III.

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.

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[1], 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

[1] 'Ueber den Ursprung des Todes,' Hamburg and Leipzig, 1883.

have not 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 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 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[1], 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[2]. 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

[1] As in the case of the bodies of monks on the Great St. Bernard, or the dried-up bodies in the well-known Capuchine Monastery at Palermo.

[2] See below.

feature in the process is the rejuvenescence of the individual. This 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 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[1]. 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[2].

[1] Professor Gruber informs me that among the Infusoria of the harbour of Genoa, he has observed a species which encysts upon one of the free-swimming Copepoda. He has often found as many as ten cysts upon one of these Copepods, and has observed the escape of their contents whenever the water under the cover-glass began to putrefy. Here advantage is probably gained in the rapid transport of the cyst by the Crustacean.

[2] The views of most biologists who have worked at this subject agree in all essentials with that expressed above. Bütschli says (Bronn's 'Klassen und Ordnungen des Thierreichs,' Protozoa, p. 148): 'The process of encystment does not appear to have originally borne any direct relation to reproduction: it appears on the contrary to have taken place originally,—as it frequently does at the present day,—either for the protection of the organism against injurious external influences, such as desiccation or the fatal effects of impure water, etc.; and also to enable the organism, after taking up an unusually abundant supply of food, to assimilate it in safety.' Balbiani ('Journ. de Micrographie,' Tom. V. 1881, p. 293) says in reference to the Infusoria, 'Un petit nombre d'espèces, au lieu de se multiplier à l'état de vie active, *se reproduisent dans une sorte d'état de repos,* dit état d'enkystement. Ces sortes de kystes peuvent être désignés sous le nom de kystes de reproduction, par opposition avec d'autres kystes, dans lesquels les Infusoires se renferment pour se soustraire à des conditions devenues défavorables du milieu qu'ils habitent, le manque d'air, le dessèchement, etc.—ceux-ci sont des kystes de conservation . . .'

When in this case, the specific organization degenerates to a certain extent, such changes 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 [1]. 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 [2] 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 [3] (l. c., p. 62).

[1] This is of importance in so far as single individuals might be thus compelled to encyst even when the existing external conditions of life do not require it. The substance which *Actinosphaerium*, for example, employs in the secretion of its thick siliceous cyst must have been gradually accumulated by means of a process peculiar to the species. We can scarcely be in error if we assume that the silica accumulated in the organism cannot increase to an unlimited extent without injury to the other vital processes and that the secretion of the cyst must take place as soon as the accumulation has exceeded a certain limit. Thus we can understand that encystment may occur without any external necessity. Similarly, certain Entomostraca (*e. g. Moina*) produce winter-eggs in a particular generation, and these are formed even when the animals are kept in a room protected from cold and desiccation.

[2] Upon this point Professor Gruber intends to publish an elaborate memoir.

[3] This view has not even been proved for *Actinosphaerium*, upon which Götte

For this reason I must strongly oppose Götte's view that an encysted individual is a germ, viz. 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

chiefly relies. The observations which we now possess merely indicate that the animal contracts to the smallest volume possible. Compare F. E. Schulze, 'Rhizopodenstudien,' I, Arch. f. mikr. Anat. Bd. 10, p. 328 ; and Karl Brandt, 'Ueber Actinosphaerium Eichhornii,' Inaug. Diss. ; Halle, 1877.

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.

First, the question arises as to how death could have been transmitted from the Monoplastides[1] 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

[1] The conception of Protozoa and Metazoa does not correspond exactly with that of unicellular and multicellular beings, for which Götte has proposed the names Mono- and Polyplastides.

absent, and in which reproduction consisted only in 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[1]. 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

[1] Among the Rhizopoda encystment is only known in fresh-water forms, and not in a single one of the far more numerous marine forms which possess shells (see Bütschli, 'Protozoa,' p. 148); the marine Rhizopoda are not exposed to the effects of desiccation or frost, and thus the strongest motives for the process of encystment do not exist, at least among forms possessing a shell.

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.

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.

