the surface of the earth and stones, and hence the female moth does not leave the ground, and generally does not even quit the pupa-case, within which it lays its eggs; as soon as this duty is finished, it dies. In relation to these habits the wings and mouth of the female are rudimentary, while the male possesses perfectly developed wings.

The causes which have regulated the length of life in these cases are obvious enough, yet still more striking illustrations are to be found among insects which live in colonies.

The duration of life varies with the sex in bees, wasps, ants, and termites: the females have a long life, the males a short one; and there can be no doubt that the explanation of this fact is to be found in adaptation to external conditions of life.

The queen-bee—the only perfect female in the hive—lives two to three years, and often as long as five years, while the male bees or drones only live four to five months. Sir John Lubbock has succeeded in keeping female and working ants alive for seven years—a great age for insects[3],—while the males only lived a few weeks.

These last examples become readily intelligible when we remember that the males neither 19 collect food nor help in building the hive. Their value to the colony ceases with the nuptial flight, and from the point of view of utility it is easy to understand why their lives should be so short [See Note 7 and Note 9]. But the case is very different with the female. The longest period of reproduction possible, when accompanied by very great fertility, is, as a rule, advantageous for the maintenance of the species. It cannot however be attained in most insects, for the capability of living long would be injurious if all individuals fell a prey to their enemies before they had completed the full period of life. Here it is otherwise: when the queen-bee returns from her nuptial flight, she remains within the hive until her death, and never leaves it. There she is almost completely secure from enemies and from dangers of all kinds; thousands of workers armed with stings protect, feed, and warm her; and in short there is every chance of her living through the full period of a life of normal length. And the case is entirely similar with the female ant. In neither of these insects is there any reason why the advantages which follow from a lengthened period of reproductive activity should be abandoned [See Note 6].

That an increase in the length of life has actually taken place in such cases seems to be indicated by the fact that both sexes of the saw-flies—the probable ancestors of bees and ants—have but a short life. On the other hand, the may-flies afford an undoubted instance of the shortening of life. Only in certain species is life as short as I have indicated above; in the majority it lasts for one or more days. The extreme cases, with a life of only a few hours, form the end of a line of development tending in the direction of a shortened life. This is made clear by the fact that one of these may-flies (*Palingenia*) does not even leave its pupa-skin, but reproduces in the so-called sub-imago stage.

It is therefore obvious that the duration of life is extremely variable, and not only depends upon physiological considerations, but also upon the external conditions of life. With every change in the structure of a species, and with the acquisition of new habits, the length of its life may, and in most cases must, be altered.

In answering the question as to the means by which the lengthening or shortening of life is brought about, our first appeal must be to the process of natural selection. Duration of life, like every other characteristic of an organism, is subject to individual fluctuations. From our experience with the human species we know that long life is hereditary. As soon as the long-lived individuals in a species obtain some advantage in the struggle for existence, they will gradually become dominant, and those with the shortest lives will be exterminated. 20

So far everything is quite simple; but hitherto we have only considered the external mechanism, and we must now further inquire as to the concomitant internal means by which such processes are rendered possible.

This brings us face to face with one of the most difficult problems in the whole range of physiology,—the question of the origin of death. As soon as we thoroughly understand the circumstances upon which normal death depends in general, we shall be able to make a further inquiry as to the circumstances which influence its earlier or later appearance, as well as to any functional changes in the organism which may produce such a result.

The changes in the organism which result in normal death,—senility so-called,—have been most accurately studied among men. We know that with advancing age certain alterations take place in the tissues, by which their functional activity is diminished; that these changes gradually increase, and finally either lead to direct or so-called normal death, or produce indirect death by rendering the organism incapable of resisting injuries due to external influences. These senile changes have been so well described from the time of Burdach and Bichat to that of Kussmaul, and are so well known, that I need not enter into further details here.

In answer to an inquiry as to the causes which induce these changes in the tissues, I can only suggest that the cells which form the vital constituents of tissues are worn out by prolonged use and activity. It is conceivable that the cells might be thus worn out in two ways; either the cells of a tissue remain the same throughout life, or else they are being continually replaced by younger generations of cells, which are themselves cast off in their turn.

In the present state of our knowledge the former alternative can hardly be maintained. Millions of blood corpuscles are continually dying and being replaced by new ones. On both the internal and external surfaces of the body countless epithelial cells are being incessantly removed, while new ones arise in their place; the activity of many and probably of all glands is accompanied by a change in their cells, for their secretions consist partly of detached and partly of dissolved cells; it is stated that even the cells of bone, connective tissue, and muscle undergo the same changes, and nervous tissue alone remains, in which it is doubtful whether such a renewal of cells takes place. And yet as regards even this tissue, certain facts are known which indicate a normal, though probably a slow renewal of the histological elements. I believe that one might reasonably defend the statement,—in fact, it has already found advocates,—that the vital processes of the higher (i.e. multicellular) animals are accompanied by a renewal of the morphological elements in most tissues. 21

This statement leads us to seek the origin of death, not in the waste of single cells, but in the limitation of their powers of reproduction. Death takes place because a worn-out tissue cannot for ever renew itself, and because a capacity for increase by means of cell-division is not everlasting, but finite [See Note 8]. This does not however imply that the immediate cause of death lies in the imperfect renewal of cells, for death would in all cases occur long before the reproductive power of the cells had been completely exhausted. Functional disturbances will appear as soon as the rate at which the worn-out cells are renewed becomes slow and insufficient.

But it must not be forgotten that death is not always preceded by senility, or a period of old age. For instance, in many of the lower animals death immediately follows the most important deed of the organism, viz. reproduction. Many Lepidoptera, all may-flies, and many other insects die of exhaustion immediately after depositing their eggs. Men have been known to die from the shock of a strong passion. Sulla is said to have died as the result of rage, whilst Leo X succumbed to an excess of joy. Here the psychical shock caused too intense an excitement of the nervous system. In the same manner the exercise of intense effort may also produce a similarly fatal excitement in the above-mentioned insects. At any rate it is certain that when, for some reason, this effort is not made, the insect lives for a somewhat longer period. 22

It is clear that in such animals as insects we can only speak figuratively of normal death, if we mean by this an end which is not due to accident. In these animals an accidental end is the rule, and is therefore, strictly speaking, normal [See Note 9].

Assuming the truth of the above-mentioned hypothesis as to the causes of normal death, it follows that the number of cell-generations which can proceed from the egg-cell is fixed for every species, at least within certain limits; and this number of cell-generations, if attained, corresponds to the maximum duration of life in the individuals of the species concerned. Shortening of life in any species must depend upon a decrease in the number of successive cell-generations, while conversely, the lengthening of life depends upon an increase in the number of cell-generations over those which were previously possible.

Such changes actually take place in plants. When an annual plant becomes perennial, the change—one in every way possible—can only happen by the production of new shoots, i. e. by an increase in the number of cell-generations. The process is not so obvious in animals, because in them the formation of young cells does not lead to the production of new and visible parts, for the new material is merely deposited in the place of that which is worn out and disappears. Among plants, on the other hand, the old material persists, its cells become lignified, and it is built over by new cells which assume the functions of life.

It is certainly true that the question as to the necessity of death in general does not seem much clearer from this point of view than from the purely physiological one. This is because we do not know why a cell must divide 10,000 or 100,000 times and then suddenly stop. It must be admitted that we can see no reason why the power of cell-multiplication should not be unlimited, and why the organism should not therefore be endowed with everlasting life. In the same manner, from a physiological point of view, we might admit that we can see no reason why the functions of the organism should ever cease.

It is only from the point of view of utility that we can understand the necessity of death. The 23 same arguments which were employed to explain the necessity for as short a life as possible, will with but slight modification serve to explain the common necessity of death[4].

Let us imagine that one of the higher animals became immortal; it then becomes perfectly obvious that it would cease to be of value to the species to which it belonged. Suppose that such an immortal individual could escape all fatal accidents, through infinite time,—a 24 supposition which is of course hardly conceivable. The individual would nevertheless be unable to avoid, from time to time, slight injuries to one or another part of its body. The injured parts could not regain their former integrity, and thus the longer the individual lived, the more defective and crippled it would become, and the less perfectly would it fulfil the purpose of its species. Individuals are injured by the operation of external forces, and for this reason alone it is necessary that new and perfect individuals should continually arise and take their place, and this necessity would remain even if the individuals possessed the power of living eternally.

From this follows, on the one hand, the necessity of reproduction, and, on the other, the utility of death. Worn-out individuals are not only valueless to the species, but they are even harmful, for they take the place of those which are sound. Hence by the operation of natural selection, the life of our hypothetically immortal individual would be shortened by the amount which was useless to the species. It would be reduced to a length which would afford the most favourable conditions for the existence of as large a number as possible of vigorous individuals, at the same time.

If by these considerations death is shown to be a beneficial occurrence, it by no means follows that it is to be solely accounted for on grounds of utility. Death might also depend upon causes which lie in the nature of life itself. The floating of ice upon water seems to us to be a useful arrangement, although the fact that it does float depends upon its molecular structure and not upon the fact that its doing so is of any advantage to us. In like manner the necessity of death has been hitherto explained as due to causes which are inherent in organic nature, and not to the fact that it may be advantageous.

I do not however believe in the validity of this explanation; I consider that death is not a primary necessity, but that it has been secondarily acquired as an adaptation. I believe that life is endowed with a fixed duration, not because it is contrary to its nature to be unlimited, but because the unlimited existence of individuals would be a luxury without any corresponding advantage. The above-mentioned hypothesis upon the origin and necessity of death leads me to believe that the organism did not finally cease to renew the worn-out cell material because 25
the nature of the cells did not permit them to multiply indefinitely, but because the power of multiplying indefinitely was lost when it ceased to be of use.

I consider that this view, if not exactly proved, can at any rate be rendered extremely probable.

It is useless to object that man (or any of the higher animals) dies from the physical necessity of his nature, just as the specific gravity of ice results from its physical nature. I am quite ready to admit that this is the case. John Hunter, supported by his experiments on *anabiosis*, hoped to prolong the life of man indefinitely by alternate freezing and thawing; and the Veronese Colonel Aless. Guaguino made his contemporaries believe that a race of men existed in Russia, of which the individuals died regularly every year on the 27th of November, and returned to life on the 24th of the following April. There cannot however be the least doubt, that the higher organisms, as they are now constructed, contain within themselves the germs of death. The question however arises as to how this has come to pass; and I reply that death is to be looked upon as an occurrence which is advantageous to the species as a concession to the outer conditions of life, and not as an absolute necessity, essentially inherent in life itself.

Death, that is the end of life, is by no means, as is usually assumed, an attribute of all organisms. An immense number of low organisms do not die, although they are easily destroyed, being killed by heat, poisons, &c. As long, however, as those conditions which are necessary for their life are fulfilled, they continue to live, and they thus carry the potentiality of unending life in themselves. I am speaking not only of the Amoebae and the low unicellular Algae, but also of far more highly organized unicellular animals, such as the Infusoria.

The process of fission in the Amoeba has been recently much discussed, and I am well aware that the life of the individual is generally believed to come to an end with the division which gives rise to two new individuals, as if death and reproduction were the same thing. But this process cannot be truly called death. Where is the dead body? what is it that dies? Nothing dies; the body of the animal only divides into two similar parts, possessing the same constitution. Each of these parts is exactly like its parent, lives in the same manner, and finally 26
also divides into two halves. As far as these organisms are concerned, death can only be spoken of in the most figurative sense.

There are no grounds for the assumption that the two halves of an Amoeba are differently constituted internally, so that after a time one of them will die while the other continues to live. Such an idea is disproved by a recently discovered fact. It has been noticed in *Euglypha* (one of the Foraminifera) and in other low animals of the same group, that when division is almost complete, and the two halves are only connected by a short strand, the protoplasm of both parts begins to circulate, and for some time passes backwards and forwards between the two halves. A complete mingling of the whole substance of the animal and a resulting identity in the constitution of each half is thus brought about before the final separation [See Note 10].

The objection might perhaps be raised that, if the parent animal does not exactly die, it nevertheless disappears as an individual. I cannot however let this pass unless it is also maintained that the man of to-day is no longer the same individual as the boy of twenty years ago. In the growth of man, neither structure nor the components of structure remain precisely the same; the material is continually changing. If we can imagine an Amoeba endowed with self-consciousness, it might think before dividing 'I will give birth to a daughter,' and I have no doubt that each half would regard the other as the daughter, and would consider itself to be the original parent. We cannot however appeal to this criterion of personality in the Amoeba, but there is nevertheless a criterion which seems to me to decide the matter: I refer to the continuity of life in the same form.

Now if numerous organisms, endowed with the potentiality of never-ending life, have real existence, the question arises as to whether the fact can be understood from the point of view of utility. If death has been shown to be a necessary adaptation for the higher organisms, why should it not be so for the lower also? Are they not decimated by enemies? are they not often imperfect? are they not worn out by contact with the external world? Although they are certainly destroyed by other animals, there is nothing comparable to that deterioration of the 27
body which takes place in the higher organisms. Unicellular animals are too simply constructed for this to be possible. If an infusorian is injured by the loss of some part of its body, it may often recover its former integrity, but if the injury is too great it dies. The alternative is always perfect integrity or complete destruction.

We may now leave this part of the subject, for it is obvious that normal death, that is to say, death which arises from internal causes, is an impossibility among these lower organisms. In those species at any rate in which fission is accompanied by a circulation of the protoplasm of the parent, the two halves must possess the same qualities. Since one of them is endowed with a potentiality for unending life, and must be so endowed if the species is to persist, it is clear that the other exactly similar half must be endowed with equal potentiality.

Let us now consider how it happened that the multicellular animals and plants, which arose from unicellular forms of life, came to lose this power of living for ever.

The answer to this question is closely bound up with the principle of division of labour which appeared among multicellular organisms at a very early stage, and which has gradually led to the production of greater and greater complexity in their structure.

The first multicellular organism was probably a cluster of similar cells, but these units soon lost their original homogeneity. As the result of mere relative position, some of the cells were especially fitted to provide for the nutrition of the colony, while others undertook the work of reproduction. Hence the single group would come to be divided into two groups of cells, which may be called somatic and reproductive—the cells of the body as opposed to those which are concerned with reproduction. This differentiation was not at first absolute, and indeed it is not always so to-day. Among the lower Metazoa, such as the polypes, the capacity for reproduction still exists to such a degree in the somatic cells, that a small number of them are able to give rise to a new organism,—in fact new individuals are normally produced by means of so-called buds. Furthermore, it is well known that many of the higher animals have retained considerable powers of regeneration; the salamander can replace its lost tail or foot, and the snail can reproduce its horns, eyes, etc.

As the complexity of the Metazoan body increased, the two groups of cells became more 28
sharply separated from each other. Very soon the somatic cells surpassed the reproductive in number, and during this increase they became more and more broken up by the principle of

the division of labour into sharply separated systems of tissues. As these changes took place, the power of reproducing large parts of the organism was lost, while the power of reproducing the whole individual became concentrated in the reproductive cells alone.

But it does not therefore follow that the somatic cells were compelled to lose the power of unlimited cell-production, although in accordance with the law of heredity, they could only give rise to cells which resembled themselves, and belonged to the same differentiated histological system. But as the fact of normal death seems to teach us that they have lost even this power, the causes of the loss must be sought outside the organism, that is to say, in the external conditions of life; and we have already seen that death can be very well explained as a secondarily acquired adaptation. The reproductive cells cannot lose the capacity for unlimited reproduction, or the species to which they belong would suffer extinction. But the somatic cells have lost this power to a gradually increasing extent, so that at length they became restricted to a fixed, though perhaps very large number of cell-generations. This restriction, which implies the continual influx of new individuals, has been explained above as a result of the impossibility of entirely protecting the individual from accidents, and from the deterioration which follows them. Normal death could not take place among unicellular organisms, because the individual and the reproductive cell are one and the same: on the other hand, normal death is possible, and as we see, has made its appearance, among multicellular organisms in which the somatic and reproductive cells are distinct.

I have endeavoured to explain death as the result of restriction in the powers of reproduction possessed by the somatic cells, and I have suggested that such restriction may conceivably follow from a limitation in the number of cell-generations possible for the cells of each organ and tissue. I am unable to indicate the molecular and chemical properties of the cell upon which the duration of its power of reproduction depends: to ask this is to demand an explanation of the nature of heredity—a problem the solution of which may still occupy many 29
generations of scientists. At present we can hardly venture to propose any explanation of the real nature of heredity.

But the question must be answered as to whether the kind and degree of reproductive power resides in the nature of the cell itself, or in any way depends upon the quality of its nutriment.

Virchow, in his ‘Cellular Pathology,’ has remarked that the cells are not only nourished, but that they actively supply themselves with food. If therefore the internal condition of the cell decides whether it shall accept or reject the nutriment which is offered, it becomes conceivable that all cells may possess the power of refusing to absorb nutriment, and therefore of ceasing to undergo further division.

Modern embryology affords us many proofs, in the segmentation of the ovum, and in the subsequent developmental changes, that the causes of the different forms of reproductive activity witnessed in cells lie in the essential nature of the cells themselves. Why does the segmentation of one half of certain eggs proceed twice as rapidly as that of the other half? why do the cells of the ectoderm divide so much more quickly than those of the endoderm? Why does not only the rate, but also the number of cells produced (so far as we can follow them) always remain the same? Why does the multiplication of cells in every part of the blastoderm take place with the exact amount of energy and rapidity necessary to produce the various elevations, folds, invaginations, etc., in which the different organs and tissues have their origin, and from which finally the organism itself arises? There can be no doubt that the causes of all these phenomena lie within the cells themselves; that in the ovum and the cells which are immediately derived from it, there exists a tendency towards a certain determined (I might almost say specific) mode and energy of cell-multiplication. And why should we regard this inherited tendency as confined to the building up of the embryo? why should it not also exist in the young, and later in the mature animal? The phenomena of heredity which make their appearance even in old age afford us proofs that a tendency towards a certain mode of cell-multiplication continues to regulate the growth of the organism during the whole of its life.

The above-mentioned considerations show us that the degree of reproductive activity present in the tissues is regulated by internal causes while the natural death of an organism is the termination—the hereditary limitation—of the process of cell-division, which began in the segmentation of the ovum. [30]

Allow me to suggest a further consideration which may be compared with the former. The organism is not only limited in time, but also in space: it not only lives for a limited period, but it can only attain a limited size. Many animals grow to their full size long before their natural end: and although many fishes, reptiles, and lower animals are said to grow during the whole of their life, we do not mean by this that they possess the power of unlimited growth any more than that of unlimited life. There is everywhere a maximum size, which, as far as our experience goes, is never surpassed. The mosquito never reaches the size of an elephant, nor the elephant that of a whale.

Upon what does this depend? Is there any external obstacle to growth? Or is the limitation entirely imposed from within?

Perhaps you may answer, that there is an established relation between the increase of surface and mass, and it cannot be denied that these relations do largely determine the size of the body. A beetle could never reach the size of an elephant, because, constituted as it is, it would be incapable of existence if it attained such dimensions. But nevertheless the relations between surface and mass do not form the only reason why any given individual does not exceed the average size of its species. Each individual does not strive to grow to the largest possible size, until the absorption from its digestive area becomes insufficient for its mass; but it ceases to grow because its cells cannot be sufficiently nourished in consequence of its increased size. The giants which occasionally appear in the human species prove that the plan upon which man is constructed can also be carried out on a scale which is far larger than the normal one. If the size of the body chiefly depends upon amount of nutriment, it would be possible to make giants and dwarfs at will. But we know, on the contrary, that the size of the body is hereditary in families to a very marked extent; in fact so much so that the size of an individual depends chiefly upon heredity, and not upon amount of food.

These observations point to the conclusion that the size of the individual is in reality pre- [31]
determined, and that it is potentially contained in the egg from which the individual developes.

We know further that the growth of the individual depends chiefly upon the multiplication of cells and only to a slight extent upon the growth of single cells. It is therefore clear that a limit of growth is imposed by a limitation in the processes by which cells are increased, both as regards the number of cells produced and the rate at which they are formed. How could we otherwise explain the fact that an animal ceases to grow long before it has reached the physiologically attainable maximum of its species, without at the same time suffering any loss of vital energy?

In many cases at least, the most important duty of an organism, viz. reproduction, follows upon the attainment of full size—a fact which induced Johannes Müller to reject the prevailing hypothesis which explained the death of animals as due to ‘the influences of the inorganic environment, which gradually wear away the life of the individual.’ He argued that, if this were the case, ‘the organic energy of an individual would steadily decrease from the beginning,’ while the facts indicate that this is not so[5].

If it is further asked why the egg should give rise to a fixed number of cell-generations, although perhaps a number which varies widely within certain limits, we may now refer to the operation of natural selection upon the relation of surface to mass, and upon other physiological necessities which are peculiar to the species. Because a certain size is the most favourable for a certain plan of organization, the process of natural selection determined that such a size should be within certain variable limits, characteristic of each species. This size is then transmitted from generation to generation, for when once established as normal for the species, the most favourable size is potentially present in the reproductive cell from which each individual is developed.

If this conclusion holds, and I believe that no essential objection can be raised against it, then we have in the limitation in space a process which is exactly analogous to the limitation in time, which we have already considered. The latter limitation—the duration of life—also depends upon the multiplication of cells, the rapid increase of which first gave rise to the characteristic form of the mature body, and then continued at a slower rate. In the mature animal, cell-reproduction still goes on, but it no longer exceeds the waste; for some time it just compensates for loss, and then begins to decline. The waste is not compensated for, the tissues perform their functions incompletely, and thus the way for death is prepared, until its final appearance by one of the three great *Atria mortis*. 32

I admit that facts are still wanting upon which to base this hypothesis. It is a pure supposition that senile changes are due to a deficient reproduction of cells: at the same time this supposition gains in probability when we are enabled to reduce the limitations of the organism in both time and space to one and the same principle. It cannot however be asserted under any circumstances that it is a pure supposition that the ovum possesses a capacity for cell-multiplication which is limited both as to numbers produced and rate of production. The fact that each species maintains an average size is a sufficient proof of the truth of this conclusion.

