I.

THE DURATION OF LIFE.

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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 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.

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.

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.

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.

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 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 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 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, 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

[1] Humboldt's 'Ansichten der Natur.'

time; it follows that, if we know the fertility 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[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

[1] See Appendix, note 1, p. 36.

lives about thirty-five years, the wild boar twenty-five, the sheep fifteen, the fox fourteen, the hare ten, the squirrel and the mouse six years[1]; 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[2]. The length of life in many molluscan species is very well known, because the age can be determined by markings on the shell[3]. But even in this group, any exact knowledge, such as would be available for our purpose, is still

[1] See Appendix, note 2, p. 38.
[2] See Appendix, note 4, p. 54.
[3] See Appendix, note 5, p. 55.

wanting concerning such necessary points as the degree of fertility, the relation to other animals, and many other factors.

Data the most exact in all respects are found among the insects[1], 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,

[1] See Appendix, note 3, p. 38.

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.

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 [1].

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

[1] See Appendix, note 3, p. 38.

completely. Even the manner in which the eggs are laid 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 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 [1].

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 [2],—while the males only lived a few weeks.

[1] 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.

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

These last examples become readily intelligible when we remember that the males neither 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 [1]. 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 [2].

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.

[1] See Appendix, notes 7 and 9, pp. 59 and 63.

[2] See Appendix, note 6, p. 58.

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.

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.

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[1]. 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

[1] See Appendix, note 8, p. 59.

reason, this effort is not made, the insect lives for a somewhat longer period.

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 [1].

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 under-

[1] See Appendix, note 9, p. 63.

stand the necessity of death. The 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 [1].

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

[1 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.]

time,—a 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 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 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 [1].

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

[1] See Appendix, note 10, p. 64.

nothing comparable to that deterioration of the 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 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 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.

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-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[1].

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

[1] Johannes Müller, 'Physiologie,' Bd. I. p. 31, Berlin, 1840.

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*.

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[1] 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

[1] See Appendix, note 12, p. 65.

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.

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.

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 case 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?

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.