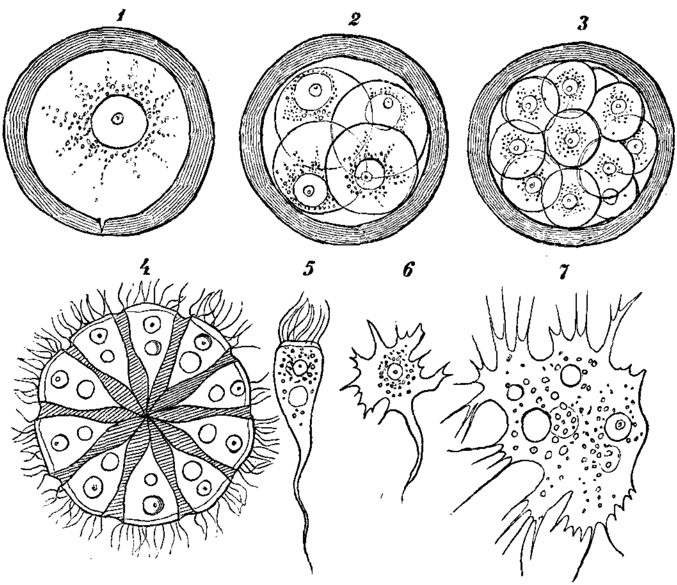
Among the higher Metazoa there can be no doubt as to what we mean by death, but the precise nature of that which dies is not equally evident, and the popular conception is not sufficient for us. It is necessary to distinguish between the mortal and the immortal part of the individual—the body in its 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*)[1].

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,

[1] I trust that it will not be objected that the germ-cells cannot be immortal, because they frequently perish in large numbers, as a result of the natural death of the individual. There are certain definite conditions under which alone a germ-cell can render its potential immortality actual, and these conditions are for the most part fulfilled with difficulty (fertilization, etc.). It follows from this fact that the germ-cells must always be produced in numbers which reach some very high multiple of the necessary number of offspring, if these latter are to be ensured for the species. If in the natural death of the individual the germ-cells must also die, the *natura* death of the *soma* becomes a cause of *accidental* death to the germ-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 that with which the cycle began. In fact, *Magosphaera* is not a perfect Polyplastid, but a transitional



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.

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.'

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 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 [1].'

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 [2].' 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

[1] l. c., p. 78. [2] l. c., p. 47.

which he 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[1] 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[2],' 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[3].

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

[1] 'Entwicklungsgeschichte der Unke,' Leipzig, 1875, p. 65.
[2] Id., p. 842.
[3] 'Ursprung des Todes,' p. 79.

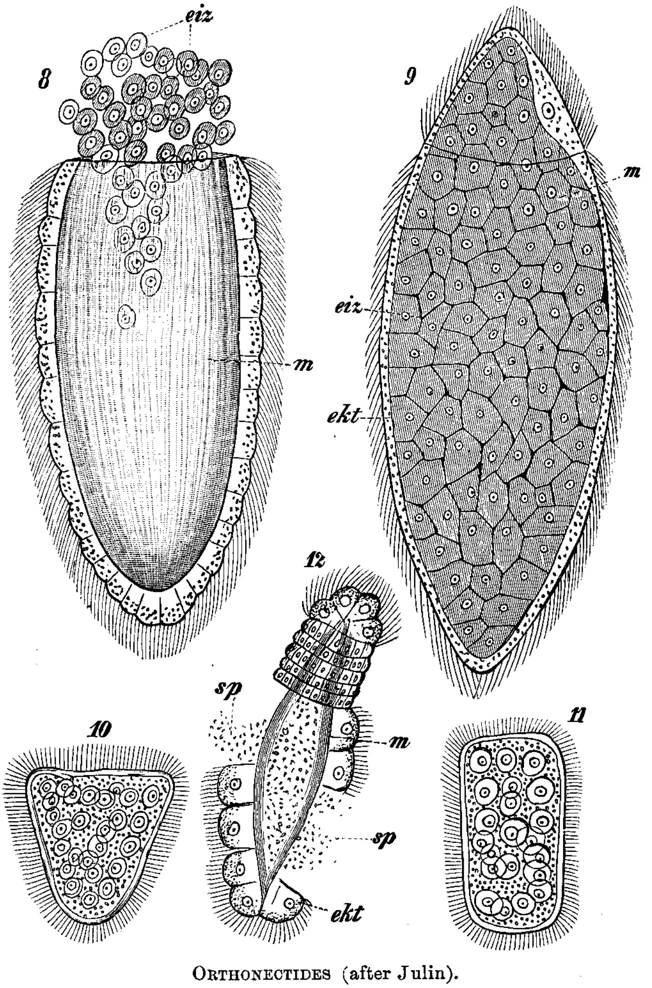
comes to an end' (l. c., p. 78). The dissolution of a cell-colony into its component living elements can only be called death in the most figurative sense, and can have nothing to do with the real death of the individuals; it only consists in a change from a higher to a lower stage of individuality. 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[1] figures them, for they not only consist of ectoderm and germ-cells, but, according to Julin[2], 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. There is nevertheless no doubt that in the first female form, when sexually mature, the greater part, not only of the