Hitherto I have only spoken of animals and have hardly mentioned plants. I should not have been able to consider them at all, had it not happened that a work of Hildebrand's [See Note 12] has recently appeared, which has, for the first time, provided us with exact observations on the duration of plant-life.

The chief results obtained by this author agree very well with the view which I have brought before you to-day. Hildebrand shows that the duration of life in plants also is by no means completely fixed, and that it may be very considerably altered through the agency of the external conditions of life. He shows that, in course of time, and under changed conditions of life, an annual plant may become perennial, or *vice versa*. The external factors which influence the duration of life are here however essentially different, as indeed we expect them to be, when we remember the very different conditions under which the animal and vegetable kingdoms exist. During the life of animals the destruction of mature individuals plays a most important part, but the existence of the mature plant is fairly well secured; their chief period of destruction is during youth, and this fact has a direct influence upon the degree of fertility, but not upon the duration of life. Climatic considerations, especially the periodical changes of summer and winter, or wet and dry seasons, are here of greater importance. 33

It must then be admitted that the dependence of the duration of life upon the external conditions of existence is alike common to plants and animals. In both kingdoms the high multicellular forms with well-differentiated organs contain the germs of death, while the low unicellular organisms are potentially immortal. Furthermore, an undying succession of reproductive cells is possessed by all the higher forms, although this may be but poor consolation to the conscious individual which perishes. Johannes Müller is therefore right, when in the sentence quoted at the beginning of my lecture, he speaks of an 'appearance of immortality' which passes from each individual into that which succeeds it. That which remains over, that which persists, is not the individual itself,—not the complex aggregate of cells which is conscious of itself,—but an individuality which is outside its consciousness, and of a low order,—an individuality which is made up of a single cell, which arises from the conscious individual. I might here conclude, but I wish first, in a few words, to protect myself against a possible misunderstanding.

I have repeatedly spoken of immortality, first of the unicellular organism, and secondly of the reproductive cell. By this word I have merely intended to imply a duration of time which appears to be endless to our human faculties. I have no wish to enter into the question of the cosmic or telluric origin of life on the earth. An answer to this question will at once decide whether the power of reproduction possessed by these cells is in reality eternal or only immensely prolonged, for that which is without beginning is, and must be, without end.

The supposition of a cosmic origin of life can only assist us if by its means we can altogether dispense with any theory of spontaneous generation. The mere shifting of the origin of life to some other far-off world cannot in any way help us. A truly cosmic origin in its widest significance will rigidly limit us to the statement—*omne vivum e vivo*—to the idea that life can only arise from life, and has always so arisen,—to the conclusion that organic beings are eternal like matter itself.

Experience cannot help us to decide this question; we do not know whether spontaneous generation was the commencement of life on the earth, nor have we any direct evidence for the idea that the process of development of the living world carries the end within itself, or for the converse idea that the end can only be brought about by means of some external force. 34

I admit that spontaneous generation, in spite of all vain efforts to demonstrate it, remains for me a logical necessity. We cannot regard organic and inorganic matter as independent of each other and both eternal, for organic matter is continually passing, without residuum, into the inorganic. If the eternal and indestructible are alone without beginning, then the non-eternal and destructible must have had a beginning. But the organic world is certainly not eternal and indestructible in that absolute sense in which we apply these terms to matter itself. We can, indeed, kill all organic beings and thus render them inorganic at will. But these changes are not the same as those which we induce in a piece of chalk by pouring sulphuric acid upon it; in this ease we only change the form, and the inorganic matter remains. But when we pour sulphuric acid upon a worm, or when we burn an oak tree, these organisms are not changed into some other animal and tree, but they disappear entirely as organized beings and are resolved into inorganic elements. But that which can be completely resolved into inorganic matter must have also arisen from it, and must owe its ultimate foundation to it. The organic might be considered eternal if we could only destroy its form, but not its nature.

It therefore follows that the organic world must once have arisen, and further that it will at some time come to an end. Hence we must speak of the eternal duration of unicellular organisms and of reproductive cells in the Metazoa and Metaphyta in that particular sense which signifies, when measured by our standards, an immensely long time.

Yet who can maintain that he has discovered the right answer to this important question? And even though the discovery were made, can any one believe that by its means the problem of life would be solved? If it were established that spontaneous generation did actually occur, a new question at once arises as to the conditions under which the occurrence became possible. How can we conceive that dead inorganic matter could have come together in such a manner as to form living protoplasm, that wonderful and complex substance which absorbs foreign material and changes it into its own substance, in other words grows and multiplies? 35

And so, in discussing this question of life and death, we come at last—as in all provinces of human research—upon problems which appear to us to be, at least for the present, insoluble. In fact it is the quest after perfected truth, not its possession, that falls to our lot, that gladdens us, fills up the measure of our life, nay! hallows it.

APPENDIX.

Note 1. The Duration of Life among Birds.

There is less exact knowledge upon this subject than we might expect, considering the existing number of ornithologists and ornithological societies with their numerous publications. It has neither been possible nor necessary for my purpose to look up all the widely-scattered references which are to be found upon the subject. Many of these are doubtless unknown to me; for we are still in want of a compilation of accurately determined observations in this department of zoology. I print the few facts which I have been able to collect, as a slight contribution towards such a compilation.

Small singing birds live from eight to eighteen years: the nightingale, in captivity, eight years, but longer according to some writers: the blackbird, in captivity, twelve years, but both these birds live longer in the natural state. A 'half-bred nightingale built its nest for nine consecutive years in the same garden' (Naumann, 'Vögel Deutschlands,' p. 76).

Canary birds in captivity attain an age of twelve to fifteen years (l. c., p. 76).

Ravens have lived for almost a hundred years in captivity (l. c., Bd. I. p. 125).

Magpies in captivity live twenty years, and, 'without doubt,' much longer in the natural state (l. c., p. 346).

Parrots 'in captivity have reached upwards of a hundred years' (l. c., p. 125).

A single instance of the cuckoo (alluded to in the text) is mentioned by Naumann as reaching the age of thirty-two years (l. c., p. 76).

Fowls live ten to twenty years, the golden pheasant fifteen years, the turkey sixteen years, and the pigeon ten years (Oken, 'Naturgeschichte, Vögel,' p. 387).

A golden eagle which 'died at Vienna in the year 1719, had been captured 104 years previously' (Brehm, 'Leben der Vögel,' p. 72). 37

A falcon (species not mentioned) is said to have attained an age of 162 years (Knauer, 'Der Naturhistoriker,' Vienna, 1880).

A white-headed vulture which was taken in 1706 died in the Zoological Gardens at Vienna (Schönbrunn) in 1824, thus living 118 years in captivity (l. c.).

The example of the bearded vulture, mentioned in the text, is quoted from Schinz's 'Vögel der Schweiz,' p. 196.

The wild goose must live for upwards of 100 years, according to Naumann (l. c., p. 127). The proof of this is not, however, forthcoming. A wild goose which had been wounded reached its eighteenth year in captivity.

Swans are said to have lived 300 years(?), (Naumann, l. c., p. 127).

It is evident that observations upon the duration of life in wild birds can only rarely be made, and that they are usually the result of chance and cannot be verified. It is on this account all the more to be desired that every ascertained fact should be collected.

If the long life of birds has been correctly interpreted as compensation for their feeble fertility and for the great mortality of their young, it will be possible to estimate the length of life in a species, without direct observation, if we only know its fertility and the percentage of individuals destroyed. This percentage can, however, at best, be known only as an average. If we consider, for example, the enormous number of sea birds which breed in summer on the rocks and cliffs of the northern seas, and if we remember that the majority of these birds lay but one, or at most two eggs yearly, and that their young are exposed to very many destructive agencies, we are forced to the conclusion that they must possess a very long life, so that the

breeding period may be many times repeated. Their number does not diminish. Year after year countless numbers of these birds cover the rocks, from summit to sea line; millions of them rest there, and rise in the air like a thick cloud whenever they are disturbed. Even in those localities which are every year visited by man in order to effect their capture, the number does not appear to decrease, unless the birds are disturbed and are therefore prompted to seek other breeding-places. From the small island of St. Kilda, off Scotland, 20,000 young gannets (*Sula*) and an immense number of eggs are annually collected; and although this bird only lays a single egg yearly and takes four years to attain maturity, the numbers do not diminish[6]. 38
30,000 sea-gulls' eggs and 20,000 terns' eggs are yearly exported from the breeding-places on the island of Sylt, but in this case it appears that a systematic disturbance of the birds is avoided by the collectors, and no decrease in their numbers has yet taken place[7]. The destruction of northern birds is not only caused by man, but also by various predaceous mammals and birds. Indeed the dense mass of birds which throng the cliffs is a cause of destruction to many of the young and to the eggs, which are pushed over the edge of the rocks. According to Brehm the foot of these cliffs is 'always covered with blood and the dead bodies of fledglings.'

Such birds must attain a great age or they would have been exterminated long ago: the minimum duration of life necessary for the maintenance of the species must in their case be a very high one.

Note 2. The Duration of Life among Mammals.

The statements upon this subject in the text are taken from many sources; from Giebel's 'Säugethiere,' from Oken's 'Naturgeschichte,' from Brehm's 'Illustrirtem Thierleben,' and from an essay of Knauer in the 'Naturhistoriker,' Vienna, 1880.

Note 3. The Duration of Life among Mature Insects.

A short statement of the best established facts which I have been able to find is given below. I have omitted the lengthening of imaginal life which is due to hybernation in certain species. In almost all orders of insects there are certain species which emerge from the pupa in the autumn, but which first reproduce in the following spring. The time spent in the torpid condition during winter cannot of course be reckoned with the active life of the species, for its vital activity is either entirely suspended for a time by freezing (*Anabiosis*: Preyer[8]), or it is at any rate never more than a *vita minima*, with a reduction of assimilation to its lowest point.

The following account does not make any claim to contain all or even most of the facts scattered through the enormous mass of entomological literature, and much less all that is privately known by individual entomologists. It must therefore be looked upon as merely a first attempt, a nucleus, around which the principal facts can be gradually collected. It is unnecessary to give any special information as to the duration of larval life, for numerous and exact observations upon this part of the subject are contained in all entomological works. 39

I. Orthoptera.

Gryllotalpa. The eggs are laid in June or July, and the young are hatched in from two to three weeks; they live through the winter, and become sexually mature in the following May or June. ‘When the female has deposited her eggs, her body collapses, and afterwards she does not survive much longer than a month.’ ‘According as the females are younger or older, they live a longer or shorter life, and hence some females are even found in the autumn’ (Rösel, ‘Insektenbelustigungen,’ Bd. II. p. 92). Rösel believes that the female watches the eggs until they are hatched, and this explains the fact that she outlives the process of oviposition by about a month. It is not stated whether the males die at an earlier period.

Gryllus campestris becomes sexually mature in May, and sings from June till October, ‘when they all die’ (Oken, ‘Naturgeschichte,’ Bd. II. Abth. iii. p. 1527). It is hardly probable that any single individual lives for the whole summer; probably, as in the case of *Gryllotalpa*, the end of the life of those individuals which first become mature, overlaps the beginning of the life of others which reach maturity at a later date.

Locusta viridissima and *L. verrucivora* are mature at the end of August; they lay their eggs in the earth during the first half of September and then die. It is probable that the females do not live for more than four weeks in the mature state. It is not known whether the males of this or other species of locusts live for a shorter period.

I have found *Locusta cantans* in plenty, from the beginning of September to the end of the month. In captivity they die after depositing their eggs: the males are probably more short-lived, for towards the middle and end of September they are much less plentiful than the 40
females.

Acridium migratorium ‘dies after the eggs are laid’ (Oken, ‘Naturgeschichte’).

The male *Termes* probably live for a short time only, although exact observations upon the point are wanting. The females ‘seem sometimes to live four or five years,’ as I gather from a letter from Dr. Hagen, of Cambridge, Mass., U.S.A.

Ephemeridae. Rösel, speaking of *Ephemera vulgata* (‘Insektenbelustigungen,’ Bd. II. der Wasserinsekten, 2te Klasse, p. 60 et seq.), says:—‘Their flight commences at sunset, and comes to an end before midnight, when the dew begins to fall.’ ‘The pairing generally takes place at night and lasts but a short time. As soon as the insects have shed their last skin, in the afternoon or evening, they fly about in thousands, and pair almost immediately; but by the next day they are all dead. They continue to emerge for many days, so that when yesterday’s swarm is dead, to-day a new swarm is seen emerging from the water towards the evening.' 'They not only drop their eggs in the water, but wherever they may happen to be,—on trees, bushes, or the earth. Birds, trout and other fish lie in wait for them.'

Dr. Hagen writes to me—'It is only in certain species that life is so short. The female *Palingenia* does not live long enough to complete the last moult of the sub-imago. I believe that a female imago has never been seen. The male imago, often half in its sub-imago skin, fertilizes the female sub-imago and immediately the contents of both ovaries are extruded, and the insect dies. It is quite possible that the eggs pass out by rupturing the abdominal segments.'

Libellula. All dragon-flies live in the imago condition for some weeks; at first they are not capable of reproduction, but after a few days they pair.

Lepisma saccharina. An individual lived for two years in a pill-box, without any food except perhaps a little *Lycopodium* dust[9].

II. Neuroptera.

Phryganids 'live in the imago stage for at least a week and probably longer, apparently without taking food' (letter from Dr. Hagen).

According to the latest researches *Phrygane grandis*[10] never contains food in its alimentary canal, but only air, although it contains the latter in such quantities that the anterior end of the chylific ventricle is dilated by it. 41

III. Strepsiptera.

The larva requires for its development a rather shorter time than that which is necessary for the grub of the bee into the body of which it has bored. The pupa stage lasts eight to ten days. The male, which flies about in a most impetuous manner, lives only two to three hours, while the female lives for some days. Possibly the pairing does not take place until the female is two to three days old. The viviparous female seems to produce young only once in a lifetime, and then dies: it is at present uncertain whether she also produces young parthenogenetically (cf. Siebold, 'Ueber Paedogenesis der Strepsipteren,' Zeitschr. f. Wissensch. Zool., Band. XX, 1870).

IV. Hemiptera.

Aphis. Bonnet ('Observations sur les Pucerons,' Paris, 1745) had a parthenogenetic female of *Aphis euonymi* in his possession for thirty-one days, from its birth, during which time it brought forth ninety-five larvae. Gleichen kept a parthenogenetic female of *Aphis mali* fifteen to twenty-three days.

Aphis foliorum ulmi. The mother of a colony which leaves the egg in May is 2‴ long at the end of July: it therefore lives for at least two and a half months (De Geer, 'Abhandlungen zur Geschichte der Insekten,' 1783, III. p. 53).

Phylloxera vastatrix. The males are merely ephemeral sexual organisms, they have no proboscis and no alimentary canal, and die immediately after fertilizing the female.

Pemphigus terebinthi. The male as well as the female sexual individuals are wingless and without a proboscis; they cannot take food and consequently live but a short time,—far shorter than the parthenogenetic females of the same species (Derbès, 'Note sur les aphides du pistachier térébinthe,' Ann. des sci. nat., Tom. XVII, 1872).

Cicada. In spite of the numerous and laborious descriptions of the Cicadas which have appeared during the last two centuries, I can only find precise statements as to the duration of life in the mature insect in a single species. P. Kalm, writing upon the North American *Cicada* 42 *septemdecim*, which sometimes appears in countless numbers, states that ‘six weeks after (such a swarm had been first seen) they had all disappeared.’ Hildreth puts the life of the female at from twenty to twenty-five days. This agrees with the fact that the Cicada lays many hundred eggs (Hildreth states a thousand); sixteen to twenty at a time being inserted into a hole which is bored in wood, so that the female takes some time to lay her eggs (Oken, ‘Naturgeschichte,’ 2ter Bd. 3te Abth. p. 1588 et seq.).

Acanthia lectularia. No observations have been made upon the bed bug from which the normal length of its life can be ascertained, but many statements tend to show that it is exceedingly long-lived, and this is advantageous for a parasite of which the food (and consequently growth and reproduction) is extremely precarious. They can endure starvation for an astonishingly long period, and can survive the most intense cold. Leunis (‘Zoologie,’ p. 659) mentions the case of a female which was shut up in a box and forgotten: after six months’ starvation it was found not only alive but surrounded by a circle of lively young ones. Göze found bugs in the hangings of an old bed which had not been used for six years: ‘they appeared white like paper.’ I have myself observed a similar case, in which the starving animals were quite transparent. De Geer placed some bugs in an unheated room in the cold winter of 1772, when the thermometer fell to -33°C: they passed the whole winter in a state of torpidity, but revived in the following May. (De Geer, Bd. III. p. 165, and Oken, ‘Naturgeschichte,’ 2ter Bd. 3te Abth. p. 1613.)

V. Diptera.

Pulex irritans. Oken says of the flea (‘Naturgeschichte,’ Bd. II. Abth. 2, p. 759) that ‘death follows the deposition of the eggs in the course of two or three days, even if the opportunity of sucking blood is given them.’ The length of time which intervenes between the emergence from the cocoon and fertilization or the deposition of eggs is not stated.

Sarcophaga carnaria. The female fly dies ten to twelve hours after the birth of the viviparous larvae; the time intervening between the exit from the cocoon and the birth of the young is not 43
given (Oken, quoting Réaumur, ‘Mém. p. s. à l’hist. Insectes,’ Paris, 1740-48, IV).

Musca domestica. In the summer the common house-fly begins to lay eggs eight days after leaving the cocoon: she then lays several times. (See Gleichen, ‘Geschichte der gemeinen Stubenfliege,’ Nuremberg, 1764.)

Eristalis tenax. The larva of this large fly lives in liquid manure, and has been described and figured by Réaumur as the rat-tailed larva. I kept a female which had just emerged from the cocoon, from August 30th till October 4th, in a large gauze-covered glass vessel. The insect soon learnt to move freely about in its prison, without attempting to escape; it flew round in circles, with a characteristic buzzing sound, and obtained abundant nourishment from a solution of sugar, provided for it. From September 12th it ceased to fly about, except when frightened, when it would fly a little way off. I thought that it was about to die, but matters took an unexpected turn, and on the 26th of September it laid a large packet of eggs, and again on the 29th of the same month another packet of similar size. The flight of the animal had been probably impeded by the weight of the mass of ripe eggs in its body. The deposition of eggs was probably considerably retarded in this case, because fertilization had not taken place. The fly died on the 4th of October, having thus lived for thirty-five days. Unfortunately, I have been unable to make any experiments as to the duration of life in the female when males are also present.

VI. Lepidoptera.

I am especially indebted to Mr. W. H. Edwards[11], of Coalburgh, W. Virginia, and to Dr. Speyer, of Rhoden, for valuable letters relating to this order.

The latter writes, speaking of the duration of life in imagos generally:—'It is, to my mind, improbable that any butterfly can live as an imago for a twelvemonth. Specimens which have lived through the winter are only rarely seen in August, even when the summer is late. A worn specimen of *Vanessa cardui* has, for instance, been found at this time' ('Entomolog. Nachrichten,' 1881, p. 146). 44

In answer to my question as to whether the fact that certain Lepidoptera take no solid or liquid food, and are, in fact, without a functional mouth, may be considered as evidence for an adaptation of the length of life to the rapid deposition of eggs, Dr. Speyer replies:—'The wingless females of the *Psychidae* do not seem to possess a mouth, at any rate I cannot find one in *Psyche unicolor* (*graminella*). They do not leave the case during life, and certainly do not drink water. The same is true of the wingless female of *Heterogynis*, and of *Orgyia ericae*, and probably of all the females of the genus *Orgyia*; and as far as I can judge from cabinet specimens, it is probably true of the males of *Heterogynis* and *Psyche*. I have never seen the day-flying *Saturnidae*, *Bombycidae*, and other Lepidoptera with a rudimentary proboscis, settle in damp places, or suck any moist substance, and I doubt if they would ever do this. The sucking apparatus is probably deficient.'

In answer to my question as to whether the males of any species of butterfly or moth are known to pass a life of different length from that of the female, Dr. Speyer stated that he knew of no observations on this point.

The following are the only instances of well-established direct observations upon single individuals, in my possession[12]:—

Pieris napi, var. *bryoniae* [male] and [female], captured on the wing: lived in confinement ten days, and were then killed.

Vanessa prorsa lived at most ten days in confinement.

Vanessa urticae lived ten to thirteen days in confinement.

Papilio ajax. According to a letter from Mr. W. H. Edwards, the female, when she leaves the pupa, contains unripe eggs in her body, and lives for about six weeks—calculating from the first appearance of this butterfly to the disappearance of the same generation[13]. The males live longer, and continue to fly when very worn and exhausted. A worn female is very seldom seen;—'I believe the female does not live long after laying her eggs, but this takes some days, and probably two weeks.'

Lycaena violacea. According to Mr. Edwards, the first brood of this species lives three to four weeks at the most.

Smerinthus tiliae. A female, which had just emerged from the pupa, was caught on June 24th; 45
on the 29th pairing took place; on the 1st of July she laid about eighty eggs, and died the following day. She lived nine days, taking no food during this period, and she only survived the deposition of eggs by a single day.

Macroglossa stellatarum. A female, captured on the wing and already fertilized, lived in confinement from June 28th to July 4th. During this time she laid about eighty eggs, at intervals and singly; she then disappeared, and must have died, although the body could not be found among the grass at the bottom of the cage in which she was confined.

Saturnia pyri. A pair which quitted the cocoons on the 24th or 25th of April, remained in coitu from the 26th until May 2nd—six or seven days; the female then laid a number of eggs, and died.

Psyche graminella. The fertilized female lives some days, and the unfertilized female over a week (Speyer).