[1] l. c., p. 42.

[2] 'Contributions à l'histoire des Mesozoaires. Recherches sur l'organisation et le développement embryonnaire des Orthonectides,' Arch. de Biologie, vol. iii. 1882.

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



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.

escaped, the thin disintegrated membrane, composed of ciliated cells, 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—an effect which is 'not only empirically necessary, but absolutely unavoidable.' Such a necessity is explained by the fact that the endoderm consists entirely of germ-cells. Now the life of the organism, being dependent upon the mutual action of both layers, must cease as soon as the whole endoderm is extruded during reproduction.

Arguments such as these pass over the presence of a mesoderm; but apart from this omission, it does not appear to me so self-evident from a purely physiological standpoint, that the ectodermal sheath with its muscle layer must die after the extrusion of the germ-cells.

In those females to which Götte refers in this passage, the whole sheath remains at first quite uninjured, with the exception of a small cap at the anterior end, which is pushed off to give exit to the ova; and inasmuch as the sheath continues to swim about in the nutritive fluids after this has taken place, the proof is at any rate wanting that it cannot support itself quite as well as before, although it has lost the germ-cells.

Then why does it die? My answer to this is simple:—because it has lived its time; because its length of life is limited to a period which corresponds with the time necessary for complete reproduction. The physical constitution of the body is so regulated that it remains capable of living until the extrusion of the reproductive cells, and then dies, however favourable external conditions may be for its further support.

The correctness of this explanation is shown by a consideration of the males and the second form of females; for in these cases the body falls to pieces, not as a consequence of reproduction, but as a preparation for it!

Götte only mentions the second female form in a note, in which he says, it appears 'that in the second female form of these animals the whole body breaks into many pieces, and the superficial layer gradually atrophies, so that it dies before the eggs are extruded.' In Julin's account[1], upon which Götte bases his statements, there are, however, some not unimportant differences. For instance, the eggs are not extruded at all, but embryonic development takes place within the body of the mother, which has previously undergone spontaneous division into several pieces. In this case, the eggs differ from those of the other female form, inasmuch as they do not constitute the whole of the endoderm, but are embedded (as was stated above) in a fairly voluminous granular mass at the expense of which, or at least by means of which, they are nourished; for they increase considerably in size during their development. But not only this granular mass, but all the layers of the body of the mother, even the ectoderm, persist during the embryonic development of the offspring. Indeed, the ectoderm must continue to grow during the division of the mother animal, for it gradually covers in the products of division on all sides, and, by means of its cilia, causes the animal to swim about in the fluids of its host. After some time the cilia are lost, and the separate parts into which the mother animal has divided, fix themselves upon some part of the body-cavity of the host; the young become free, and the remains of the body of the mother probably disappear by dissolution and resorption[2]. In this case the remains of the mother animal seem to be, to some extent, consumed by the embryos,—a process which sometimes, although very rarely, happens elsewhere. We can scarcely consider this as a primitive arrangement, or look upon it as a proof that 'reproduction' has a necessarily fatal effect upon the Polyplastid organism.