Solenobia triquetrella. 'The parthenogenetic form (I refer to the one which I have shown to be parthenogenetic in Oken's 'Isis,' 1846, p. 30) lays a mass of eggs in the abandoned case, soon after emergence. The oviposition causes her body to shrivel up, and some hours afterwards she dies. The non-parthenogenetic female of the same species remains for many days, waiting to be fertilized; if this does not occur, she lives over a week.' 'The parthenogenetic female lives for hardly a day, and the same is true of the parthenogenetic females of another species of *Solenobia*' (*S. inconspicuella*?). Letter from Dr. Speyer.

Psyche calcella, O. The males live a very short time; 'those which leave the cocoon in the evening are found dead on the following morning, with their wings fallen off, at the bottom of their cage.' Dr. Speyer.

Eupithecia, sp. (*Geometridae*), 'when well-fed, live for three to four weeks in confinement; the males fertilize the females frequently, and the latter continue to lay eggs when they are very feeble, and are incapable of creeping or flying.' Dr. Speyer.

The conclusions and speculations in the text seem to be sufficiently supported from this short series of observations. There remains, as we see, much to be done in this field, and it would well repay a lepidopterist to undertake some exact observations upon the length of life in different butterflies and moths, with reference to the conditions of life—the mode of egg- 46
laying, the degeneracy of the wings, and of the external mouth-parts or the closure of the mouth itself. It would be well to ascertain whether such closure does really take place, as it undoubtedly does in certain plant-lice.

VII. Coleoptera.

Melolontha vulgaris. Cockchafers, which I kept in an airy cage with fresh food and abundant moisture, did not in any case live longer than thirty-nine days. One female only, out of a total number of forty-nine, lived for this period; a second lived thirty-six days, a third thirty-five, and a fourth and fifth twenty-four days; all the rest died earlier. Of the males, only one lived as long as twenty-nine days. These periods are less by some days than the true maximum duration of life, for the beetles were captured in the field, and had lived for at least a day; but the difference cannot be great, when we remember that out of forty-nine beetles, only three females lived thirty-five to thirty-nine days, and only one male twenty-nine days. Those that died earlier had probably lived for some considerable time before being caught.

Exact experiments with pupae which have survived the winter would show whether the female really lives for ten days more than the male, or whether the results of my experiment were merely accidental. I may add that coitus frequently took place during the period of captivity. One pair, observed in this condition on the 17th, separated in the evening; they paired again on the morning of the 18th, and separated in the middle of the day. Coitus took place between another pair on the 22nd, and again on the 26th.

I watched the gradual approach of death in many individuals: some days before it ensued, the insects became sluggish, ceased to fly and to eat, and only crept a little way off when disturbed: they then fell to the ground and remained motionless, apparently dead, but moved their legs when irritated, and sometimes automatically. Death came on gradually and imperceptibly; from time to time there was a slow movement of the legs, and at last, after some hours, all signs of life ceased.

In one case only I found bacteria present in great numbers in the blood and tissues; in the other individuals which had recently died, the only noticeable change was the unusual dryness 47
of the tissues.

Carabus auratus. An experiment with an individual, caught on May 27th, gave the length of life at fourteen days; this is probably below the average, since the beetles are found, in the wild state, from the end of May until the beginning of July.

Lucanus cervus. Captured individuals, kept in confinement, and fed on a solution of sugar, never lived longer than fourteen days, and as a rule not so long. The beetles appear in June and July, and certainly cannot live much over a month. As is the case with many beetles appearing during certain months, the length of the individual life is shorter than the period over which they are found. Accurate information, especially as to any difference between the lengths of life in the sexes, is not obtainable.

Isolated accounts of remarkably long lives among beetles are to be found scattered throughout the literature of the subject. Dr. Hagen, of Cambridge, Mass., has been kind enough to draw my attention to these, and to send me some observations of his own.

Cerambyx heros. One individual lived in confinement from August until the following year[14].

Saperda carcharias. An individual lived from the 5th of July until the 24th of July of the next year[15].

Buprestis splendens. A living individual was removed from a desk which had stood in a London counting-house for thirty years; from the condition of the wood it was evident that the larva had been in it before the desk was made[16].

Blaps mortisaga. One individual lived three months, and two others three years.

Blaps fatidica. One individual which was left in a box and forgotten, was found alive when the box was opened six years afterwards.

Blaps obtusa. One lived a year and a half in confinement.

Eleodes grandis and *E. dentipes*. Eight of these beetles from California were kept in confinement and without food for two years by Dr. Gissler, of Brooklyn; they were then sent to Dr. Hagen who kept them another year.

Goliathus cacicus. One individual lived in a hot-house for five months.

In addition to these cases, Dr. Hagen writes to me: ‘Among the beetles which live for more than a year,—*Blaps*, *Pasimachus*, (*Carabidae*)—and among ants, almost thirty per cent. are found with the cuticle worn out and cracked, and the powerful mandibles so greatly worn down that species were formerly founded upon this point. The mandibles are sometimes worn down to the hypodermis.’ 48

From the data before me I am inclined to believe that in certain beetles the normal length of life extends over some years, and this is especially the case with the *Blapidae*. It seems probable that in these cases another factor is present,—a *vita minima*, or apparent death, a sinking of the vital processes to a minimum in consequence of starvation, which we might call the hunger sleep, after the analogy of winter sleep. The winter sleep is usually ascribed to cold alone, and some insects certainly become so torpid that they appear to be dead when the temperature is low. But cold does not affect all insects in this way. Among bees, for example, the activity of the insects diminishes to a marked extent at the beginning of winter, but if the temperature continues to fall, they become active again, run about, and as the bee-keepers say, ‘try to warm themselves by exercise’; by this means they keep some life in them. If the frost is very severe, they die. In the tropics the period of hibernation for many animals coincides with the time of maximum heat and drought. This shows that the organism can be brought into the condition of a *vita minima* in various ways, and it would not be at all remarkable if such a state were induced in certain insects by hunger. Exact experiments however are the only means by which such a suggestion can be tested, and I have already commenced a series of experiments. The fact that certain beetles live without food for many years (even six) can hardly be explained on any other supposition, for these insects consume a fair amount of food under normal conditions, and it is inconceivable that they could live for years without food, if the metabolism were carried on with its usual energy.

A very striking example, showing that longevity may be induced by the lengthening of the period of reproductive activity, is communicated to me by Dr. Adler in the following note: ‘Three years ago I accidentally noticed that ovoviviparous development takes place in

Chrysomela varians,—a fact which I afterwards discovered had been already described by another entomologist.

‘The egg passes through all the developmental stages in the ovary; when these are completed the egg is laid, and a minute or two afterwards the larva breaks through the egg-shell. In each division of the ovary the eggs undergo development one at a time; it therefore follows that they are laid at considerable intervals, so that a long life becomes necessary in order to ensure the development of a sufficiently long series of eggs. Hence it comes about that the females live a full year. Among other species of *Chrysomela* two generations succeed each other in a year, and the duration of life in the individual varies from a few months to half a year.’ 49

VIII. Hymenoptera.

Cynipidae. I have been unable to find any accurate accounts of the duration of life in the imagos of saw-flies or ichneumons; but on the other hand I owe to the kindness of Dr. Adler, an excellent observer of the *Cynipidae*, the precise accounts of that family which are in my possession. I asked Dr. Adler the general question as to whether there was any variation in the duration of life among the *Cynipidae* corresponding to the conditions under which the deposition of eggs took place; whether those species which lay many eggs, or of which the oviposition is laborious and protracted, lived longer than those species which lay relatively few eggs, or easily and quickly find the suitable places in which to deposit them.

Dr. Adler fully confirmed my suppositions and supported them by the following statements:—

‘The summer generation of *Neuroterus* (*Spathegaster*) has the shortest life of all *Cynipidae*. Whether captured or reared from the galls I have only kept them alive on an average for three to four days. In this generation the work of oviposition requires the shortest time and the least expenditure of energy, for the eggs are simply laid on the surface of a leaf. The number of eggs in the ovary is also smaller than that of other species, averaging about 200. This form of *Cynips* can easily lay 100 eggs a day.

‘The summer generation of *Dryophanta* (*Spathegaster Taschenbergi*, *verrucosus*, etc.) lives somewhat longer; I have kept them in confinement for six to eight days. The oviposition requires a considerable expenditure of time and strength, for the ovipositor has to pierce the rather tough mid-rib or vein of a leaf. The number of eggs in the ovary averages 300 to 400.

‘The summer generation of *Andricus*, which belongs to the extensive genus *Aphilotrix*, have also a long life. I have kept the smaller *Andricus* (such as *A. nudus*, *A. cirratus*, *A. noduli*) alive for a week, and the larger (*A. inflator*, *A. curvator*, *A. ramuli*) for two weeks. The smaller species pierce the young buds when quite soft, but the larger ones bore through the fully grown buds protected by tough scales. The ovary of the former contains 400 to 500 eggs, that of the latter over 600. 50

‘The agamic winter generations live much longer. The species of *Neuroterus* have the shortest life; they live for two weeks at the outside; on the other hand, species of *Aphilotrix* live quite four weeks, and *Dryophanta* and *Biorhiza* even longer. I have kept *Dryophanta scutellaris* alive for three months. The number of eggs in these agamic *Cynipidae* is much larger: *Dryophanta* and *Aphilotrix* contain 1200 and *Neuroterus* about 1000.’

It is evidently, therefore, a general rule that the duration of life is directly proportional to the number of eggs and to the time and energy expended in oviposition. It must of course be understood that, here as in all other instances, these are not the only factors which determine the duration of life, but many other factors, at present unknown, may be in combination with them and assist in producing the result. For example, it is very probable that the time of year at which the imagos appear exerts some indirect influence. The long-lived *Biorhiza* emerges from the gall in the middle of winter, and at once begins to deposit eggs in the oak buds. Although the insect is not sensitive to low temperature, for I have myself seen oviposition proceeding when the thermometer stood at 5° R., yet very severe frost would certainly lead to interruption and would cause the insect to shelter itself among dead leaves on the ground. Such interruptions may be of long duration and frequently repeated, so that the remarkably long life of this species may perhaps be looked upon as an adaptation to its winter life.

Ants. *Lasius flavus* lays its eggs in the autumn, and the young larvae pass the winter in the nest. The males and females leave the cocoons in June, and pair during July and August. The males fly out of the nest with the females, but they do not return to it; 'they die shortly after pairing.' It is also believed that the females do not return to the nest, but found new colonies; this point is however one of the most uncertain in the natural history of ants. On the other 51
hand it is quite certain that the female may live for years within the nest, continuing to lay fertilized eggs. Old females are sometimes found in the colony, with their jaws worn down to the hypodermis.

Breeding experiments confirm these statements. P. Huber[17] and Christ have already put the life of the female at three to four years, and Sir John Lubbock, who has been lately occupied with the natural history of ants, was able to keep a female worker of *Formica sanguinea* alive for five years; and he has been kind enough to write and inform me that two females of *Formica fusca*, which he captured in a wood together with ten workers, in December 1874, are still alive (July 1881), so that these insects live as imagos for six and a half years or more[18].

On the other hand, Sir John Lubbock never succeeded in keeping the males 'alive longer than 52
a few weeks.' Both the older and more recent observers agree in stating that female ants, like queen bees, are always protected as completely as possible from injury and danger. Dr. A. Forel, whose thorough knowledge of Swiss ants is well known, writes to me,—'The female ants are only once fertilized, and are then tended by the workers, being cleaned and fed in the middle of the nest: one often finds them with only three legs, and with their chitinous armour greatly worn. They never leave the centre of the nest, and their only duty is to lay eggs.'

With regard to the workers, Forel believes that their constitution would enable them to live as long as the females (as the experiments of Lubbock also indicate), and the fact that in the wild state they generally die sooner than the females is 'certainly connected with the fact that they are exposed to far greater dangers.' The same relation seems also to obtain among bees, but with them it has not been shown that in confinement the workers live as long as the queens.

Bees. According to von Berlepsch[19] the queen may as an exception live for five years, but as a rule survives only two or three years. The workers always seem to live for a much shorter period, generally less than a year. Direct experiments upon isolated or confined bees, or upon marked individuals in the wild state, do not prove this, but the statistics obtained by bee-keepers confirm the above. Every winter the numbers in a hive diminish from 12,000-20,000 to 2000-3000. The queen lays the largest number of eggs in the spring, and the workers which die before the winter are replaced by those which emerge in the summer, autumn or during a mild winter. The queen lays eggs at such a variable rate throughout the year that the above-mentioned inequality in numbers is explained. The workers do not often live for more than six to seven months, and at the time of their greatest labour, (May to July), only three months. An attempt to calculate the length of life of the workers and drones by taking stock at the end of summer, gives six months for the former and four months for the latter[20]. 53

The drones do not as a rule live so long as four months, for they meet with a violent death before the end of this period. The well-known slaughter of the drones is not, according to the latest observations, brought about directly by means of the stings of the workers, but by these latter driving away the useless drones from the food so that they perish of starvation.

Wasps. It is interesting that among these near relations of the bees, the life of the female should be much shorter, corresponding to the much lower degree of specialization found in the colonies. The females of *Polistes gallica* and of *Vespa* not only lay eggs but take part in building the cells and in collecting food; they are therefore obliged to use all parts of the body more actively and especially the wings, and are exposed to greater danger from enemies.

It is well known from Leuckart's observations, that the so-called 'workers' of *Polistes gallica* and *Bombus* are not arrested females like the workers of a bee-hive, but are females which although certainly smaller, are in every way capable of being fertilized and of reproduction. Von Siebold has nevertheless proved that they are not fertilized, but reproduce parthenogenetically.

The fertilized female which survives the winter, commences to found a colony at the beginning of May: the larvæ, which hatch from the first eggs, which are about fifteen in number, become pupæ at the beginning of June, and the imagos appear towards the end of the same month. These are all small 'workers,' and they perform such good service in tending the second brood, that the latter attain the size of the female which founded the colony; only differing from her in the perfect condition of their wings, for by this time her wings are greatly worn away.

The males appear at the beginning of July; their spermatozoa are mature in August, and pairing then takes place with certain 'special females which require fertilization' which have in the meantime emerged from their cocoons. These are the females which live through the winter and found new colonies in the following spring. The old females of the previous winter die, and do not live beyond the summer at the beginning of which they founded colonies. At 54
the first appearance of frost, the young fertilized females seek out winter quarters; the males which never survive the winter, do not take this course, but perish in October. The parthenogenetic females, which remain in the nest during the nuptial flight, also perish.

The males of *Polistes gallica* do not live longer than three months—from July to the beginning of October; the parthenogenetic females live a fortnight longer at the outside—from the middle of June to October, but the later generations have a shorter life. The sexual females alone live for about a year, including the winter sleep.

A similar course of events takes place in the genus *Vespa*. In both these genera the possibility of reproduction is not restricted to a single female in the nest, but is shared by a number of females. In the genus *Apis* alone is the division of labour complete, so that only a single female (the queen) is at any one time capable of reproduction, a power which differentiates it from the sterile workers.

Note 4. The Duration of Life of the Lower Marine Animals.

I have only met with one definite statement in the literature of this part of the subject. It concerns a sea anemone,—which is a solitary and not a colonial form. The English zoologist Dalyell, in August, 1828, removed an *Actinia mesembryanthemum* from the sea and placed it in an aquarium[21]. It was a very fine individual, although it had not quite attained the largest size; and it must have been at least seven years old, as proved by comparison with other individuals reared from the egg. In the year 1848, it was about thirty years old, and in the twenty years during which it had been in captivity it had produced 334 young Actiniae. Prof. Dohrn, of Naples, tells me that this Actinia is still living to-day, and is shown as a curiosity to those who visit the Botanical Gardens in Edinburgh. It is now (1882) at least sixty-one years old[22].

Note 5. The Duration of Life in Indigenous Terrestrial and Fresh-water Mollusca. 55

I am indebted to Herr Clessin—the celebrated student of our mollusca—for some valuable notes upon our indigenous snails and bivalves (*Lamellibranchiata*). I could not incorporate them in the text, for a number of necessary details as to the conditions of life are at present entirely unknown, or are at least only known in a very fragmentary manner. No statistics as to the amount of destruction suffered by the young are available, and even the number of eggs produced annually is only known for a few species. I nevertheless include Herr Clessin's very interesting communications, as a commencement to the life statistics of the Mollusca.

(1) '*Vitrinae* are annual; the old animals die in the spring, after having produced the spawn from which the young develope. These continue to grow until the following spring.'

(2) 'The *Succineae* are mostly biennial; *Succinea putris* probably triennial. Fertilization takes place from June till the beginning of August, and the young develope until the autumn. *Succinea Pfeifferi* and *S. elegans* live through the winter, and the fact is proved by very distinct annual markings. Reproduction takes place in July and August of the following year, and they die in the autumn. They continue to grow until their death.'

(3) 'The shells of our native species of *Pupa*, *Clausilia*, and *Bulimus* (with the exception of *Bulimus detritus*) show but faint annual markings. They can hardly require more than two years for their complete development. The great number of living individuals with full-sized shells belonging to these genera, as compared with the number which possess smaller shells, makes it probable that these animals live in the mature condition longer than our other *Helicidae*. I have always found full-sized shells present in at least two-thirds of the individuals of these genera characterized by much-coiled shells—a proportion which I have never seen among our larger *Helicidae*. Nevertheless direct observations as to the length of life in the mature condition are still wanting.'

(4) 'The *Helicidae* live from two to four years; *Helix sericea*, *H. hispida*, two to three years; *H. hortensis*, *H. nemoralis*, *H. arbustorum*, as a rule three years; *H. pomatia* four years. Fertilization is not in these species strictly confined to any one time of year, but in the case of 56
old animals takes place in the spring, as soon as the winter sleep is over; while in the two-year-old animals it also happens later in the summer.'

(5) 'The *Hyalineae* are mostly biennial: they seldom live three years, and even in the largest species such an age is probably exceptional. The smallest *Hyalineae* and *Helicidae* live at most two years. The length of life is dependent upon the time at which the parents are fertilized, for this decides whether the young begin to shift for themselves early in the summer or later in the autumn, and so whether the first year's growth is large or small.'

(6) 'The species of *Limnaeus*, *Planorbis*, and *Ancylus* live two to three years, that is they take two to three years to attain the full size. *L. auricularis* is mostly biennial, *L. palustris* and *L. pereger* two to three years: I have found that the latter, in the mountains at Oberstorf in the Bavarian Alps, may exceptionally attain the age of four years, that is, it may possess three clearly defined annual markings, whilst the specimens from the plain never showed more than two.'

(7) 'The *Paludinidae* attain an age of three or four years.'

(8) 'The smaller bivalves, *Pisidium* and *Cyclas*, do not often live for more than two years: the larger *Najadae*, on the other hand, often live for more than ten years, and indeed they are not full grown until they possess ten to fourteen annual markings. It is possible that habitat may have great influence upon the length of life in this order.'

'*Unio* and *Anodonta* become sexually mature in the third to the fifth year.'

As far as I am aware but few statements exist upon the length of life in marine mollusca, and these are for the most part very inexact. The giant bivalve *Tridacna gigas* must attain an age of 60 to 100 years[23]. All *Cephalopods* live for at least over a year, and most of them well over ten years; and the giant forms, sometimes mistaken for 'sea-serpents,' must require many decades in which to attain such a remarkable size. L. Agassiz has determined the length of life in a large sea snail, *Natica heros*, by sorting a great number of individuals according to their sizes: he places it at 30 years[24].

I am glad to be able to communicate an observation made at the Zoological Station at Naples upon the length of life in *Ascidians*. The beautiful white *Cionea intestinalis* has settled in great numbers in an aquarium at the Station, and Professor Dohrn tells me that it produces three generations annually, and that each individual lives for about five months, and then reproduces itself and dies. External conditions accounting for this early death have not been discovered. 57

It is known that the freshwater *Polyzoa* are annual, but it is not known whether the first individuals produced from a colony in the spring, live for the whole summer. The length of life is also unknown in single individuals of any marine Polyzoon.

Clessin's accurate statements upon the freshwater Mollusca, previously quoted, show that a surprisingly short length of life is the general rule. Only those forms of which the large size requires that many years shall elapse before the attainment of sexual maturity, live ten years or over (*Unio*, *Anodonta*); indeed, our largest native snail (*Helix pomatia*) only lives for four years, and many small species only one year, or two years if the former time is insufficient to render them sexually mature. These facts seem to indicate, as I think, that these molluscs are exposed to great destruction in the adult state, indeed to a greater extent than when they are young, or, at any rate, to an equal extent. The facts appear to be the reverse of those found among birds. The fertility is enormous; a single mussel contains several hundred thousand eggs; the destruction of young as compared with the number of eggs produced is distinctly smaller than in birds, therefore a much shorter duration of the life of each mature individual is rendered possible, and further becomes advantageous because the mature individuals are exposed to severe destruction.

However it can only be vaguely suggested that this is the case, for positive proofs are entirely absent. Perhaps the destruction of single mature individuals does not play so important a part as the destruction of their generative organs. The ravages of parasitic animals (*Trematodes*) in the internal organs of snails and bivalves are well known to zoologists. The ovaries of the latter are often entirely filled with parasites, and such animals are then incapable of reproduction.

Besides, molluscs have many enemies, which destroy them both on land and in water. In the water,—fish, frogs, newts, ducks and other water-fowl, and on land many birds, the hedgehog, toads, etc., largely depend upon them for food. 58

If the principles developed in this essay apply to the freshwater Mollusca, we must then infer that snails which maintain the mature condition—the capability of reproduction—for one year, are in this state more exposed to destruction from the attacks of enemies than those species which remain sexually mature for two or three years, or that the latter suffer from a greater proportional loss of eggs and young.

Note 6. Unequal Length of Life in the two Sexes.

This inequality is frequently found among insects. The males of the remarkable little parasites infesting bees, the *Strepsiptera*, only live for two to three hours in the mature condition, while the wingless, maggot-like, female lives eight days: in this case, therefore, the female lives sixty-four times as long as the male. The explanation of these relations is obvious; a long life for the male would be useless to the species, while the relatively long life of the female is a necessity for the species, inasmuch as she is viviparous, and must nourish her young until their birth.

Again, the male of *Phylloxera vastatrix* lives for a much shorter period than the female, and is devoid of proboscis and stomach, and takes no food: it fertilizes the female as soon as the last skin has been shed and then dies.

Insects are not the only animals among which we find inequality in the length of life of the two sexes. Very little attention has been hitherto directed to this matter, and we therefore possess little or no accurate information as to the duration of life in the sexes, but in some cases we can draw inferences either from anatomical structure or from the mode of development. Thus, male *Rotifers* never possess mouth, stomach, or intestine, they cannot take food, and without doubt live much shorter lives than the females, which are provided with a complete alimentary canal. Again, the dwarf males of many parasitic *Copepods*—low Crustacea—and the ‘complementary males’ of *Cirrhipedes* (or barnacles) are devoid of stomach, and must live for a much shorter time than the females; and the male *Entoniscidae* (a family of which the species are endo-parasitic in the larger Crustacea), although they can feed, 59
die after fertilizing the females; while the latter then take to a parasitic life, produce eggs, and continue to live for some time. It is supposed that the dwarf male of *Bonellia viridis* does not live so long by several years as the hundred times larger female, and it too has no mouth to its alimentary canal. These examples might be further increased by reference to zoological literature.

In most cases the female lives longer than the male, and this needs no special explanation; but the converse relation is conceivable, when, for instance, the females are much rarer than the males, and the latter lose much time in seeking them. The above-mentioned case of *Aglia tau* probably belongs to this category.

We cannot always decide conclusively whether the life of one sex has been lengthened or that of the other shortened; both these changes must have taken place in different cases. There is no doubt that a lengthening of life in the female has arisen in the bees and ants, for both sexes of the saw-flies, which are believed to be the ancestors of bees, only live for a few weeks. But among the *Strepsiptera* the shorter life of the male must have been secondarily acquired, since we only rarely meet with such an extreme case in insects.

Note 7. Bees.

It has not been experimentally determined whether the workers, which are usually killed after some months, would live as long as the queen, if they were artificially protected from danger in the hive; but I think that this is probable, because it is the case among ants, and because the peculiarity of longevity must be latent in the egg. As is well known, the egg which gives rise to the queen is identical with that which produces a worker, and differences in the nutrition alone decide whether a queen or a worker shall be formed. It is therefore probable that the duration of life in queen and worker is potentially the same.

Note 8. Death of the Cells in higher Organisms.

The opinion has been often expressed that the inevitable appearance of normal ‘death’ is dependent on the wearing out of the tissues in consequence of their functional activity. Bertin 60
says, referring to animal life[25]:—‘L’observation des faits y attache l’idée d’une terminaison fatale, bien que la raison ne découvre nullement les motifs de cette nécessité. Chez les êtres qui font partie du règne animal l’exercise même de la rénovation moléculaire finit par user le principe qui l’entretient sans doute parceque le travail d’échange ne s’accomplissant pas avec une perfection mathématique, il s’établit dans la figure, comme dans la substance de l’être vivant, une déviation insensible, et que l’accumulation des écarts finit par amener un type chimique ou morphologique incompatible avec la persistance de ce travail.’

Here the replacement of the used-up elements of tissue by new ones is not taken into account, but an attempt is made to show that the functions of the whole organism necessarily cause it to waste away. But the question at once arises, whether such a result does not depend upon the fact that the single histological elements,—the cells,—are worn out by the exercise of function. Bertin admits this to be the case, and this idea of the importance of changes in the cells themselves is everywhere gaining ground. But although we must admit that the histological elements do, as a matter of fact, wear out, in multicellular animals, this would not prove that, nor explain why, such changes must follow from the nature of the cell and the vital processes which take place within it. Such an admission would merely suggest the question:—how is it that the cells in the tissues of higher animals are worn out by their function, while cells which exist in the form of free and independent organisms possess the power of living for ever? Why should not the cells of any tissue, of which the equilibrium is momentarily disturbed by metabolism, be again restored, so that the same cells continue to perform their functions for ever:—why cannot they live without their properties suffering alteration? I have not sufficiently touched upon this point in the text, and as it is obviously important it demands further consideration.

In the first place, I think we may conclude with certainty from the unending duration of unicellular organisms, that such wearing out of tissue cells is a secondary adaptation, that the death of the cell, like general death, has arisen with the complex, higher organisms. Waste
does not depend upon the intrinsic nature of the cells, as the primitive organisms prove to us, 61
but it has appeared as an adaptation of the cells to the new conditions by which they are surrounded when they come into combination, and thus form the cell-republic of the metazoan body. The replacement of cells in the tissues must be more advantageous for the functions of the whole organism than the unlimited activity of the same cells, inasmuch as the power of single cells would be much increased by this means. In certain cases, these advantages are obvious, as for example in many glands of which the secretions are made up of cast-off cells. Such cells must die and be separated from the organism, or the secretion would come to an end. In many cases, however, the facts are obscure, and await physiological investigation. But in the meantime we may draw some conclusions from the effects of growth, which are necessarily bound up with a certain rate of production of new cells. In the process of growth a certain degree of choice between the old cells which have performed their functions up to any particular time, and the new ones which have appeared between them, is as it were left to the organism.

The organism may thus, figuratively speaking, venture to demand from the various specific cells of tissues a greater amount of work than they are able to bear, during the normal length of their life, and with the normal amount of their strength. The advantages gained by the whole organism might more than compensate for the disadvantages which follow from the disappearance of single cells. The glandular secretions which are composed of cell-detritus, prove that the cells of a complex organism may acquire functions which result in the

loosening of their connexion with the living cell-community of the body, and their final separation from it. And the same facts hold with the blood corpuscles, for the exercise of their function results in ultimate dissolution. Hence it is not only conceivable, but in every way probable, that many other functions in the higher organisms involve the death of the cells which perform them, not because the living cell is necessarily worn out and finally killed by the exercise of any ordinary vital process, but because the specific functions in the economy of the cell community which such cells undertake to perform, involve the death of the cells themselves. But the fact that such functions have appeared,—involving as they do the sacrifice of a great number of cells,—entirely depends upon the replacement of the old by newly 62
formed cells, that is by the process of reproduction in cells[26].

We cannot *a priori* dispute the possibility of the existence of tissues in which the cells are not worn out by the performance of function, but such an occurrence appears to be improbable when we recollect that the cells of all tissues owe their constitution to a very far-reaching process of division of labour, which leaves them comparatively one-sided, and involves the loss of many properties of the unicellular, self-sufficient organism. At any rate we only know of potential immortality in the cells which constitute independent unicellular organisms, and the nature of these is such that they are continually undergoing a complete process of reformation.

If we did not find any replacement of cells in the higher organism, we should be induced to look upon death itself as the direct result of the division of labour among the cells, and to conclude that the specific cells of tissues have lost, as a consequence of the one-sided development of their activities, the power of unending life, which belongs to all independent primitive cells. We should argue that they could only perform their functions for a certain time, and would then die, and with them the organism whose life is dependent upon their activity. The longer they are occupied with the performance of special functions, the less completely do they carry out the phenomena of life, and hence they lead to the appearance of retrogressive changes. But the replacement of cells is certain in many tissues (in glands, blood, etc.), so that we can never seek a satisfactory explanation in the train of reasoning indicated above, but we must assume the existence of limits to the replacement of cells. In my opinion, we can find an explanation of this in the general relations of the single individual to its species, and to the whole of the external conditions of life; and this is the explanation which I have suggested and have attempted to work out in the text.

Note 9. Death by Sudden Shock. 63

The most remarkable example of this kind of death known to me, is that of the male bees. It has been long known that the drone perishes while pairing, and it was usually believed that the queen bites it to death. Later observations have however shown that this is not the case, but that the male suddenly dies during copulation, and that the queen afterwards bites through the male intromittent organ, in order to free herself from the dead body. In this case death is obviously due to sudden excitement, for when the latter is artificially induced, death immediately follows. Von Berlepsch made some very interesting observations on this point, 'If one catches a drone by the wings, during the nuptial flight, and holds it free in the air without touching any other part, the penis is protruded and the animal instantly dies, becoming motionless as though killed by a shock. The same thing happens if one gently stimulates the dorsal surface of the drone on a similar occasion. The male is in such an excited and irritable condition that the slightest muscular movement or disturbance causes the penis to be protruded[27].' In this case death is caused by the so-called nervous shock. The humble-bees are not similarly constituted, for the male does not die after fertilizing the female, 'but withdraws its penis and flies away.' But the death of male bees, during pairing, must not be regarded as normal death. Experiment has shown that these insects can live for more than four months[28]. They do not, as a matter of fact, generally live so long; for—although the workers do not, as was formerly believed, kill them after the fertilization of the queen, by direct means—they prevent them from eating the honey and drive them from the hive, so that they die of hunger[29].

We must also look upon death which immediately, or very quickly, follows upon the deposition of eggs as death by sudden shock. The females of certain species of *Psychidae*, when they reproduce sexually, may remain alive for more than a week waiting for a male: after fertilization, however, they lay their eggs and die, while the parthenogenetic females of the same species lay their eggs and die immediately after leaving the cocoon; so that while the 64
former live for many days, the latter do not last for more than twenty-four hours. 'The parthenogenetic form of *Solenobia triquetrella*, soon after emergence, lays all her eggs together in the empty case, becomes much shrunken, and dies in a few hours.' (Letter from Dr. Speyer, Rhoden.)

Note 10. Intermingling during the Fission of Unicellular Organisms[30].

Fission is quite symmetrical in *Amoebae*, so that it is impossible to recognise mother and daughter in the two resulting organisms. But in *Euglypha* and allied forms the existence of a shell introduces a distinguishing mark by which it is possible to discriminate between the products of fission; so that the offspring can be differentiated from the parent. The parent organism, before division, builds the parts of the shell for the daughter form. These parts are arranged on the surface of that part of the protoplasm, external to the old shell, which will be subsequently separated as the daughter-cell. On this part the spicules are arranged and unite to form the new shell. The division of the nucleus takes place after that of the protoplasm, so that the daughter-cell is for some time without a nucleus. Although we can in this species recognise the daughter-cell for some time after separation from the parent by the greater transparency of its younger shell, it is nevertheless impossible to admit that the characteristics of the two animals are in any way different, for just before the separation of the two individuals a circulation of the protoplasm through both shells takes place after the manner described in the text, and there is therefore a complete intermingling of the substance of the two bodies.

The difference between the products is even greater after transverse fission of the *Infusoria*, for a new anus must be formed at the anterior part and a new mouth posteriorly. It is not known whether any circulation of the protoplasm takes place, as in *Euglypha*. But even if this does not occur, there is no reason for believing that the two products of division possess a different duration of life. 65

The process of fission in the *Diatomaceae* seems to me to be theoretically important, because here, as in the previously-mentioned *Monothalamia* (*Euglypha*, etc.), the new silicious skeleton is built up within the primary organism, but not, as in *Euglypha*, for the new individual only, but for both parent and daughter-cell alike[31]. If we compare the diatom shell to a box, then the two halves of the old shell would form two lids, one for each of the products of fission, while a new box is built up afresh for each of them. In this case there is an absolute equality between the products of fission, so far as the shell is concerned.

Note 11. Regeneration.

A number of experiments have been recently undertaken, in connection with a prize thesis at Würzburg, in order to test the powers of regeneration possessed by various animals. In all essential respects the results confirm the statements of the older observers, such as Spallanzani. Carrière has also proved that snails can regenerate not only their horns and eyes, but also part of the head when it has been cut off, although he has shown that Spallanzani's old statement that they can regenerate the whole head, including the nervous system, is erroneous[32].

Note 12. The Duration of Life in Plants.

The title of the work on this subject mentioned in the Text is ‘Die Lebensdauer und Vegetationsweise der Pflanzen, ihre Ursache und ihre Entwicklung,’ F. Hildebrand, Engler’s botanische Jahrbücher, Bd. II. 1. und 2. Heft, Leipzig, 1881.

NOTE 13.

[Many interesting facts and conclusions upon the subject of this essay will be found in a volume by Professor E. Ray Lankester, ‘On comparative Longevity in Man and the lower Animals,’ Macmillan and Co., 1870.—E. B. P.]

Footnotes for the Appendix to Essay I.

66

1. Humboldt's 'Ausichten der Natur.'

2. This estimate is derived from observation of the time during which these insects are to be seen upon the wing. Direct observations upon the duration of life in this species are unknown to me.

3. [Sir John Lubbock has now kept a queen ant alive for nearly 15 years. See note 2 {note 18 below} on p. 51.—E. B. P.]

4. [After reading these proofs Dr. A. R. Wallace kindly sent me an unpublished note upon the production of death by means of natural selection, written by him some time between 1865 and 1870. The note contains some ideas on the subject, which were jotted down for further elaboration, and were then forgotten until recalled by the argument of this Essay. The note is of great interest in relation to Dr. Weismann's suggestions, and with Dr. Wallace's permission I print it in full below.

   'The Action of Natural Selection in Producing Old Age, Decay, and Death.

   'Supposing organisms ever existed that had not the power of natural reproduction, then since the absorptive surface would only increase as the square of the dimensions while the bulk to be nourished and renewed would increase as the cube, there must soon arrive a limit of growth. Now if such an organism did not produce its like, accidental destruction would put an end to the species. Any organism therefore that, by accidental or spontaneous fission, could become two organisms, and thus multiply itself indefinitely without increasing in size beyond the limits most favourable for nourishment and existence, could not be thus exterminated: since the individual only could be accidentally destroyed,—the race would survive. But if individuals did not die they would soon multiply inordinately and would interfere with each other's healthy existence. Food would become scarce, and hence the larger individuals would probably decompose or diminish in size. The deficiency of nourishment would lead to parts of the organism not being renewed; they would become fixed, and liable to more or less slow decomposition as dead parts within a living body. The smaller organisms would have a better chance of finding food, the larger ones less chance. That one which gave off several small portions to form each a new organism would have a better chance of leaving descendants like itself than one which divided equally or gave off a large part of itself. Hence it would happen that those which gave off very small portions would probably soon after cease to maintain their own existence while they would leave a numerous offspring. This state of things would be in any case for the advantage of the race, and would therefore, by natural selection, soon become established as the regular course of things, and thus we have the origin of *old age*, *decay*, and *death*; for it is evident that when one or more individuals have provided a sufficient number of successors they themselves, as consumers of nourishment in a constantly increasing degree, are an injury to those successors. Natural selection therefore weeds them out, and in many cases favours such races as die almost immediately after they have left successors. Many moths and other insects are in this condition, living only to propagate their kind and then immediately dying, some not even taking any food in the perfect and reproductive state.'—E. B. P.]

5. Johannes Müller, 'Physiologie,' Bd. I. p. 31, Berlin, 1840.

6. Oken, 'Naturgeschichte,' Stuttgart, 1837, Bd. IV. Abth. 1.

7. Brehm, 'Leben der Vögel,' p. 278.

8. 'Naturwissenschaftliche Thatsachen und Probleme,' Populäre Vorträge, Berlin, 1880; *vide* Appendix.

9. 'Entomolog. Mag.,' vol. i. p. 527, 1833.

10. Imhof, 'Beiträge zur Anatomie der *Perla maxima*,' Inaug. Diss., Aarau, 1881.

11. Mr. Edwards has meanwhile published these communications in full; cf. 'On the length of life of Butterflies,' Canadian Entomologist, 1881, p. 205.

12. When no authority is given, the observations are my own.

13. In the paper quoted above, Edwards, after weighing all the evidence, reduces the length of life from three to four weeks.

14. 'Entomolog. Mag.,' vol. i. p. 527, 1823.

15. Ibid.

16. Ibid.

17. 'Recherches sur les mœurs des Fourmis indigènes,' Genève, 1810.

18. These two female ants were still alive on the 25th of September following Sir John Lubbock's letter, so that they live at least seven years. Cf. 'Observations on Ants, Bees, and Wasps,' Part VIII. p. 385; Linn. Soc. Journ. Zool., vol. xv. 1881.

    [Sir John Lubbock has kindly given me further information upon the duration of life of these two queen ants. Since the receipt of his letter, the facts have been published in the Journal of the Linnean Society (Zoology), vol. xx. p. 133. I quote in full the passage which refers to these ants:—

    'Longevity.—It may be remembered that my nests have enabled me to keep ants under observation for long periods, and that I have identified workers of *Lasius niger* and *Formica fusca* which were at least seven years old, and two queens of *Formica fusca* which have lived with me ever since December 1874. One of these queens, after ailing for some days, died on the 30th July, 1887. She must then have been more than thirteen years old. I was at first afraid that the other one might be affected by the death of her companion. She lived, however, until the 8th August, 1888, when she must have been nearly fifteen years old, and is therefore by far the oldest insect on record.

    'Moreover, what is very extraordinary, she continued to lay fertile eggs. This remarkable fact is most interesting from a physiological point of view. Fertilization took place in 1874 at the latest. There has been no male in the nest since then, and, moreover, it is, I believe, well established that queen ants and queen bees are fertilized once for all. Hence the spermatozoa of 1874 must have retained their life and energy for thirteen years, a fact, I believe, unparalleled in physiology.'

    'I had another queen of *Formica fusca* which lived to be thirteen years old, and I have now a queen of *Lasius niger* which is more than nine years old, and still lays fertile eggs, which produce female ants.'

Both the above-mentioned queens may have been considerably older, for it is impossible to estimate their age at the time of capture. It is only certain (as Sir John Lubbock informs me in his letter) that they must have been at least nine months old (when captured), as the eggs of *F. fusca* are laid in March or early in April.' The queens became gradually 'somewhat lethargic and stiff in their movements (before their death), but there was no loss of any limb nor any abrasion.' This last observation seems to indicate that queen ants may live for a much longer period in the wild state, for it is stated above that the chitin is often greatly worn, and some of the limbs lost (see pp. 48, 51, and 52).—E. B. P.]

19. A. von Berlepsch, 'Die Biene und ihre Zucht,' etc., 3rd ed.; Mannheim, 1872.

20. E. Bevan, 'Ueber die Honigbiene und die Länge ihres Lebens;' abstract in Oken's 'Isis,' 1844, p. 506.

21. Dalyell, 'Rare and Remarkable Animals of Scotland,' vol. ii. p. 203; London, 1848.

22. [Mr. J. S. Haldane has kindly obtained details of the death of the sea anemone referred to by the author. It died, by a natural death, on August 4, 1887, after having appeared to become gradually weaker for some months previous to this date. It had lived ever since 1828 in the same small glass jar in which it was placed by Sir John Dalyell. It must have been at least 66 years old when it died.—E.B.P.]

23. Bronn, 'Klassen und Ordnungen des Thierreichs,' Bd. III. p. 466; Leipzig.

24. Bronn, l. c.

25. Cf. the article 'Mort' in the 'Encyclop. Scienc. Méd.' vol. M. p. 520.

26. Roux, in his work 'Der Kampf der Theile im Organismus,' Jena 1881, has attempted to explain the manner in which division of labour has arisen among the cells of the higher organisms, and to render intelligible the mechanical processes by which the purposeful adaptations of the organism have arisen.

27. von Berlepsch, 'Die Biene und ihre Zucht,' etc.

28. Oken, 'Isis,' 1844, p. 506.

29. von Berlepsch, l. c., p. 165.

30. Cf. August Gruber, 'Der Theilungsvorgang bei Euglypha alveolata,' and 'Die Theilung der monothalamen Rhizopoden,' Z. f. W. Z., Bd. XXXV. and XXXVI., p. 104, 1881.

31. Cf. Victor Hensen, 'Physiologie d. Zeugung,' p. 152.

32. Cf. J. Carrière, 'Ueber Regeneration bei Landpulmonaten,' Tagebl. der 52. Versammlg. deutsch. Naturf. pp. 225-226.

II. 67

ON HEREDITY.

1883.

ON HEREDITY.

PREFACE.

The following essay was my inaugural lecture as Pro-Rector of the University of Freiburg, and was delivered publicly in the hall of the University, on June 21, 1883; it first appeared in print in the following August. Only a few copies of the first edition were available for the public, and it is therefore now reprinted as a second edition, which only differs from the first in a few not unimportant improvements and additions.

The title which I have chosen requires some explanation. I do not propose to treat of the whole problem of heredity, but only of a certain aspect of it—the transmission of acquired characters which has been hitherto assumed to occur. In taking this course I may say that it was impossible to avoid going back to the foundation of all the phenomena of heredity, and to determine the substance with which they must be connected. In my opinion this can only be the substance of the germ-cells; and this substance transfers its hereditary tendencies from generation to generation, at first unchanged, and always uninfluenced in any corresponding manner, by that which happens during the life of the individual which bears it. If these views, which are indicated rather than elaborated in this paper, be correct, all our ideas upon the transformation of species require thorough modification, for the whole principle of evolution by means of exercise (use and disuse), as proposed by Lamarck, and accepted in some cases by Darwin, entirely collapses.

The nature of the present paper—which is a lecture and not an elaborate treatise—necessitates that only suggestions and not an exhaustive treatment of the subject could be given. I have [70] also abstained from giving further details in the form of an appendix, chiefly because I could hardly have attempted to complete a treatment of the whole range of the subject, and I hope to refer again to these questions in the future, when new experiments and observations have been made.

I am very glad to see that such an important authority as Pflüger[33] has in the meantime come to the same opinion, from an entirely different direction—an opinion which forms the foundation of the views here brought forward, namely, that heredity depends upon the continuity of the molecular substance of the germ from generation to generation.

A. W.

[71]

II.

ON HEREDITY.

With your permission I wish to bring before you to-day my views on a problem of general biological interest—the problem of heredity.