In the male, the mass of spermatozoa does not swell out the body to such an extent that its walls must give way and thus permit an exit, but the large ectoderm cells atrophy spontaneously at the time of maturity, and as they fall off, exit is given to the spermatozoa here and there. In this instance also the dissolution of the body is not a consequence of reproduction, but reproduction can only take place when the dissolution of the body has preceded it!

[1] l. c., p. 37.

[2] Julin does not enter into further details on this point, and it is not quite clear at what precise time the cells of the ectoderm atrophy; but this is irrelevant to the origin of death, since the granular mass surrounding the egg-cells at any rate belongs to the *soma* of the mother.

In this remarkable arrangement we cannot discern anything except an evident adaptation of the life of the body-cells to reproductive purposes, and this adaptation was rendered possible because, after the evacuation of the sexual cells, the body ceased to be of any value for the maintenance of the species.

But even if we assume, that the death of the Orthonectides is, in Götte's sense, a consequence of reproduction, inasmuch as, in the two forms of females as well as in the male, the extrusion of a mass of developed germ-cells or embryos deprives the organism of the physiological possibility of living longer, how can we explain the necessity of death as a direct consequence of reproduction in all Polyplastides? Is the body—the *soma*—of the Metazoa so imperfectly developed, as compared with the reproductive cells, that the extrusion of the latter involves the death of the former? As a matter of fact in the majority of cases the relations are reversed; the number of body-cells usually exceeds the germ-cells a hundred- or a thousand-fold, and the body is, as regards nutrition, so completely independent of the reproductive cells, that it need not be in the least disadvantageously affected by their extrusion. And if the Orthonectid-like ancestors of the Metazoa were compelled to give up their insignificant somatic part after the extrusion of their germ-cells, because it could now no longer support itself, does it therefore follow that the somatic cells had for ever lost the power of surviving, even when their phyletic descendants were surrounded by more favourable conditions? Had they to inherit 'the necessity of death' for all time? Whence came this great change in the nature of organisms which, before the differentiation of Homoplastids into Heteroplastids, were endowed with the immortality of unicellular beings?

And it must be remembered that it is only an assumption which places the Orthonectides among the lowest Metazoa (Heteroplastids). I do not intend to greatly emphasize this point, but the formation of the Gastrula by embole, and the absence of a mouth and alimentary canal, shows that these parasites are extremely degenerate, and the same may be said of almost all endoparasites. The Gastrula, as an independent organism, was without doubt primitively provided with both mouth and stomach, and the mass of ova filling the female Orthonectid is an adaptation to a parasitic life, which on the one side renders the possession of a stomach a superfluity, and on the other demands the production of a great number of germ-cells[1]. It is certain that the Orthonectides, as at present constituted, cannot have lived in the free condition, and also that their adaptation to parasitism cannot have arisen at the beginning of the phyletic development of Metazoa, because they inhabit starfishes and Nemertines—both relatively highly developed Metazoa. Hence it is, at any rate, doubtful whether the Orthonectides can claim to pass as typical forms of the lowest Heteroplastids, and whether their reproduction can be looked upon 'as typical for the unknown ancestors of all Polyplastids' (l. c., p. 45). If, however, we accept some organism resembling these Orthonectides as the most ancient Heteroplastid, being a free-living organism, it must have had a stomach, and the cells surrounding it must—as a whole or in part—have possessed the power of digesting; at any rate, they cannot all have been germ-cells, and therefore it is improbable that death would be the direct result of the extrusion of the germ-cells.

Let us now consider the manner in which Götte has endeavoured to explain the transmission of the cause of death—which first appeared in the Orthonectides—from these organisms to all later Metazoa, until the very highest forms are reached. Exact proofs of this supposition are unfortunately wanting, and the evidence is confined to the collection of a number of cases in which death and reproduction take place nearly or quite simultaneously. These would prove nothing, even if *post hoc* were always *propter hoc*; and there are, opposed to them, a number of cases in which reproduction and death take place at different times. In obtaining evidence for 'the fatal influence of reproduction,' is it possible to point to every case of sudden death after the act of oviposition or fertilization? These cases occur among many of the higher animals, especially in Insects, and were collected by me in an earlier work[2]. It is