Heredity is the process which renders possible that persistence of organic beings throughout successive generations, which is generally thought to be so well understood and to need no special explanation. Nevertheless our minds cannot fail to be much perplexed by the multiplicity of its manifestations, and to be greatly puzzled as to its real nature. A celebrated German physiologist says[34], 'Although many hands have at all times endeavoured to break the seal which hides the theory of heredity from our view, the results achieved have been but small; and we are in a certain degree justified in looking with little hope upon new efforts undertaken in this direction. We must nevertheless endeavour from time to time to ascertain how far we have advanced towards a complete explanation.'

Such a course is in every way advisable, for we are not dealing with phenomena which from their very nature are incomprehensible by man. The great complexity of the subject has alone rendered it hitherto insuperable, but in the province of heredity we certainly have not reached the limits of attainable knowledge.

From this point of view heredity bears some resemblance to certain anatomical and physiological problems, e. g. the structure and function of the human brain. Its structure—with so many millions of nerve-fibres and nerve-cells—is of such extraordinary complexity that we might well despair of ever completely understanding it. Each fibre is nevertheless distinct in itself, while its connection with the nearest nerve-cell can be frequently traced, and the function of many groups of cell elements is already known. But it would seem to be impossible to unravel the excessively complex network into which the cells and fibres are knit 72
together; and hence to arrive at the function of each single element appears to be also beyond our reach. We have not however commenced to untie this Gordian knot without some hope of success, for who can say how far human perseverance may be able to penetrate into the mechanism of the brain, and to reveal a connected structure and a common principle in its countless elements? But surely this work will be most materially assisted by the simultaneous investigation of the structure and function of the nervous system in the lower forms of life—in the polypes and jelly-fish, worms and Crustacea. In the same way we should not abandon the hope of arriving at a satisfactory knowledge of the processes of heredity, if we consider the simplest processes of the lower animals as well as the more complex processes met with in the higher forms.

The word heredity in its common acceptation, means that property of an organism by which its peculiar nature is transmitted to its descendants. From an eagle's egg an eagle of the same species developes; and not only are the characteristics of the species transmitted to the following generation, but even the individual peculiarities. The offspring resemble their parents among animals as well as among men.

On what does this common property of all organisms depend?

Häckel was probably the first to describe reproduction as 'an overgrowth of the individual,' and he attempted to explain heredity as a simple continuity of growth. This definition might be considered as a play upon words, but it is more than this; and such an interpretation rightly applied, points to the only path which, in my opinion, can lead to the comprehension of heredity.

Unicellular organisms, such as Rhizopoda and Infusoria, increase by means of fission. Each individual grows to a certain size, and then divides into two parts, which are exactly alike in size and structure, so that it is impossible to decide whether one of them is younger or older than the other. Hence in a certain sense these organisms possess immortality: they can, it is true, be destroyed, but, if protected from a violent death, they would live on indefinitely, and would only from time to time reduce the size of their overgrown bodies by division. Each individual of any such unicellular species living on the earth to-day is far older than mankind, and is almost as old as life itself.

From these unicellular organisms we can to a certain extent understand why the offspring, being in fact a part of its parents, must therefore resemble the latter. The question as to why the part should resemble the whole leads us to a new problem, that of assimilation, which also awaits solution. It is, at any rate, an undoubted fact that the organism possesses the power of taking up certain foreign substances, viz. food, and of converting them into the substance of its own body. 73

Among these unicellular organisms, heredity depends upon the continuity of the individual during the continual increase of its body by means of assimilation.

But how is it with the multicellular organisms which do not reproduce by means of simple division, and in which the whole body of the parent does not pass over into the offspring?

In such animals sexual reproduction is the chief means of multiplication. In no case has it always been completely wanting, and in the majority of cases it is the only kind of reproduction.

In these animals the power of reproduction is connected with certain cells which, as germ-cells, may be contrasted with those which form the rest of the body; for the former have a totally different rôle to play; they are without significance for the life of the individual[35], and yet they alone possess the power of preserving the species. Each of them can, under certain conditions, develope into a complete organism of the same species as the parent, with every individual peculiarity of the latter reproduced more or less completely. How can such hereditary transmission of the characters of the parent take place? how can a single reproductive cell reproduce the whole body in all its details?

Such a question could be easily answered if we were only concerned with the continuity of the substance of the reproductive cells from one generation to another; for this can be demonstrated in some cases, and is very probable in all. In certain insects the development of the egg into the embryo, that is the segmentation of the egg, begins with the separation of a few small cells from the main body of the egg. These are the reproductive cells, and at a later period they are taken into the interior of the animal and form its reproductive organs. Again, in certain small freshwater Crustacea (*Daphnidae*) the future reproductive cells become distinct 74
at a very early period, although not quite at the beginning of segmentation, i. e. when the egg has divided into not more than thirty segments. Here also the cells which are separated early form the reproductive organs of the animal. The separation of the reproductive cells from those of the body takes place at a still later period, viz. at the close of segmentation, in *Sagitta*—a pelagic free-swimming form. In Vertebrata they do not become distinct from the other cells of the body until the embryo is completely formed. Thus, as their development shows, a marked antithesis exists between the substance of the undying reproductive cells and that of the perishable body-cells. We cannot explain this fact except by the supposition that each reproductive cell potentially contains two kinds of substance, which at a variable time after the commencement of embryonic development, separate from one another, and finally produce two sharply contrasted groups of cells.

It is evidently unimportant, as regards the question of heredity, whether this separation takes place early or late, inasmuch as the molecular constitution of the reproductive substance is determined before the beginning of development. In order to understand the growth and multiplication of cells, it must be conceded that all protoplasmic molecules possess the power of growing, that is of assimilating food, and of increasing by means of division. In the same manner the molecules of the reproductive protoplasm, when well nourished, grow and increase without altering their peculiar nature, and without modifying the hereditary tendencies derived from the parents. It is therefore quite conceivable that the reproductive cells might separate from the somatic cells much later than in the examples mentioned above, without changing the hereditary tendencies of which they are the bearers. There may be in fact cases in which such separation does not take place until after the animal is completely formed, and others, as I believe that I have shown[36], in which it first arises one or more generations later, viz. in the buds produced by the parent. Here also there is no ground for the belief that the hereditary tendencies of the reproductive molecules are in any way changed by the length of time which elapses before their separation from the somatic molecules. And this theoretical 75 deduction is confirmed by observation, for from the egg of a Medusa, produced by the budding of a Polype, a Polype, in the first instance, and not a Medusa arises. Here the molecules of the reproductive substance first formed part of the Polype, and later, part of the Medusa bud, and, although they separated from the somatic cells in the bud, they nevertheless always retain the tendency to develope into a Polype.

We thus find that the reproduction of multicellular organisms is essentially similar to the corresponding process in unicellular forms; for it consists in the continual division of the reproductive cell; the only difference being that in the former case the reproductive cell does not form the whole individual, for the latter is composed of the millions of somatic cells by which the reproductive cell is surrounded. The question, ‘How can a single reproductive cell contain the germ of a complete and highly complex individual?’ must therefore be re-stated more precisely in the following form, ‘How can the substance of the reproductive cells potentially contain the somatic substance with all its characteristic properties?’

The problem which this question suggests, becomes clearer when we employ it for the explanation of a definite instance, such as the origin of multicellular from unicellular animals. There can be no doubt that the former have originated from the latter, and that the physiological principle upon which such an origin depended, is the principle of division of labour. In the course of the phyletic development of the organized world, it must have happened that certain unicellular individuals did not separate from one another immediately after division, but lived together, at first as equivalent elements, each of which retained all the animal functions, including that of reproduction. The *Magosphaera planula* of Häckel proves that such perfectly homogeneous cell-colonies exist[37], even at the present day. Division of labour would produce a differentiation of the single cells in such a colony: thus certain cells would be set apart for obtaining food and for locomotion, while certain other cells would be exclusively reproductive. In this way colonies consisting of somatic and of reproductive cells must have arisen, and among these for the first time death appeared. For in each case the 76 somatic cells must have perished after a certain time, while the reproductive cells alone retained the immortality inherited from the Protozoa. We must now ask how it becomes possible that one kind of cell in such a colony, can produce the other kind by division? Before the differentiation of the colony each cell always produced others similar to itself. How can the cells, after the nature of one part of the colony is changed, have undergone such changes in *their* nature that they can now produce more than one kind of cell?

Two theories can be brought forward to solve this problem. We may turn to the old and long since abandoned *nisus formativus*, or adapting the name to modern times, to a phyletic force of development which causes the organism to change from time to time. This *vis a tergo* or teleological force compels the organism to undergo new transformations without any reference to the external conditions of life. This theory throws no light upon the numerous adaptations which are met with in every organism; and it possesses no value as a scientific explanation.

Another supposition is that the primary reproductive cells are influenced by the secondary cells of the colony, which, by their adaptability to the external conditions of life, have become somatic cells: that the latter give off minute particles which entering into the former, cause such changes in their nature that at the next succeeding cell-division they are compelled to break up into dissimilar parts.

At first sight this hypothesis seems to be quite reasonable. It is not only conceivable that particles might proceed from the somatic to the reproductive cells, but the very nutrition of the latter at the expense of the former is a demonstration that such a passage actually takes place. But a closer examination reveals immense difficulties. In the first place, the molecules of the body devoured are never simply added to those of the feeding individual without undergoing any change, but as far as we know, they are really assimilated[38], that is, converted into the molecules of the latter. We cannot therefore gain much by assuming that a number of molecules can pass from the growing somatic cells into the growing reproductive cells, and can be deposited unchanged in the latter, so that, at their next division, the molecules are 77
separated to become the somatic cells of the following generation. How can such a process be conceivable, when the colony becomes more complex, when the number of somatic cells becomes so large that they surround the reproductive cells with many layers, and when at the same time by an increasing division of labour a great number of different tissues and cells are produced, all of which must originate *de novo* from a single reproductive cell? Each of these various elements must, *ex hypothesi*, give up certain molecules to the reproductive cells; hence those which are in immediate contact with the latter would obviously possess an advantage over those which are more remote. If then any somatic cell must send the same number of molecules to each reproductive cell[39], we are compelled to suspend all known physical and physiological conceptions, and must make the entirely gratuitous assumption of an affinity on the part of the molecules for the reproductive cells. Even if we admit the existence of this affinity, its origin and means of control remain perfectly unintelligible if we suppose that it has arisen from differentiation of the complete colony. An unknown controlling force must be added to this mysterious arrangement, in order to marshal the molecules which enter the reproductive cell in such a manner that their arrangement corresponds with the order in which they must emerge as cells at a later period. In short, we become lost in unfounded hypotheses.

It is well known that Darwin has attempted to explain the phenomena of heredity by means of a hypothesis which corresponds to a considerable extent with that just described. If we substitute gemmules for molecules we have the fundamental idea of Darwin's provisional hypothesis of pangenesis. Particles of an excessively minute size are continually given off from all the cells of the body; these particles collect in the reproductive cells, and hence any change arising in the organism, at any time during its life, is represented in the reproductive cell[40]. Darwin believed that he had by this means rendered the transmission of acquired characters intelligible, a conception which he held to be necessary in order to explain the 78
development of species. He himself pointed out that the hypothesis was merely provisional, and that it was only an expression of immediate, and by no means satisfactory knowledge of these phenomena.

It is always dangerous to invoke some entirely new force in order to understand phenomena which cannot be readily explained by the forces which are already known.

I believe that an explanation can in this case be reached by an appeal to known forces, if we suppose that characters acquired (in the true sense of the term) by the parent cannot appear in the course of the development of the offspring, but that all the characters exhibited by the latter are due to primary changes in the germ.

This supposition can obviously be made with regard to the above-mentioned colony with its constituent elements differentiated into somatic and reproductive cells. It is conceivable that the differentiation of the somatic cells was not primarily caused by a change in their own structure, but that it was prepared for by changes in the molecular structure of the reproductive cell from which the colony arose.

The generally received idea assumes that changes in the external conditions can, in connection with natural selection, call forth persistent changes in an organism; and if this view be accepted it must be as true of all Metazoa as it is of unicellular or of homogeneous multicellular organisms. Supposing that the hypothetical colonies, which were at first entirely made up of similar cells, were to gain some advantages, if in the course of development, the molecules of the reproductive cells, from which each colony arose became distributed irregularly in the resulting organism, there would be a tendency towards the perpetuation of such a change, wherever it appeared as the result of individual variability. As a result of this change the colony would no longer remain homogeneous, and its cells would become dissimilar from the first, because of the altered arrangement of the molecules in the reproductive cells. Nothing prevents us from assuming that, at the same time, the nature of a part of the molecule may undergo still further change, for the molecules are by nature complex, and may split up or combine together.

If then the reproductive cells have undergone such changes that they can produce a heterogeneous colony as the result of continual division, it follows that succeeding generations 79
must behave in exactly the same manner, for each of them is developed from a portion of the reproductive cell from which the previous generation arose, and consists of the same reproductive substance as the latter.

From this point of view the exact manner in which we imagine the subsequent differentiation of the colony to be potentially present in the reproductive cell, becomes a matter of comparatively small importance. It may consist in a different molecular arrangement, or in some change of chemical constitution, or it may be due to both these causes combined. The essential point is that the differentiation was originally due to some change in the reproductive cells, just as this change itself produces all the differentiations which appear in the ontogeny of all species at the present day. No one doubts that the reason why this or that form of segmentation takes place, or why this or that species finally appears, is to be found in the ultimate structure of the reproductive cells. And, as a matter of fact, molecular differentiation and grouping, whether present from the beginning or first appearing in the course of development, plays a rôle which can be almost directly observed in certain species. The first segmentation furrow divides the egg of such species into an opaque and a clear half, or, as is often the case among Medusae, into a granular outer layer and a clear central part, corresponding respectively with the ectoderm and endoderm which are formed at a later period. Such early differentiations are only the visible proofs of certain highly complex molecular rearrangements in the cells, and the fact appears to indicate that we cannot be far wrong in maintaining that differentiations which appear in the course of ontogeny depend upon the chemical and physical constitution of the molecules in the reproductive cell.

At the first appearance of the earliest Metazoa alluded to above, only two kinds of cells, somatic and reproductive, arose from the segmentation of the reproductive cell. The reproductive cells thus formed must have possessed exactly the same molecular structure as the mother reproductive cell, and would therefore pass through precisely the same developmental changes. We can easily imagine that all the succeeding stages in the development of the Metazoa have been due to the same causes which were efficient at the earliest period. Variations in the molecular structure of the reproductive cells would continue 80
to appear, and these would be increased and rendered permanent by means of natural selection, when their results, in the alteration of certain cells in the body, were advantageous to the species. The only condition necessary for the transmission of such changes is that a part of the reproductive substance (the germ-plasm) should always remain unchanged during segmentation and the subsequent building up of the body, or in other words, that such unchanged substance should pass into the organism, and after the lapse of a variable period, should reappear as the reproductive cells. Only in this way can we render to some extent intelligible the transmission of those changes which have arisen in the phylogeny of the species; only thus can we imagine the manner in which the first somatic cells gradually developed in numbers and in complexity.

It is only by supposing that these changes arose from molecular alterations in the reproductive cell that we can understand how the reproductive cells of the next generation can originate the same changes in the cells which are developed from them; and it is impossible to imagine any way in which the transmission of changes, produced by the direct action of external forces upon the somatic cells, can be brought about[41].

The difficulty or the impossibility of rendering the transmission of acquired characters intelligible by an appeal to any known force has been often felt, but no one has hitherto attempted to cast doubts upon the very existence of such a form of heredity.

There are two reasons for this: first, observations have been recorded which appear to prove the existence of such transmission; and secondly, it has seemed impossible to do without the supposition of the transmission of acquired characters, because it has always played such an important part in the explanation of the transformation of species.

It is perfectly right to defer an explanation, and to hesitate before we declare a supposed phenomenon to be impossible, because we are unable to refer it to any of the known forces. 81
No one can believe that we are acquainted with all the forces of nature. But, on the other hand, we must use the greatest caution in dealing with unknown forces; and clear and indubitable facts must be brought forward to prove that the supposed phenomena have a real existence, and that their acceptance is unavoidable.

It has never been proved that acquired characters are transmitted, and it has never been demonstrated that, without the aid of such transmission, the evolution of the organic world becomes unintelligible.

The inheritance of acquired characters has never been proved, either by means of direct observation or by experiment[42]. It must be admitted that there are in existence numerous descriptions of cases which tend to prove that such mutilations as the loss of fingers, the scars of wounds, etc., are inherited by the offspring, but in these descriptions the previous history is invariably obscure, and hence the evidence loses all scientific value.

As a typical example of the scientific value of such cases I may mention the frequently quoted instance of the cow, which lost its left horn from suppuration, induced by some ‘unknown cause,’ and which afterwards produced two calves with a rudimentary left horn in each case. But as Hensen[43] has rightly remarked, the loss of the cow’s horn may have arisen from a congenital malformation, which would certainly be transmitted, but which was not an acquired character.

The only cases worthy of scientific discussion are the well-known experiments upon guinea-pigs, conducted by the French physiologist Brown-Séquard. But the explanation of his results is, in my opinion, open to discussion. In these cases we have to do with the apparent transmission of artificially produced malformations. The division of important nerves, or of the spinal cord, or the removal of parts of the brain, produced certain symptoms which 82
reappeared in the descendants of the mutilated animals. Epilepsy was produced by dividing the great sciatic nerve; the ear became deformed when the sympathetic nerve was severed in the throat; and prolapsus of the eye-ball followed the removal of a certain part of the brain—the corpora restiformia. All these effects were said to be transmitted to the descendants as far as the fifth or sixth generation.

But we must inquire whether these cases are really due to heredity and not to simple infection. In the case of epilepsy, at any rate, it is easy to imagine that the passage of some specific organism through the reproductive cells may take place, as in the case of syphilis. We are, however, entirely ignorant of the nature of the former disease. This suggested explanation may not perhaps apply to the other cases: but we must remember that animals which have been subjected to such severe operations upon the nervous system have sustained a great shock, and if they are capable of breeding, it is only probable that they will produce weak descendants, and such as are easily affected by disease. Such a result does not however explain why the offspring should suffer from the same disease as that which was artificially induced in the parents. But this does not appear to have been by any means invariably the case. Brown-Séquard himself says, ‘The changes in the eye of the offspring were of a very variable nature, and were only occasionally exactly similar to those observed in the parents.’

There is no doubt, however, that these experiments demand careful consideration, but before they can claim scientific recognition, they must be subjected to rigid criticism as to the precautions taken, the number and nature of the control experiments, etc.

Up to the present time such necessary conditions have not been sufficiently observed. The recent experiments themselves are only described in short preliminary notices, which, as regards their accuracy, the possibility of mistake, the precautions taken, and the exact succession of individuals affected, afford no data upon which a scientific opinion can be founded. Until the publication of a complete series of experiments, we must say with Du Bois Reymond[44], ‘The hereditary transmission of acquired characters remains an unintelligible 83
hypothesis, which is only deduced from the facts which it attempts to explain.’

We therefore naturally ask whether the hypothesis is really necessary for the explanation of known facts.

At the first sight it certainly seems to be necessary, and it appears rash to attempt to dispense with its aid. Many phenomena only appear to be intelligible if we assume the hereditary transmission of such acquired characters as the changes which we ascribe to the use or disuse of particular organs, or to the direct influence of climate. Furthermore, how can we explain instinct as hereditary habit unless it has gradually arisen by the accumulation, through heredity, of habits which were practised in succeeding generations?

I will now attempt to prove that even these cases, so far as they depend upon clear and indubitable facts, do not force us to accept the supposition of the transmission of acquired characters.

It seems difficult and well nigh impossible to deny the transmission of acquired characters when we remember the influence which use and disuse have exercised upon certain special organs. It is well known that Lamarck attempted to explain the structure of the organism as almost entirely due to this principle alone. According to his theory the long neck of the giraffe arose by constant stretching after the leaves of trees, and the web between the toes of a water-bird’s foot by the extension of the toes, in an attempt to oppose as large a surface of water as possible in swimming. There can be no doubt that those muscles which are frequently used increase in size and strength, and that glands which often enter into activity become larger and not smaller, and that their functional powers increase. Indeed, the whole effect which exercise produces upon the single parts of the body is dependent upon the fact that frequently used organs increase in strength. This conclusion also refers to the nervous system, for a pianist who performs with lightning rapidity certain pre-arranged, highly complex, and combined movements of the muscles of his hands and fingers has, as Du Bois Reymond pointed out, not only exercised the muscles, but also those ganglionic centres of the brain which determine the combination of muscular movement. Other functions of the brain, such as memory, can be similarly increased and strengthened by exercise, and the question to be settled is whether characters acquired in this way by exercise and practice can be transmitted to the following 84
generations. Lamarck’s theory assumes that such transmission takes place, for without it no accumulation or increase of the characters in question would be possible, as a result of their exercise during any number of successive generations.

Against this we may urge that whenever, in the course of nature, an organ becomes stronger by exercise, it must possess a certain degree of importance for the life of the individual, and when this is the case it becomes subject to improvement by natural selection, for only those individuals which possess the organ in its most perfect form will be able to reproduce them. The perfection of form of an organ does not however depend upon the amount of exercise undergone by it during the life of the organism, but primarily and principally upon the fact that the germ from which the individual arose was predisposed to produce a perfect organ. The increase to which any organ can attain by exercise during a single life is bounded by certain limits, which are themselves fixed by the primary tendencies of the organ in question. We cannot by excessive feeding make a giant out of the germ destined to form a dwarf; we cannot, by means of exercise, transform the muscles of an individual destined to be feeble into those of a Hercules, or the brain of a predestined fool into that of a Leibnitz or a Kant, by means of much thinking. With the same amount of exercise the organ which is destined to be strong, will attain a higher degree of functional activity than one that is destined to be weak. Hence natural selection, in destroying the least fitted individuals, destroys those which from the germ were feebly disposed. Thus the result of exercise during the individual life does not acquire so much importance, for, as compared with differences in predisposition, the amount of exercise undergone by all the individuals of a species becomes relatively uniform. The increase of an organ in the course of generations does not depend upon the summation of the exercise taken during single lives, but upon the summation of more favourable predispositions in the germs.