[1] Leuckart finds such a great resemblance between the newly born young of *Distoma* and the Orthonectides, that he is inclined to believe that the latter are Trematodes, 'which in spite of sexual maturity have not developed further than the embryonic condition of the *Distoma*' ('Zur Entwicklungsgeschichte des Leberegels,' Zool. Anzeiger, 1881, No. 99). In reference to the Dicyemidae, which resemble the Orthonectides in their manner of living and in their structure, Gegenbaur has stated his opinion that they belong to a 'stage in the development of Platyhelminthes' (Grundriss d. vergleich. Anatomie). Giard includes both in the 'phylum Vermes,' and regards them as much degenerated by parasitism; and Whitman—the latest investigator of the Dicyemids—speaks of them in a similar manner in his excellent work 'Contributions to the Life-history and Classification of Dicyemids' (Leipzig, 1882).

[2] 'Dauer des Lebens;' translated as the first essay in this volume.

obvious that such cases are exceptional, but in a restricted sense it is quite true, as far as these individual instances are concerned, that death appears as a consequence of reproduction. The male bee, which invariably dies while pairing, *is undoubtedly killed in consequence* of a very powerful nervous shock; and the female Psychid, which has laid all her eggs at once, dies of 'exhaustion'—however we may attempt to explain the term on physiological principles.

Can we conclude from these cases that the effects of reproduction are, in Götte's sense, universally fatal; that reproduction is the positive and 'exclusive explanation of natural death'? (l. c., p. 32.) I need not linger over these isolated examples, but I turn at once to the foundation of the whole conclusion—a foundation which is obviously unable to support the superstructure erected on it. Götte formally derives the idea that death is a necessary condition *of reproduction, from a very heterogeneous collection of facts.* When we examine this collection we find that the process which is taken to be death is not the same thing in all these instances, while the same is true of the influence of reproduction by which death is supposed to be caused. The whole conception arises out of the process of encystment, which is regarded as the building-up of reproductive material—that is, as true reproduction; and since, according to Götte's view, the formation of germs is always intimately connected with an arrest of life, and since, by his own definition, this stand-still of life is equivalent to death, it follows that, with such a theory, reproduction, in its essential nature, must *be inseparably connected with death.* It is necessary at this juncture to remember what Götte means by the process of rejuvenescence, and to point out that he is dealing with something quite different from 'the fatal influence of reproduction,' which was just now mentioned with regard to insects. 'Rejuvenescence,' bound up as it is with encystment and reproduction, is, according to Götte, 'a re-coining of the specific protoplasm, by means of which the identity of its substance is fixed by heredity,' a 'marvellous process in which phenomena the most important in the whole life of the animal, and in fact of all organisms—reproduction and death—have their roots' (l. c., p. 81). Whether such re-coining really takes place or not, at any rate I claim to have shown above that it does not correspond with death in the Metazoa, and—if it is represented at all in these latter—that it ought to be looked for in the reproductive cells; and indeed, in another passage, Götte himself has placed the process in these cells.

While, among the Monoplastids, according to Götte, the causes of the supposed death lie hidden in this mysterious change of the organism into reproductive material, Götte asserts that among the Polyplastids (such as *Magosphaera*, hypothetically perfected so as to form a genuine Polyplastid), the causes of death operate so that the organism breaks up into its component cells, all these being still reproductive cells—a process which, unlike 'rejuvenescence,' has nothing mysterious about it, and which is certainly not genuine death. In the Orthonectid-like animals death does not occur as a consequence of the dispersal of the reproductive cells, but rather because the part of the animal which remains is so small and effete that, being unable to support itself, it necessarily dies. From this point at least the object of death and the conception of it remain the same, but now the idea of reproduction undergoes a change. When the Rhabdite females of *Ascaris* are eaten up by their offspring, is this mode of death connected with the 'rejuvenescence of protoplasm'? (l. c., p. 34.) Is there any deep underlying relationship between such an end and the essential nature of reproduction? The same question may be asked with regard to the 'Redia or the Sporocyst of Trematodes, which are converted into slowly dying sacs during the growth of the Cercariae within them.' We cannot speak of the 'fatal influence of reproduction' among tape-worms just because 'in the ripe segments the whole organization degenerates under the influence of the excessive growth of the uterus.' It certainly degenerates, but only so far as the developing mass of eggs demands. In fact, at a sufficiently high temperature, death does not occur, and such mature segments of tape-worms creep about of their own accord. We cannot fail to recognize that in this as well as in the above-mentioned cases we have to do with adaptation to certain very special conditions of existence—an adaptation leading to an immense development of reproductive cells in a mother organism which can no longer take in nourishment, or which has become entirely superfluous because its duty to its species is already fulfilled. If this is an example of death inherent in the essential nature of reproduction, then so is the death of a mature segment of a tape-worm in the gastric juices of the pig that eats it.