In criticizing these arguments, it may be questioned whether the single individuals of a species which is undergoing modification do, as a matter of fact, exercise themselves in the same manner and to the same extent. But the consideration of a definite example clearly shows that 85
this must be the case. When the wild duck became domesticated, and lived in a farm-yard, all the individuals were compelled to walk and stand more than they had done previously, and the muscles of the legs were used to a correspondingly greater degree. The same thing happens in the wild state, when any change in the conditions of life compels an organ to be more largely used. No individual will be able to entirely avoid this extra use, and each will endeavour to accommodate itself to the new conditions according to its power. The amount of this power depends upon the predisposition of the germ; and natural selection, while it apparently decides between individuals of various degrees of strength, is in truth operating upon the stronger and weaker germs.

But the very conclusions which have been drawn from the increase of activity which has arisen from exercise, must also be drawn from the instances of atrophy or degeneration following from the disuse of organs.

Darwin long ago called attention to the fact that the degeneration of an organ may, under certain circumstances, be beneficial to the species. For example, he first proved in the instance of Madeira, that the loss of wings may be of advantage to many beetles inhabiting oceanic islands. The individuals with imperfectly developed or atrophied wings have an advantage, because they are not carried out to sea by the frequent winds. The small eyes, buried in fur, possessed by moles and other subterranean mammals, can be similarly explained by means of natural selection. So also, the complete disappearance of the limbs of snakes is evidently a real advantage to animals which creep through narrow holes and clefts; and the degeneration of the wings in the ostrich and penguin is, in part, explicable as a favourable modification of the organ of flight into an organ for striking air or water respectively.

But when the degeneration of disused organs confers no benefits upon the individual, the explanation becomes less simple. Thus we find that the eyes of animals which inhabit dark caves (such as insects, crabs, fish, Amphibia, etc.) have undergone degeneration; yet this can hardly be of direct advantage to the animals, for they could live quite as well in the dark with well-developed eyes. But we are here brought into contact with a very important aspect of natural selection, viz. the power of conservation exerted by it. Not only does the survival of 86
the fittest select the best, but it also maintains it[45]. The struggle for existence does not cease with the foundation of a new specific type, or with some perfect adaptation to the external or internal conditions of life, but it becomes, on the contrary, even more severe, so that the most minute differences of structure determine the issue between life and death.

The sharpest sight possessed by birds is found in birds of prey, but if one of them entered the world with eyes rather below the average in this respect, it could not, in the long run, escape death from hunger, because it would always be at a disadvantage as compared with others.

Hence the sharp sight of these birds is maintained by means of the continued operation of natural selection, by which the individuals with the weakest sight are being continually exterminated. But all this would be changed at once, if a bird of prey of a certain species were compelled to live in absolute darkness. The quality of the eyes would then be immaterial, for it could make no difference to the existence of the individual, or the maintenance of the species. The sharp sight might, perhaps, be transmitted through numerous generations; but when weaker eyes arose from time to time, these would also be transmitted, for even very short-sighted or imperfect eyes would bring no disadvantage to their owner. Hence, by continual crossing between individuals with the most varied degrees of perfection in this respect, the average of perfection would gradually decline from the point attained before the species lived in the dark.

We do not at present know of any bird living in perfect darkness, and it is improbable that such a bird will ever be found; but we are acquainted with blind fish and Amphibia, and among these the eyes are present it is true, but they are small and hidden under the skin. I think it is difficult to reconcile the facts of the case with the ordinary theory that the eyes of these animals have simply degenerated through disuse. If disuse were able to bring about the complete atrophy of an organ, it follows that every trace of it would be effaced. We know that, as a matter of fact, the olfactory organ of the frog completely degenerates when the olfactory nerve is divided; and that great degeneration of the eye may be brought about by the artificial destruction of the optic centre in the brain. Since, therefore, the effects of disuse are so striking in a single life, we should certainly expect, if such effects can be transmitted, that all traces of an eye would soon disappear from a species which lives in the dark. 87

The caverns in Carniola and Carinthia, in which the blind *Proteus* and so many other blind animals live, belong geologically to the Jurassic formation; and although we do not exactly know when for example the *Proteus* first entered them, the low organization of this amphibian certainly indicates that it has been sheltered there for a very long period of time, and that thousands of generations of this species have succeeded one another in the caves.

Hence there is no reason to wonder at the extent to which the degeneration of the eye has been already carried in the *Proteus*; even if we assume that it is merely due to the cessation of the conserving influence of natural selection.

But it is unnecessary to depend upon this assumption alone, for when a useless organ degenerates, there are also other factors which demand consideration, namely, the higher development of other organs which compensate for the loss of the degenerating structure, or the increase in size of adjacent parts. If these newer developments are of advantage to the species, they finally come to take the place of the organ which natural selection has failed to preserve at its point of highest perfection.

In the first place, a certain form of correlation, which Roux[46] calls 'the struggle of the parts in the organism,' plays a most important part. Cases of atrophy, following disuse, appear to be always attended by a corresponding increase of other organs: blind animals always possess very strongly developed organs of touch, hearing, and smell, and the degeneration of the wing-muscles of the ostrich is accompanied by a great increase in the strength of the muscles of the leg. If the average amount of food which an animal can assimilate every day remains constant for a considerable time, it follows that a strong influx towards one organ must be accompanied by a drain upon others, and this tendency will increase, from generation to generation, in proportion to the development of the growing organ, which is favoured by natural selection in its increased blood-supply, etc.; while the operation of natural selection has also determined the organ which can bear a corresponding loss without detriment to the organism as a whole. 88

Without the operation of natural selection upon different individuals, the struggle between the organs of a single individual would be unable to encourage a predisposition in the germ

towards the degeneration or non-development of a useless organ, and it could only limit and degrade the development of an organ in the lifetime of the individual. If, therefore, acquired characters are not transmitted, the disposition to develope such an organ would be present in the same degree in each successive generation, although the realization would be less perfect. The complete disappearance of a rudimentary organ can only take place by the operation of natural selection; this principle will lead to its elimination, inasmuch as the disappearing structure takes the place and the nutriment of other useful and important organs. Hence the process of natural selection tends to entirely remove the former. The predisposition towards a weaker development of the organ is thus advantageous, and there is every reason for the belief that the advantages would continue to be gained, and that therefore the processes of natural selection would remain in operation, until the germ had entirely lost all tendency towards the development of the organ in question. The extreme slowness with which this process takes place, and the extraordinary persistence of rudimentary organs, at any rate in the embryo, together with their gradual but finally complete disappearance, can be clearly seen in the limbs of certain vertebrates and arthropods. The blind-worms have no limbs, but a rudimentary shoulder-girdle is present close under the skin, and the interesting fact has been quite recently established[47] that the fore-limbs are present in the embryo in the form of short stumps, which entirely disappear at a later stage. In most snakes all traces of limbs have been lost in the adult, but we do not yet know for certain whether they are also wanting in the embryo. I might further mention the very different stages of degeneration witnessed in the limbs of various salamanders; and the anterior limbs of *Hesperornis*—the remarkable toothed bird from the cretaceous rocks—which, according to Marsh[48], consists only of a very thin and relatively 89
small humerus, which was probably concealed beneath the skin. The water-fleas (*Daphnidae*) possess in the embryonic state three complete and almost equal pairs of jaws, but two of these entirely disappear, and do not develope into jaws in any species. In the same way, the embryo of the maggot-like legless larva of bees and wasps possesses three pairs of ancestral limbs.

There are, however, cases in which, apparently, acquired variations of characters are transmitted without natural selection playing any active part in the change. Such a case is afforded by the short-sightedness so common in civilized nations.

This affection is certainly hereditary in some cases, and it may well have been explained as an example of the transmission of acquired changes. It has been argued that acquired short-sightedness can be in a slight degree transmitted, and that each successive generation has developed a further degree of the disease by habitually holding books etc. close to the eyes, so that the inborn predisposition to short-sightedness is continually accumulating.

But we must remember that variations in the refraction of the human eye have been for a long time independent of the preserving control of natural selection. In the struggle for existence, a blind man would certainly disappear before those endowed with sight, but myopia does not prevent any one from gaining a living.

A short-sighted lynx, hawk, or gazelle, or even a short-sighted Indian, would be eliminated by natural selection, but a short-sighted European of the higher class finds no difficulty in earning his bread.

Those fluctuations on either side of the average which we call myopia and hypermetropia, occur in the same manner, and are due to the same causes, as those which operate in producing degeneration in the eyes of cave-dwelling animals. If, therefore, we not infrequently meet with families in which myopia is hereditary, such results may be attributed to the transmission of an accidental disposition on the part of the germ, instead of to the transmission of acquired short-sightedness. A very large proportion of short-sighted people do not owe their affliction to inheritance at all, but have acquired it for themselves; for there is no doubt that a normal eye may be rendered myopic in the course of a life-time by continually looking at objects from a 90
very short distance, even when no hereditary predisposition towards the disease can be shown to exist. Such a change would of course appear more readily if there was also a corresponding predisposition on the part of the eye. But I should not explain this widely spread

predisposition towards myopia as due to the transmission of acquired short-sightedness, but to the greater variability of the eye, which necessarily results from the cessation of the controlling influence of natural selection.

This suspension of the preserving influence of natural selection may be termed *Panmixia*, for all individuals can reproduce themselves and thus stamp their characters upon the species, and not only those which are in all respects, or in respect to some single organ, the fittest. In my opinion, the greater number of those variations which are usually attributed to the direct influence of external conditions of life, are to be ascribed to panmixia. For example, the great variability of most domesticated animals essentially depends upon this principle.

A goose or a duck must possess strong powers of flight in the natural state, but such powers are no longer necessary for obtaining food when it is brought into the poultry-yard, so that a rigid selection of individuals with well-developed wings, at once ceases among its descendants. Hence in the course of generations, a deterioration of the organs of flight must necessarily ensue, and the other members and organs of the bird will be similarly affected.

This example very clearly indicates that the degeneration of an organ does not depend upon its disuse; for although our domestic poultry very rarely make use of their wings, the muscles of flight have not disappeared, and, at any rate in the goose, do not seem to have undergone any marked degeneration.

The numerous and exact observations conducted by Darwin upon the weight and measurement of the bones in domestic fowls, seem to me to possess a significance beyond that which he attributed to them.

If the weight of the wing-bones of the domestic duck bears a smaller proportion to the weight of the leg-bones than in the wild duck, and if, as Darwin rightly assumes, this depends not only upon the diminution of the wings, but also upon the increase of the legs, it by no means follows that this latter increase in organs which are now more frequently used, is dependent upon hereditary influences alone. 91

It is quite possible that it depends, on the one hand, upon the suspension of natural selection, or panmixia (and these effects would be transmitted), and on the other hand upon the direct influence of increased use during the course of a single life. We do not yet know with any accuracy, the amount of change which may be produced by increased use in the course of a single life. If it is desired to prove that use and disuse produce hereditary effects without the assistance of natural selection, it will be necessary to domesticate wild animals (for example the wild duck) and preserve all their descendants, thus excluding the operation of natural selection. If then all individuals of the second, third, fourth and later generations of these tame ducks possess identical variations, which increase from generation to generation, and if the nature of these changes proves that they must have been due to the effect of use or disuse, then perhaps the transmission of such effects may be admitted; but it must always be remembered that domestication itself influences the organism,—not only directly, but also indirectly, by the increase of variability as a result of the suspension of natural selection. Such experiments have not yet been carried out in sufficient detail[49].

It is usually considered that the origin and variation of instincts are also dependent upon the exercise of certain groups of muscles and nerves during a single life-time; and that the gradual improvement which is thus caused by practice, is accumulated by hereditary transmission. I believe that this is an entirely erroneous view, and I hold that all instinct is entirely due to the operation of natural selection, and has its foundation, not upon inherited experiences, but upon the variations of the germ.

Why, for instance, should not the instinct to fly from enemies have arisen by the survival of those individuals which are naturally timid and easily startled, together with the extermination of those which are unwary? It may be urged in opposition to this explanation that the birds of uninhabited islands which are not at first shy of man, acquire in a few generations an instinctive dread of him, an instinct which cannot have arisen in so short a time by means of natural selection. But, in this case are we really dealing with the origin of a new instinct, or only with the addition of one new perception ('Wahrnehmung,' Schneider)[50], of the same kind as those which incite to the instinct of flight—an instinct which had been previously developed in past ages but had never been called forth by man? Again, has any one ascertained whether the young birds of the second or third generation are frightened by man? May it not be that the experience of a single life-time plays a great part in the origin of the habit? For my part, I am inclined to believe that the habit of flying from man is developed in the first generation which encounters him as a foe[51]. We see how wary and cautious a flock of birds become as soon as a few shots have been fired at them, and yet shortly before this occurrence they were perhaps playing carelessly close to the sportsmen. Intelligence plays a considerable part in the life of birds, and it by no means follows that the transmission of individual habits explains the above-mentioned phenomena. The long-continued operation of natural selection may very well have been necessary before the perception of man could awake the instinct to flee in young, inexperienced birds. Unfortunately the observations upon these points are far too indefinite to enable us to draw conclusions. 92

There is again the frequently-quoted instance of the young pointer, 'which, untrained, and without any example which might have been imitated, pointed at a lizard in a subtropical jungle, just as many of its forefathers had pointed at partridges on the plain of St. Denis,' and which, without knowing the effect of a shot, sprang forward barking, at the first discharge, to bring in the game. This conduct must not be attributed to the inheritance of any mental picture, such as the effect of a shot, but to the inheritance of a certain reflex mechanism. The young pointer does not spring forward at the shot because he has inherited from his forefathers a certain association of ideas,—shot and game,—but because he has inherited a reflex mechanism, which impels him to start forward on hearing a report. We cannot yet determine without more experiments how such an impulse due to perception ('Wahrnehmungstrieb,' Schneider) has arisen; but, in my opinion, it is almost inconceivable that artificial breeding has had nothing to do with it; and that we are here concerned—not with the inheritance of the effects of training—but with some predisposition on the part of the germ, which has been increased by artificial selection. 93

The necessity for extreme caution in appealing to the supposed hereditary effects of use, is well shown in the case of those numerous instincts, which only come into play once in a lifetime, and which do not therefore admit of improvement by practice. The queen-bee takes her nuptial flight only once, and yet how many and complex are the instincts and the reflex mechanisms which come into play on that occasion. Again, in many insects the deposition of eggs occurs but once in a life-time, and yet such insects always fulfil the necessary conditions with unfailing accuracy, either simply dropping the eggs into water, or carefully fixing them on the surface of the earth beneath some stone, or laying them on a particular part of a certain species of plant; and in all these cases the most complicated actions are performed. It is indeed astonishing to watch one of the *Cynipidae* (*Rhodites rosae*) depositing her eggs in the tissue of a young bud. She first carefully examines the bud on all sides, and feels it with her legs and antennae. Then she slowly inserts her long ovipositor between the closely-rolled leaves of the bud, but if it does not reach exactly the right spot, she will withdraw and re-insert it many times, until at length, when the proper place has been found, she will slowly bore deep into the very centre of the bud, so that the egg will reach the exact spot, where the necessary conditions for its development alone exist.

But each *Cynips* lays eggs many times, and it may be argued that practice may have led to improvement in this case; we cannot however, as a matter of fact, expect much improvement in a process which is repeated, perhaps a dozen times, at short intervals of time, and which is of such an excessively complex nature.

It is the same with the deposition of eggs in most insects. How can practice have had any influence upon the origin of the instinct which leads one of our butterflies—(*Vanessa levana*) 94

—to lay its green eggs in single file, as columns, which project freely from the stem or leaf, so that protection is gained by their close resemblance to the flower-buds of the stinging-nettle, which forms the food-plant of their caterpillars?

Of course the butterfly is not aware of the advantage which follows from such a proceeding; intelligence has no part in the process. The entire operation depends upon certain inherent anatomical and physiological arrangements:—on the structure of the ovary and oviducts, on the simultaneous ripening of a certain number of eggs, and on certain very complex reflex mechanisms which compel the butterfly to lay its eggs on certain parts of certain plants. Schneider is certainly right when he maintains that this mechanism is released by a sensation, arising from the perception (whether by sight or smell, or both together) of the particular plant or part of the plant upon which the eggs are to be laid[52]. At any rate, we cannot, in such cases, appeal to the effects of constant use and the transmission of acquired characters, as an explanation; and the origin of the impulse can only be understood as a result of the process of natural selection.

The protective cocoons by which the pupae of many insects are surrounded also belong to the same category, and improvement by practice is entirely out of the question, for they are only constructed once in the course of a life-time. And yet these cocoons are often remarkably complex: think, for instance, of the cocoon spun by the caterpillar of the emperor moth (*Saturnia carpini*), which is so tough that it can hardly be torn, and which the moth would be unable to leave, if an opening were not provided for the purpose; while, on the other hand, the pupa would not be defended against enemies if the opening were not furnished with a circle of pointed bristles, converging outwards, on the principle of the lobster pot, so that the moth can easily emerge, although no enemy can enter. The impulse which leads to the production of such a structure can only have arisen by the operation of natural selection—not, of course, during the history of a single species, but during the development of numerous, consecutive species—by gradual and unceasing improvements in the initial stages of cocoon-building. A 95
number of species exists at the present day, of which the cocoons can be arranged in a complete series, becoming gradually less and less complex, from that described above, down to a loosely-constructed, spherical case in which the pupa is contained.

The cocoon spun by the larva of *Saturnia carpini* differs but little in complexity from the web of the spider, and if the former is constructed without assistance from the experience of the single individual—and this must certainly be admitted—it follows that the latter may be also built without the aid of experience, while there is neither reason nor necessity for appealing to the entirely unproved transmission of acquired skill in order to explain this and a thousand other operations.

It may be objected that, in man, in addition to the instincts inherent in every individual, special individual predispositions are also found, of such a nature that it is impossible that they can have arisen by individual variations of the germ. On the other hand, these predispositions—which we call talents—cannot have arisen through natural selection, because life is in no way dependent upon their presence, and there seems to be no way of explaining their origin except by an assumption of the summation of the skill attained by exercise in the course of each single life. In this case, therefore, we seem at first sight to be compelled to accept the transmission of acquired characters.

Now it cannot be denied that all predispositions may be improved by practice during the course of a life-time,—and, in truth, very remarkably improved. If we could explain the existence of great talent, such as, for example, a gift for music, painting, sculpture, or mathematics, as due to the presence or absence of a special organ in the brain, it follows that we could only understand its origin and increase (natural selection being excluded) by accumulation, due to the transmission of the results of practice through a series of generations. But talents are not dependent upon the possession of special organs in the brain. They are not simple mental dispositions, but combinations of many dispositions, and often of a most complex nature: they depend upon a certain degree of irritability, and a power of readily

transmitting impulses along the nerve-tracts of the brain, as well as upon the especial development of single parts of the brain. In my opinion, there is absolutely no trustworthy proof that talents have been improved by their exercise through the course of a long series of 96
generations. The Bach family shows that musical talent, and the Bernoulli family that mathematical power, can be transmitted from generation to generation, but this teaches us nothing as to the origin of such talents. In both families the high-water mark of talent lies, not at the end of the series of generations, as it should do if the results of practice are transmitted, but in the middle. Again, talents frequently appear in some single member of a family which has not been previously distinguished.

Gauss was not the son of a mathematician; Handel's father was a surgeon, of whose musical powers nothing is known; Titian was the son and also the nephew of a lawyer, while he and his brother, Francesco Vecellio, were the first painters in a family which produced a succession of seven other artists with diminishing talents. These facts do not, however, prove that the condition of the nerve-tracts and centres of the brain, which determine the specific talent, appeared for the first time in these men: the appropriate condition surely existed previously in their parents, although it did not achieve expression. They prove, as it seems to me, that a high degree of endowment in a special direction, which we call talent, cannot have arisen from the experience of previous generations, that is, by the exercise of the brain in the same specific direction.

It appears to me that talent consists in a happy combination of exceptionally high gifts, developed in one special direction. At present, it is of course impossible to understand the physiological conditions which render the origin of such combinations possible, but it is very probable that the crossing of the mental dispositions of the parents plays a great part in it. This has been admirably and concisely expressed by Goethe in describing his own characteristics—

Vom Vater hab' ich die Statur
Des Lebens ernstes Führen,
Vom Mütterchen die Frohnatur
Die Lust zum Fabuliren, etc.

The combination of talents frequently found in one individual, and the appearance of different remarkable talents in the various branches of one and the same family, indicate that talents are only special combinations of certain highly-developed mental dispositions which are found in every brain. Many painters have been admirable musicians, and we very frequently find both these talents developed to a slighter extent in a single individual. In the Feuerbach family we 97
find a distinguished jurist, a remarkable philosopher, and a highly-talented artist; and among the Mendelssohns a philosopher as well as a musician.

The sudden and yet widespread appearance of a particular talent in correspondence with the general intellectual excitement of a certain epoch points in the same direction. How many poets arose in Germany during the period of sentiment which marked the close of the last century, and how completely all poetic gifts seem to have disappeared during the Thirty Years' War. How numerous were the philosophers that appeared in the epoch which succeeded Kant; while all philosophic talent seemed to have deserted the German nation during the sway of the antagonistic 'exact science,' with its contempt for speculation.

Wherever academies are founded, there the Schwanthalers, Defreggers, and Lenbachs emerge from the masses which had shown no sign of artistic endowment through long periods of time[53]. At the present day there are many men of science who, had they lived at the time of Bürger, Uhland, or Schelling, would probably have been poets or philosophers. And the man of science also cannot dispense with that mental disposition directed in a certain course, which we call talent, although the specific part of it may not be so obvious: we may, indeed, go further, and maintain that the Physicist and the Chemist are characterized by a combination of mental dispositions which differ from those of the Botanist and the Zoologist. Nevertheless, a man is not born a physicist or a botanist, and in most cases chance alone determines whether his endowments are developed in either direction.

Lessing has asked whether Raphael would have been a less distinguished artist had he been born without hands: we might also enquire whether he might not have been as great a musician as he was painter if, instead of living during the historical high-water mark of painting, he had lived, under favourable personal influences, at the time of highly-developed and widespread musical genius. A great artist is always a great man, and if he finds the outlet for his talent closed on one side, he forces his way through on the other.

From all these examples I wish to show that, in my opinion, talents do not appear to depend upon the improvement of any special mental quality by continued practice, but they are the expression, and to a certain extent the bye-product, of the human mind, which is so highly developed in all directions. 98

But if any one asks whether this high mental development, acquired in the course of innumerable generations of men, is not dependent upon the hereditary effects of use, I would remind him that human intelligence in general is the chief means and the chief weapon which has served and still serves the human species in the struggle for existence[54]. Even in the present state of civilization—distorted as it is by numerous artificial encroachments and unnatural conditions—the degree of intelligence possessed by the individual chiefly decides between destruction and life; and in a natural state, or still better in a state of low civilization, this result is even more striking.

Here again, therefore, we encounter the effects of natural selection, and to this power we must attribute, at any rate, a great part of the phenomena we have been discussing, and it cannot be shown that—in addition to its operation—the transmission of characters acquired by practice plays any part in nature.

I only know of one class of changes in the organism which is with difficulty explained by the supposition of changes in the germ; these are the modifications which appear as the direct consequence of some alteration in the surroundings. But our knowledge on this subject is still very defective, and we do not know the facts with sufficient precision to enable us to pronounce a final verdict as to the cause of such changes: and for this reason, I do not propose to consider the subject in detail.

These changes—such, for example, as are produced by a strange climate—have been always looked at under the supposition that they are transmitted and intensified from generation to generation, and for this reason the observations are not always sufficiently precise. It is difficult to say whether the changed climate may not have first changed the germ, and if this were the case the accumulation of effects through the action of heredity would present no difficulty. For instance, it is well known that increased nourishment not only causes a plant to grow more luxuriantly, but it alters the plant in some distinct way, and it would be wonderful 99 indeed if the seeds were not also larger and better furnished with nutritive material. If the increased nourishment be repeated in the next generation, a still further increase in the size of the seed, in the luxuriance of the plant, and in all other changes which ensue, is at any rate conceivable if it is not a necessity. But this would not be an instance of the transmission of acquired characters, but only the consequence of a direct influence upon the germ-cells, and of better nourishment during growth.

A similar interpretation explains the converse change. When horses of normal size are introduced into the Falkland Islands, the next generation is smaller in consequence of poor nourishment and the damp climate, and after a few generations they have deteriorated to a marked extent. In such a case we have only to assume that the climate which is unfavourable and the nutriment which is insufficient for horses, affect not only the animal as a whole, but also its germ-cells. This would result in the diminution in size of the germ-cells, the effects upon the offspring being still further intensified by the insufficient nourishment supplied during growth. But such results would not depend upon the transmission by the germ-cells of certain peculiarities due to the unfavourable climate, which only appear in the full-grown horse.

It must be admitted that there are cases, such as the climatic varieties of certain butterflies, which raise some difficulties against this explanation. I myself, some years ago, experimentally investigated one such case[55], and even now I cannot explain the facts otherwise than by supposing the passive acquisition of characters produced by the direct influence of climate.

It must be remembered, however, that my experiments, which have been repeated upon several American species by H. W. Edwards, with results confirmatory of my own in all essential respects, were not undertaken with the object of investigating the question from this point of view alone. New experiments, under varying conditions, will be necessary to afford the true explanation of this aspect of the question; and I have already begun to undertake them.

Leaving on one side, for the moment, these doubtful, and insufficiently investigated cases, we 100
may still maintain that the assumption that changes induced by external conditions in the organism as a whole, are communicated to the germ-cells after the manner indicated in Darwin's hypothesis of pangenesis,—is wholly unnecessary for the explanation of these phenomena. Still we cannot exclude the possibility of such a transmission occasionally occurring, for, even if the greater part of the effects must be attributed to natural selection, there might be a smaller part in certain cases which depends on this exceptional factor.

A complete and satisfactory refutation of such an opinion cannot be brought forward at present: we can only point out that such an assumption introduces new and entirely obscure forces, and that innumerable cases exist in which we can certainly exclude all assistance from the transmission of acquired characters. In most cases of variation in colour we have no explanation but the survival of the fittest[56], and the same holds good for all changes of form which cannot be influenced by the will of the animal. Very numerous adaptations, such, for instance, as occur in the eggs of animals,—the markings, and appendages which conceal them from enemies, the complex coverings which prevent them from drying up or protect them from the injurious influence of cold,—must have all arisen entirely independently of any expression of will, or of any conscious or unconscious action on the part of the animals. I will not mention here the case of plants, which as every one knows are unconscious, for they are beyond my province. In this matter, there can be no suggestion of adaptation depending upon a struggle between the various parts of the organism (Roux)[57]. Natural selection cannot operate upon the different epithelial cells which secrete the egg-shell of *Apus*, since it is of no consequence to the animal which secretes the egg-shell whether a good or a bad shell is produced. Natural selection first operates among the offspring, and the egg with a shell incapable of resisting cold or drought is destroyed. The different cells of the same individual are not selected, but the different individuals themselves.

In all such cases we have no explanation except the operation of natural selection, and if we
cannot accept this, we may as well abandon any attempt at a natural explanation. But, in my 101
opinion, there is no reason why natural selection should be considered inadequate to the task. It is true that the objection has been lately urged, that it is inconceivable that all the wonderful adaptations of the organism to its surroundings can have arisen through the selection of individuals; and that for this purpose an infinite number of individuals and infinite time would be required; and stress is laid upon the fact that the wished-for useful changes can only arise singly and very rarely among a great number of individuals.

This last objection to the modern conception of natural selection has apparently some weight, for, as a matter of fact, useful variations of a conspicuous kind seldom appear, and are often entirely absent for many generations. If we expect to find that qualitative changes take place by sudden leaps, we can never escape this difficulty. But, I think, we must not look for conspicuous variations—such as occur among domesticated animals and plants—in the process of the evolution of species as it goes on in nature. Natural selection does not deal with qualitative but quantitative changes in the individual, and the latter are always present.

A simple example will make this clearer. Let us suppose that it was advantageous to some species—for instance the ancestors of the giraffe—to lengthen some part of the body, such as the neck: this result could be obtained in a relatively short time, for the members of the species already possessed necks of varying length, and the variations which form the material for natural selection were already in existence. Now all the organs of every species vary in size, and any one of them will undergo constant and progressive increase, as soon as it acquires exceptional usefulness. But not only will the organ fluctuate as a whole, but also the parts composing it will become larger or smaller under given conditions, will increase or diminish by the operation of natural selection. I believe that qualitative variations always depend upon differences in the size and number of the component parts of the whole. A skin appears to be naked, when it is really covered with a number of small fine hairs: if these grow larger and increase in number, a thick covering is formed, and we say that the skin is woolly or furry. In the same way the skin of many worms and Crustacea is apparently colourless, but 102
the microscope reveals the presence of a number of beautiful pigment spots; and not until these have increased enormously does the skin appear coloured to the naked eye. The presence or absence of colour and its quality when present are here dependent upon the quantity of the most minute particles, and on the distance at which the object in question is observed. Again, the first appearance of colour, or the change from a green to a yellow or red colour depends upon slight variations in the position or in the number of the oxygen atoms which enter into the chemical combination in question. Fluctuations in the chemical composition of the molecules of a unicellular organism (for example) must continually arise, just as fluctuations are always occurring in the number of pigment granules in a certain cell, or in the number of pigment cells in a certain region of the body, or even in the size of the various parts of the body.

All these quantitative relations are exposed to individual fluctuations in every species; and natural selection can strengthen the fluctuations of any part, and thus cause it to develope further in any given direction.

From this point of view, it becomes less astonishing and less inconceivable that organisms adapt themselves—as we see that they obviously do—in all their parts to any condition of existence, and that they behave like a plastic mass which can be moulded into almost any imaginable form in the course of time.

If we ask in what lies the cause of this variability, the answer must undoubtedly be that it lies in the germ-cells. From the moment when the phenomena which precede segmentation commence in the egg, the exact kind of organism which will be developed is already determined—whether it will be larger or smaller, more like its father or its mother, which of its parts will resemble the one and which the other, even to the minutest detail. In spite of this, there still remains a certain scope for the influence of external conditions upon the organism. But this scope is limited, and forms but a small area round the fixed central point which is determined by heredity. Abundant nourishment can make the body large and strong, but can never make a giant out of the germ-cell destined to become a dwarf. Unhealthy sedentary habits or insufficient nourishment makes the factory-hand pale and stunted; life on board ship, 103
with plenty of exercise and sea air, gives the sailor bodily strength and a tanned skin; but when once the resemblance to father or mother, or to both, is established in the germ-cell it can never be effaced, let the habit of life be what it will.

But if the essential nature of the germ-cell dominates over the organism which will grow from it, so also the quantitative individual differences, to which I referred just now, are, by the same principle, established in the germ, and—whatever be the cause which determines their presence—they must be looked upon as inherent in it. It therefore follows that, although natural selection appears to operate upon the qualities of the developed organism alone, it in truth works upon peculiarities which lie hidden in the germ-cells. Just as the final development of any predisposition in the germ, and just as any character in the mature organism vibrates with a certain amplitude around a fixed central point, so the predisposition of the germ itself fluctuates, and it is on this that the possibility of an increase of the predisposition in question, and its average result, depends.

If we trace all the permanent hereditary variations from generation to generation back to the quantitative variations of the germ, as I have sought to do, the question naturally occurs as to the source from which these variations arose in the germ itself. I will not enter into this subject at any length on the present occasion, for I have already expressed my opinion upon it[58].

I believe however that they can be referred to the various external influences to which the germ is exposed before the commencement of embryonic development. Hence we may fairly attribute to the adult organism influences which determine the phyletic development of its descendants. For the germ-cells are contained in the organism, and the external influences which affect them are intimately connected with the state of the organism in which they lie hid. If it be well nourished, the germ-cells will have abundant nutriment; and, conversely, if it be weak and sickly, the germ-cells will be arrested in their growth. It is even possible that the 104 effects of these influences may be more specialized; that is to say, they may act only upon certain parts of the germ-cells. But this is indeed very different from believing that the changes of the organism which result from external stimuli can be transmitted to the germ-cells and will re-develope in the next generation at the same time as that at which they arose in the parent, and in the same part of the organism.

We have an obvious means by which the inheritance of all transmitted peculiarities takes place, in *the continuity of the substance of the germ-cells, or germ-plasm*. If, as I believe, the substance of the germ-cells, the germ-plasm, has remained in perpetual continuity from the first origin of life, and if the germ-plasm and the substance of the body, the somatoplasm, have always occupied different spheres, and if changes in the latter only arise when they have been preceded by corresponding changes in the former, then we can, up to a certain point, understand the principle of heredity; or, at any rate, we can conceive that the human mind may at some time be capable of understanding it. We may at least maintain that it has been rendered intelligible, for we can thus trace heredity back to growth; we can thus look upon reproduction as an overgrowth of the individual, and can thus distinguish between a succession of species and a succession of individuals, because in the latter succession the germ-plasm remains similar, while in the succession of the former it becomes different. Thus individuals, as they arise, are always assuming new and more complex forms, until the interval between the simple unicellular protozoon and the most complex of all organisms—man himself—is bridged over.

I have not been able to throw light upon all sides of the question which we are here discussing. There are still some essential points which I must leave for the present; and, furthermore, I am not yet in a position to explain satisfactorily all the details which arise at every step of the argument. But it appeared to me to be necessary to state this weighty and fundamental question, and to formulate it concisely and definitely; for only in this way will it be possible to arrive at a true and lasting solution of the problem. We must however be clear on this point—that the understanding of the phenomena of heredity is only possible on the fundamental supposition of the continuity of the germ-plasm. The value of experiment in relation to this 105 question is somewhat doubtful. A careful collection and arrangement of facts is far more likely to decide whether, and to what extent, the continuity of germ-plasm is reconcilable with the assumption of the transmission of acquired characters from the parent body to the germ, and from the germ to the body of the offspring. At present such transmission is neither proved as a fact, nor has its assumption been shown to be unquestionably necessary.

Footnotes for Essay II.

33. Pflüger, ‘Ueber den Einfluss der Schwerkraft auf die Theilung der Zellen und auf die Entwicklung des Embryo,’ Arch. f. Physiol. Bd. XXXII. p. 68, 1883.

34. Victor Hensen in his ‘Physiologie der Zeugung,’ Leipzig, 1881, p. 216.

35. That is for the preservation of its life.

36. Compare Weismann, ‘Die Entstehung der Sexualzellen bei den Hydromedusen,’ Jena, 1883.

37. It is doubtful whether *Magosphaera* should be looked upon as a mature form; but nothing hinders us from believing that species have lived, and are still living, in which the ciliated sphere has held together until the encystment, that is the reproduction, of the constituent single cells.

38. Or is an exception perhaps afforded by the nutritive cells of the egg, which occur in many animals?

39. Or more precisely, they must give up as many molecules as would correspond to the number of the kind of cell in question found in the mature organism.

40. See Darwin, ‘The Variation of Animals and Plants under Domestication,’ 1875, vol. ii. chapter xxvii. pp. 349-399.

41. To this class of phenomena of course belong those acts of will which call forth the functional activity of certain groups of cells. It is quite clear that such impulses do not originate in the constitution of the tissue in question, but are due to the operation of external causes. The activity does not arise directly from any natural disposition of the germ, but is the result of accidental external impressions. A domesticated duck uses its legs in a different manner from, and more frequently than a wild duck, but such functional changes are the consequence of changed external conditions, and are not due to the constitution of the germ.

42. Upon this subject Pflüger states—‘I have made myself accurately acquainted with all facts which are supposed to prove the inheritance of acquired characters,—that is of characters which are not due to the peculiar organization of the ovum and spermatozoon from which the individual is formed, but which follow from the incidence of accidental external influences upon the organism at any time in its life. Not one of these facts can be accepted as a proof of the transmission of acquired characters.’ *l. c.* p. 68.

43. ‘Physiologie der Zeugung.’

44. See ‘Ueber die Uebung,’ Berlin, 1881.

45. This principle was, I believe, first pointed out by Seidlitz. Compare Seidlitz, ‘Die Darwin’sche Theorie,’ Leipzig, 1875, p. 198.

46. W. Roux, ‘Der Kampf der Theile im Organismus,’ Leipzig, 1881.

47. Compare Born in ‘Zoolog. Anzeiger,’ 1883, No. 150, p. 537.

48. O. C. Marsh, 'Odontornithes, a Monograph on the extinct toothed Birds of North America,' Washington, 1880.

49. C. Darwin, 'Variation of Animals and Plants under Domestication.' Vol. I.

50. Compare 'Der thierische Wille,' Leipzig, 1880.

51. Steller's interesting account of the Sea-cow (*Rhytina Stelleri*) proves that this suggestion is valid. This large mammal was living in great numbers in Behring Strait at the end of the last century, but has since been entirely exterminated by man. Steller, who was compelled by shipwreck to remain in the locality for a whole year, tells us that the animals were at first without any fear of man, so that they could be approached in boats and could thus be killed. After a few months however the survivors became wary, and did not allow Steller's men to approach them, so that they were difficult to catch.—A. W., 1888.

52. Compare Schneider, 'Der thierische Wille.'

53. [The author refers to the Academy of Arts at Munich. S. S.]

54. Compare Darwin's 'Descent of Man.'

55. 'Studien zur Descendenztheorie, I. Ueber den Saison-Dimorphismus der Schmetterlinge.' Leipzig, 1875. English edition translated and edited by Professor Meldola, 'Studies in the Theory of Descent,' Part I.

56. The colours which have been called forth by sexual selection must also be included here.

57. Wilhelm Roux, 'Der Kampf der Theile im Organismus.' Leipzig, 1881.

58. Consult 'Studien zur Descendenztheorie, IV. Über die mechanische Auffassung der Natur,' p. 303, etc. Translated and edited by Professor Meldola; see 'Studies in the Theory of Descent,' p. 677, &c.

III. 107

LIFE AND DEATH.

1883.

LIFE AND DEATH.

PREFACE.

The following paper was first printed as an academic lecture in the summer of the present year (1883), with the title ‘Upon the Eternal Duration of Life’ (‘Über die Ewigkeit des Lebens’). In now bringing it before a larger public in an expanded and improved form, I have chosen a title which seemed to me to correspond better with the present contents of the paper.

The stimulus which led to this biological investigation was given in a memoir by Götte, in which this author opposes views which I had previously expressed. Although such an origin has naturally caused my paper to take the form of a reply, my intention was not merely to controvert the views of my opponent, but rather—using those opposed views as a starting-point—to throw new light upon certain questions which demand consideration; to give additional support to thoughts which I have previously expressed, and to penetrate, if possible, more deeply into the problem of life and death.

If, in making this attempt, the views of my opponent have been severely criticized, it will be acknowledged that the criticisms do not form the purpose of my paper, but only the means by which the way to a more correct understanding of the problems before us may be indicated.

A. W.

Freiburg i. Breisgau,
Oct. 18, 1883.

III.

LIFE AND DEATH.

In the previous essay, entitled 'The Duration of Life,' I have endeavoured to show that the limitation of life in single individuals by death is not, as has been hitherto assumed, an inevitable phenomenon, essential to the very nature of life itself; but that it is an adaptation which first appeared when, in consequence of a certain complexity of structure, an unending life became disadvantageous to the species. I pointed out that we could not speak of natural death among unicellular animals, for their growth has no termination which is comparable with death. The origin of new individuals is not connected with the death of the old; but increase by division takes place in such a way that the two parts into which an organism separates are exactly equivalent one to another, and neither of them is older or younger than the other. In this way countless numbers of individuals arise, each of which is as old as the species itself, while each possesses the capability of living on indefinitely, by means of division.

I suggested that the Metazoa have lost this power of unending life by being constructed of numerous cells, and by the consequent division of labour which became established between the various cells of the body. Here also reproduction takes place by means of cell-division, but every cell does not possess the power of reproducing the whole organism. The cells of the organism are differentiated into two essentially different groups, the reproductive cells—ova or spermatozoa, and the somatic cells, or cells of the body, in the narrower sense. The immortality of the unicellular organism has only passed over to the former; the others must die, and since the body of the individual is chiefly composed of them, it must die also.

I have endeavoured to explain this fact as an adaptation to the general conditions of life. In my opinion life became limited in its duration, not because it was contrary to its very nature to be unlimited, but because an unlimited persistence of the individual would be a luxury without a purpose. Among unicellular organisms natural death was impossible, because the reproductive cell and the individual were one and the same: among multicellular animals it was possible, and we see that it has arisen. 112

Natural death appeared to me to be explicable on the principle of utility, as an adaptation.

These opinions, to which I shall return in greater detail in a later part of this paper, have been opposed by Götte[59], who does not attribute death to utility, but considers it to be a necessity inherent in life itself. He considers that it occurs not only in the Metazoa or multicellular animals, but also in unicellular forms of life, where it is represented by the process of encystment, which is to be regarded as the death of the individual. This encystment is a process of rejuvenescence, which, after a longer or shorter interval, interrupts multiplication by means of fission. According to Götte, this process of rejuvenescence consists in the dissolution of the specific structure of the individual, or in the retrogression of the individual to a form of organic matter which is no longer living but which is comparable to the yolk of an egg. This matter is, by means of its internal energy, and in consequence of the law of growth which is inherent in its constitution, enabled to give rise to a new individual of the same species. Furthermore, the process of rejuvenescence among unicellular beings corresponds to the formation of germs in the higher organisms. The phenomena of death were transmitted by heredity from the unicellular forms to the Metazoa when they arose. Death does not therefore appear for the first time in the Metazoa, but it is an extremely ancient process which 'goes back to the first origin of organic beings' (l. c., p. 81).

It is obvious, from this short *résumé*, that Götte's view is totally opposed to mine. Inasmuch as only one of these views can be fundamentally right, it is worth while to compare the two; and although we cannot at present hope to explain the ultimate physiological processes which involve life and death, I think nevertheless that it is quite possible to arrive at definite conclusions as to the general causes of these phenomena. At any rate, existing facts have not 113 been so completely thought out that it is useless to consider them once more.

The question—what do we understand by death? must be decided before we can speak of the origin of death. Götte says, 'we are not able to explain this general expression quite definitely and in all its details, because the moment of death, or perhaps more exactly the moment when death is complete, can in no case be precisely indicated. We can only say that in the death of the higher animals, all those phenomena which make up the life of the individual cease, and further that all the cells and elements of tissue which form the dead organism, die, and are resolved into their elements.'

This definition would suffice if it did not include that which is to be defined. For it assumes that under the expression 'dead organism' we must include those organisms which have brought to an end the whole of their vital functions, but of which the component cells and elements may still be living. This view is afterwards more accurately explained, and in fact there is no doubt that the cessation of the activity of life in the multicellular organism rarely implies any direct connection with the cessation of vital functions in all its constituents. The question however arises, whether it is right or useful to limit the conception of death to the cessation of the functions of the organism. Our conceptions of death have been derived from the higher organisms alone, and hence it is quite possible that the conception may be too limited. The limitation might perhaps be removed by accurate and scientific comparison with the somewhat corresponding phenomena among unicellular organisms, and we might then arrive at a more comprehensive definition. Science has without doubt the right to make use of popular terms and conceptions, and by a more profound insight to widen or restrict them. But the main idea must always be retained, so that nothing quite new or strange may appear in the widened conception. The conception of death, as it has been expressed with perfect uniformity in all languages, has arisen from observations on the higher animals alone; and it signifies not only the cessation of the vital functions of the whole organism, but at the same time the cessation of life in its single parts, as is shown by the impossibility of revival. The *post-mortem* death of the cells is also part of death, and was so, long before science established the fact that an organism is built up of numerous very minute living elements, of which the vital 114 processes partially continue for some time after the cessation of those of the whole organism. It is precisely this incapacity on the part of the organism to reproduce the phenomena of life anew, which distinguishes genuine death from the arrest of life or trance; and the incapacity depends upon the fact that the death of the cells and tissues follows upon the cessation of the vital functions as a whole. I would, for this reason, define death as an arrest of life, from which no lengthened revival, either of the whole or any of its parts, can take place; or, to put it concisely, as a definite arrest of life. I believe that in this definition I have expressed the exact meaning of the conception which language has sought to convey in the word death. For our present purpose, the cause which gives rise to this phenomenon is of no importance,—whether it is simultaneous or successive in the various parts of the organism, whether it makes its appearance slowly or rapidly. For the conception itself it is also quite immaterial whether we are able to decide if death has really taken place in any particular case; however uncertain we might be, the state which we call death would be not less sharply and definitely limited. We might consider the caterpillar of *Euprepia flavia* to be dead when frozen in ice, but if it recovered after thawing and became an imago, we should say that it had only been apparently dead, that life stood still for a time, but had not ceased for ever. It is only the irretrievable loss of life in an organism which we call death, and we ought to hold fast to this conception, so that it will not slip from us, and become worthless, because we no longer know what we mean by it.

We cannot escape this danger if we look upon the *post-mortem* death of the cells of the body as a phenomenon which may accompany death, but which may sometimes be wanting. An experiment might be made in which some part of a dead animal, such as the comb of a cock, might be transplanted, before the death of the cells, to some other living animal: such a part might live in its new position, thus showing that single members may survive after the appearance of death, as I understand it. But the objection might be raised that in such a case the cock's comb has become a member of another organism, so that it would be lost labour to insert a clause in our definition of death which would include this phenomenon. The same objection might be raised if the transplantation took place a day or even a year before the 115
death of the cock.

Götte is decidedly in error when he considers that the idea of death merely expresses an 'arrest of the sum of vital actions in the individual,' without at the same time including that definite arrest which involves the impossibility of any revival. Decomposition is not quite essential to our definition, inasmuch as death may be followed by drying-up[60], or by perpetual entombment in Siberian ice (as in the well-known case of the mammoth), or by digestion in the stomach of a beast of prey. But the notion of a dead body is indeed inseparably connected with that of death, and I believe that I was right in distinguishing between the division of an Infusorian into two daughter-cells, and the death of a Metazoon, which leaves offspring behind it, by calling attention to the absence of a dead body in the process of fission among Infusoria (See below.). The real proof of death is that the organized substance which previously gave rise to the phenomena of life, for ever ceases to originate such phenomena. This, and this alone, is what mankind has hitherto understood by death, and we must start from this definition if we wish to retain a firm basis for our considerations.

We must now consider whether this definition, derived from observation of higher animals, may be also applied without alteration to the lower, or whether the corresponding phenomena which arise in these latter, differ in detail from those of the higher animals, so that a narrower limitation of the above definition is rendered necessary.

Götte believes the process of encystment which takes place in so many unicellular animals (Monoplastides) to be the analogue of death. According to this authority, the individuals in question, not only undergo a kind of winter sleep—a period of latent life—but when surrounded by the cyst they lose their former specific organization; they become a 'homogeneous substance,' and are resolved into a germ, from which, by a process of development, a new individual of the same species once more arises. The division of the contents of the cyst, viz. its multiplication, is, according to this view, of secondary importance, and the essential feature in the process is the rejuvenescence of the individual. This 116
rejuvenescence however is said to not only consist in the simple transformation of the old individual, but in its death, followed by the building up anew of another individual. 'The parent organism and its offspring are two successive living stages of the same substance—separated, and at the same time connected, by the condition of rejuvenescence which lies between them' (l. c., p. 79). An 'absolute continuity of life does not exist'; it is only the dead organic matter which establishes the connection, and the 'identity of this matter ensures heredity.'

It is certainly surprising that Götte should identify encystment with a cessation of life, and we may well inquire for the evidence which is believed to support such a view. The only evidence lies in a certain degree of degeneration in the structure of the individual, and in the cessation of the visible external phenomena of life, such as feeding and moving. Does Götte really believe that it is an incorrect interpretation of the facts to assume that a *vita minima* continues to exist in the protoplasm, after its complexity has diminished? Are we compelled to invoke a mystical explanation of the facts, by an appeal to such an indefinite principle as Götte's rejuvenescence? Would not the oxygen, dissolved in the water, affect the organic substance the life of which it formerly maintained, and would it not cause its decomposition, if it were in reality dead?

I, too, hold that the division of the encysted mass is of secondary importance, and that the encystment itself, without the resulting multiplication, is the original and essential part of the phenomenon. But it does not follow from this that the encystment should be considered as a process of rejuvenescence. What is there to be rejuvenated? Certainly not the substance of the animal, for nothing is added to it, and it can therefore acquire no new energy; and the forms of energy which it manifests cannot be changed, since the form of the matter is just the same after quitting the cyst as it was before. Rejuvenescence has also been mentioned in connection with the process of conjugation, but this is quite another thing. It is quite reasonable, at least in a certain sense, to maintain the connection of rejuvenescence with conjugation; for a fusion of the substance of two individuals takes place, to a greater or lesser extent, in conjugation, and the matter which composes each individual is therefore really altered. But in simple encystment, rejuvenescence can only be understood in the sense in which we speak of the 117
fable of the Phœnix, which, when old, was believed to be consumed by fire, and to rise again from its own ashes as a young bird. I doubt whether this idea is in agreement with the physiology of to-day, or with the laws of the conservation of energy. It is easy to pull down an old house with rotten beams and crumbling walls, but it would be impossible to build it anew with the old material, even if we used new mortar, represented in Götte's hypothesis by water and oxygen. For these reasons I consider the idea of rejuvenescence of the encysted individual to be contrary to our present physiological knowledge.

It is much more simple and natural to regard encystment as adapted for the protection of certain individuals in a colony from destruction by being dried up or frozen, or for the protection of the individual during multiplication by division, when it is helpless, and would easily fall a prey to enemies, or to secure advantages in some other way[61]. The case of *Actinosphaerium*, mentioned by Götte, clearly demonstrates that rejuvenescence of the individual is not the only event which happens during encystment, for this would scarcely require six months. The long duration of latent life, from summer to the next spring, clearly proves that encystment is of the highest importance for the species, in order to maintain the life of the individual through the dangers of an unfavourable season[62].

When in this case, the specific organization degenerates to a certain extent, such changes 118
depend in part upon the endeavour to diminish as far as possible the size of the organism—the pseudopodia being drawn in, while the vacuoles contract and completely disappear. The degeneration may also, perhaps, depend in part upon the secretion of the cyst itself, which implies a certain loss of substance[63]. But degeneration chiefly depends upon the fact that the encystment is accompanied by reproduction in the way of fission, which seems to begin with a simplification of the organization, that is, with a fusion of the numerous nuclei. It is well known that many unicellular animals contain several nuclei—in other words, that the nuclear substance is scattered in small parts throughout the whole cell. But when the animal prepares for division, these pieces of nuclear substance fuse into a single nucleus which itself undergoes division into two equal parts[64] during the division of the animal. It is evident that the equal division of the whole nuclear substance only becomes possible in this way.

There are, however, numerous cases which prove that the bodies of encysted animals may retain, during the whole process, exactly the same structure and differentiation, which were previously characteristic of them. Thus the large Infusorian *Tillina magna*, described by Gruber, can be seen through the thin-walled cyst to retain the characteristic structure of its ectoplasm, and the whole of its organization. Even the movements of the enclosed animal do not cease; it continues to rotate actively in the narrow cyst, as do the two or four parts into which it subsequently divides. Such observations prove that Götte's view that 'every characteristic of the previous organization is lost,' is quite out of the question[65] (l. c., p. 62).

For this reason I must strongly oppose Götte's view that an encysted individual is a germ, viz. 119
an organic mass still unorganized which can only become an adult individual by means of a

process of development. I believe that an encysted individual is one possessing a protective membrane, in structure more or less simplified as an adaptation to the narrow space within the cyst, and to a possible subsequent increase by division, in short one in which active life is reduced to a minimum, and sometimes even completely in abeyance, as happens when it is frozen.

It is evident from the above considerations that encystment in no way corresponds with that which every one, including myself, understands by death, because during encystment one and the same being is first apparently dead and then again alive; and we merely witness a condition of rest, from which active life will again emerge. This would remain true even if it were proved that life is, in reality, suspended for a time. But such proof is still wanting, and Götte was apparently only influenced by theoretical considerations, when he imagined that death intervened where unprejudiced observers have only recognised a condition of rest. He apparently entirely overlooked the fact that it is possible to test his views; for all unicellular beings are in reality capable of dying: we can kill them, for example, by boiling, and they are then really dead and cannot be revived. But this state of the organism differs chemically and physically from the encysted condition, although we do not know all the details of the difference. The encysted animal, when placed in fresh water, presently originates a living individual, but the one killed by boiling only results in decomposition of the dead organic matter. Hence we see that the same external conditions give rise to different results in two different states of the organism. It cannot be right to apply the same term to two totally different states. There is only one phenomenon which can be called death, although it may be produced by widely different causes. But if the encysted condition is not identical with the death which we can produce at will, then natural death, viz. that arising from internal causes, does not exist at all among unicellular organisms.

These facts refute Götte's peculiar view, which depends on the existence of natural death among the Monoplastid organisms; upon proof of the contradictory, his whole theory collapses. But there is nevertheless a certain interest in following it further, for we shall thus reach many ideas worthy of consideration. 120

First, the question arises as to how death could have been transmitted from the Monoplastides[66] to the Polyplastides, a process which must have taken place according to Götte. I will for the present omit the fact that I cannot accept the supposition that the process of encystment represents death. We may then inquire whether death has taken the place of encystment among the Polyplastides, or, if this is not the case, whether any process comparable to encystment exists among the Polyplastides.

Götte believes that death is always connected with reproduction, and is a consequence of the latter in both Protozoa and Metazoa. Reproduction has, in his opinion, a directly 'fatal effect,' and the reproducing individual must die. Thus the may-fly and the butterfly die directly after laying their eggs, and the male bee dies immediately after pairing; the Orthonectides expire after expelling their germ-cells, while *Magosphaera* resolves itself into germ-cells, and nothing persists except these elements. It is but a step from this latter organism to the unicellular animals which transform themselves as a whole into germ-cells; but in order to achieve this they must undergo the process of rejuvenescence, which Götte assumes to be the same as death.

These views contain many fallacies quite apart from the soundness or unsoundness of their foundation. The process of encystment, as Götte thinks, represents, in the Monoplastides, true reproduction to which multiplication by means of division has been secondarily added. This encystment cannot be dispensed with, for internal causes determine that it must occasionally interrupt the process of multiplication by simple division. But, on the other hand, Götte also considers the division of the contents of the cyst to be a secondary process. The essential characteristic of encystment is a simple process of rejuvenescence without multiplication. Hence we are forced to accept a primitive condition in which simple division as well as the division of the encysted individual were absent, and in which reproduction consisted only in 121 an often-repeated process of rejuvenescence among existing individuals, without any increase in their number. Such a condition is inconceivable because it would involve a rapid disappearance of the species, and the whole consideration clearly shows us that division of un-encysted individuals must have existed from the first, and that this, and not a vague and mysterious rejuvenescence, has always been the real and primitive reproduction of the Monoplastides. The fact that encystment does not always lead to the division of the contents of the cyst proves, in my opinion, that not reproduction but preservation against injury from without, was the primitive meaning of encystment. It is possible that at the present time there are but few Monoplastides which are able to go through an infinite number of divisions without the interposition of the resting condition implied by encystment; although it has not yet been demonstrated for all species[67]. But it is not right to conclude from this that there is an internal necessity which leads to encystment, that is to say to identify this process with rejuvenescence. It is much more probable that encystment is merely an adaptation to continual changes in the external conditions of life, such as drought and frost, and perhaps also the want of food which arises from the over-population of small areas. The same phenomenon is known in certain low Crustacea—the *Daphnidae*—which possess an ephippium or protective case for their winter-eggs. This case is only developed after a certain definite number of generations has been run through, an event which may happen at any time in the year in species living in pools which are liable to be often dried-up; but only in the autumn in such as live in lakes which are never dry. No one ever doubted that the periodical formation of the ephippium in certain generations was an adaptation to changes in the external conditions of life.

Even if the process of rejuvenescence in the Monoplastides were really equivalent to the death of the higher animals, we could not conclude from this that it is necessarily associated with reproduction. Encystment alone is not reproduction, and it first becomes a form of reproduction when it is associated with the division of the encysted animal. Simple division was the true and original form of reproduction in Monoplastides, and even now it is the principal and fundamental form. 122

Hence we see that among the Monoplastides reproduction is not connected with death, even if we accept Götte's view and allow that encystment represents death. I shall return later on to the relation between death and reproduction in the Metazoa; but the question first arises whether encystment, if it is not death, has any analogue in the higher animals, and further whether death takes that place in their development which is occupied by encystment in the Monoplastides.

Among the higher Metazoa there can be no doubt as to what we mean by death, but the precise nature of that which dies is not equally evident, and the popular conception is not sufficient for us. It is necessary to distinguish between the mortal and the immortal part of the individual—the body in its narrower sense (*soma*) and the germ-cells. Death only affects the former; the germ-cells are potentially immortal, in so far as they are able, under favourable circumstances, to develope into a new individual, or, in other words, to surround themselves with a new body (*soma*)[68].

But how is it with the lowest Polyplastides in which there is no antithesis between the somatic and germ-cells, and among which each of the component cells of the multicellular body has retained all the animal functions of the Monoplastides, even including reproduction?

Götte believes that the natural death of these organisms (which he rightly calls Homoplastides) consists in 'the dissolution of the cell-colony.' As an example of such dissolution Götte takes Häckel's *Magosphaera planula*, a marine free-swimming organism in the form of a sphere composed of a single layer of ciliated cells, imbedded in a jelly. (For figure see below.) This organism cannot however be 'considered as a genuine perfect Polyplastid, for at a certain time the component cells part from one another and then continue to live independently in the condition of Monoplastides.' These free amoebiform organisms increase considerably in size, encyst, and finally undergo numerous divisions—a kind of segmentation within the cyst. The result of the division is a sphere of ciliated cells similar to 123 that with which the cycle began. In fact, *Magosphaera* is not a perfect Polyplastid, but a transitional form between Polyplastides and Monoplastides, as the discoverer of the group of animals of which it is the only representative, indicated, when he named the group ‘Catallacta.’

Development of Magosphaera Planula (after Häckel).

1. Encysted amoeboid form. 2 and 3. Two stages in the division of the same. 4. Free ciliated sphere, the cells of which are connected by a gelatinous mass. 5. One of the ciliated cells which has become free by the breaking up of the sphere. 6. The same in the amoeboid form. 7. The same grown to a larger size.

According to Götte, the natural death of *Magosphaera* consists, as in the undoubted Protozoa, in a process of rejuvenescence by encystment. The dissolution of the ciliated sphere into single cells ‘cannot be identical with natural death. For the regular and complete separation of 124
the *Magosphaera*-cells proves that their individuality has not been completely subordinated to that of the whole colony, and it proves that the latter is not completely individualised[69].’

Nothing can be said against this, if we agree in identifying death with the encystment of the Monoplastides. Now we could, as Götte rightly remarks, derive the lower forms of Polyplastides from *Magosphaera* if ‘the connection between the cells of the ciliated sphere were retained until encystment, viz. until the reproduction of the single cells had taken place[70].’ After this had been accomplished, Götte considers that death would consist ‘in the complete separation of the cells from one another, accompanied in all probability by their simultaneous change into germ-cells.’ The fallacy in this is evident; if death is represented in one case by the encystment during which single cells change into germ-cells, then this must apply to the other case also, for nothing has changed except the duration of the cell-colony. The nature of encystment cannot be affected by the fact that the cells separate from one another a little earlier or a little later. If it is true that death is represented by encystment among the Monoplastides, then the same conclusion must also hold for the Polyplastides; or rather death must be represented in them by the process of rejuvenescence, which Götte considers to be the essential part of encystment. Götte ought not to identify death with the dissolution of the cell-colony of which the lowest and highest Polyplastides are alike composed; but he should seek it in the process of rejuvenescence which takes place within the germ-cells. If it is essential to the nature of reproduction that the cells set apart for that purpose should pass through a process of rejuvenescence, which is equivalent to death, then this must be true for the reproductive cells of all organisms. If these conclusions hold good, there is nothing to prevent us from assuming that such a process of rejuvenescence actually occurs in the higher animals. Götte evidently holds this view, as is plainly shown in the last pages of his essay. He there attempts to bring his views of the death and rejuvenescence of the germ into harmony with his previously developed idea of the derivation of death among the Polyplastides from the dissolution of the cell-colonies. Götte still clings to the view which he 125
propounded in describing the development of *Bombinator*, according to which the egg-cell of the higher Metazoa must pass through a process of rejuvenescence representing death, before it can become a germ.

According to Götte’s[71] idea ‘the egg of a *Bombinator igneus* before fertilization cannot be considered to be a cell either wholly or in part; and this is equally true of it at its origin and after its complete development; it is only an essentially homogeneous organic mass enclosed by a membrane which has been deposited externally.’ This mass is ‘unorganised and not living[72],’ and ‘during the first phenomena of its development all vital powers must be excluded.' In this way the continuity of life between two successive individuals is always interrupted; or, as Götte says in his last essay:—'The continuity of life between individuals of which one is derived from the other by means of reproduction, exists neither in the rejuvenescence of the Monoplastides nor in the condition of the germ among the Polyplastides —a condition which is derived from the former[73].'

This is quite logical, although in my opinion it is both unproved and incorrect. But, on the other hand, it is certainly illogical for Götte to derive the death of the Metazoa in a totally different way, i. e. from the dissolution of their cell-colonies. It is quite plain that the death of the Metazoa does not especially concern the reproductive cells, but the individual which bears them; Götte must therefore seek for some other origin of death—an origin which will enable it to reach the body (*soma*)—as opposed to the germ-cells. If there still remained any doubt about the failure to establish a correspondence between death and the encystment of the Monoplastides, we have here, at any rate, a final demonstration of the failure!

But there is yet another great fallacy concealed in this derivation of the death of the Polyplastides.

Among the lowest Polyplastides, where all the cells still remain similar, and where each cell is also a reproductive cell, the dissolution of the cell-colony is, according to Götte, to be regarded as death, inasmuch as 'the integrity of the mother-individual absolutely comes to an 126 end' (l. c., p. 78). The dissolution of a cell-colony into its component living elements can only be called death in the most figurative sense, and can have nothing to do with the real death of the individuals; it only consists in a change from a higher to a lower stage of individuality. Could we not kill a *Magosphaera* by boiling or by some other artificial means, and would not the state which followed be death? Even if we define death as an arrest of life, the dissolution of *Magosphaera* into many single cells which still live, is not death, for life does not cease in the organic matter of which the sphere was composed, but expresses itself in another form. It is mere sophistry to say that life ceases because the cells are no longer combined into a colony. Life does not in truth cease for a moment. Nothing concrete dies in the dissolution of *Magosphaera*; there is no death of a cell-colony, but only of a conception. The Homoplastides, that is cell-colonies built up of equal cells, have not yet gained any natural death, because each of their cells is, at the same time, a somatic as well as a reproductive cell: and they cannot be subject to natural death, or the species would become extinct.

It is more to the purpose that Götte has sought for an illustration of death among those remarkable parasites, the Orthonectides, because in them we do at any rate meet with real death. They are indeed very low organisms; but nevertheless they stand far above *Magosphaera*, even if the latter were hypothetically perfected up to the level of a true Homoplastid, for the cells which compose the body of the Orthonectides are not all similar, but are so far differentiated that they are even arranged in the primitive germ-layers, and a form results which has rightly been compared with that of the Gastrula. It is true they are not quite so simple as Götte[74] figures them, for they not only consist of ectoderm and germ-cells, but, according to Julin[75], the endoderm is arranged in two layers—the germ-cells and a layer which forms during development a strong muscular coat; and in the second female form the egg-cells are surrounded by a tolerably thick granular tissue.

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ORTHONECTIDES (after Julin).

8. First female form: the cap-like anterior part has become detached and the egg-cells (*eiz*) are escaping.
9. Second female form: *eiz* = egg-cells; outside these are the muscular layer (*m*) and the ectoderm (*ekt*).
10 and 11. Two fragments of such a female broken to pieces by

spontaneous division: the egg-cells are embedded in a granular mass, and undergo embryonic development in it at a later period; the whole is surrounded by ciliated cells.

12. Male discharging the spermatozoa by the breaking up of the ectoderm (*ekt*); *sp* spermatozoa; *m* muscle.

There is nevertheless no doubt that in the first female form, when sexually mature, the greater part, not only of the endoderm but of the whole body, is made up of ova, so that the animal resembles a thin-walled sac full of eggs. The ova escape by the bursting of the thin ectoderm, and when they have all escaped, the thin disintegrated membrane, composed of ciliated cells, 128 is no longer in a condition to live, and dies at once. This is the course of events as described by Götte, and he is probably correct in his interpretation. This is the real death of the Orthonectides, and if we regard them as low primitive forms (Mesozoa), here for the first time in the ascending series we meet with natural death. But the causes of this are scarcely so clear as Götte seems to think when he ascribes it to the effect of reproduction—a