With Götte, the conception of reproduction, like the conception of death, is a protean form, which he welcomes in any shape, if only he can use it as evidence. If death is a necessary consequence of *reproduction, its cause must be always essentially the same,* and might be expressed in one of the following suggestions:—(1) in the necessity for a 're-coining' of the protoplasm of the germ-cells; but here death could only affect the germ-cells themselves: (2) perhaps in the withdrawal of nourishment by the mass of developing reproductive material, just as death occurs sometimes among men by the excessive drain on the system caused by morbid tumours: (3) or in consequence of the development of the offspring in the body of the mother; this however would only affect the females, and could therefore have no deep and general significance: (4) from the extrusion of the sexual cells,—ova or spermatozoa,—and in the impossibility of further nourishment which is consequent upon this extrusion—(Orthonectides?): or (5) finally in an excessively powerful nervous shock brought about by the ejection of the reproductive cells.

But no one of these alternatives is the universal and inevitable cause of death. This proves irrefutably that death does not proceed as an intrinsic necessity from reproduction, although it may be connected with the latter, sometimes in one way and sometimes in another. But we must not overlook the fact that in many cases death is not connected with reproduction at all; for many Metazoa survive for a longer or shorter period after the reproductive processes have ceased.

In fact, I believe I have definitely shown that no process exists among unicellular animals which is at all comparable with the natural death of the higher organisms. Natural death first appeared among multicellular beings, and among these first in the Heteroplastids. Furthermore, it was not introduced from any absolute intrinsic necessity inherent in the nature of living matter, but on grounds of utility, that is from necessities which sprang up, not from the general conditions of life, but from those special conditions which dominate the life of multicellular organisms. If this were not so, unicellular beings must also have been endowed with natural death. I have already expressed these ideas elsewhere[1], and have briefly indicated how far, in my opinion,

[1] See the first essay upon 'The Duration of Life,' p. 22 et seq.

natural death is expedient for multicellular organisms. I found the essential reason for confining the life of the Metazoa to a fixed and limited period, in the wear and tear to which an individual is exposed in the course of a life-time. For this reason, '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' (l. c., p. 24). Death seemed to me to be expedient since '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' (l. c., p. 24).

I still adhere entirely to this explanation; not of course in the sense that an actual physical struggle has ever taken place between the mortal and immortal varieties of any species. If Götte understood me thus, he may be justified by the brief explanations given in the essay to which I have alluded; but when he also attributes to me the opinion that such hypothetically immortal Metazoa had but a very limited period for reproduction, I fail to see what part of the essay in question can be brought forward in support of his statement. Only under some such supposition can I be reproached with having assumed the existence of a process of natural selection which could never be effective, because any advantage which accrued to the species from the shortening of the duration of life could not make itself felt in a more rapid propagation of the short-lived individuals. The statement 'that in this and in every other case it is a sufficient explanation of the processes of natural selection to render it probable that any kind of advantage is gained'[1] is indeed erroneous. The explanation ought rather to be 'that the forms in question would for ever transmit their characters to a greater number of descendants than the other forms.' I have not however as yet attempted to think out in detail such processes of natural selection as would limit the somatic part of the Metazoan body to a short term of existence, and I only wished to emphasize the general principle lying at the basis of the whole process, without stating the precise manner in which it operates.

If I now attempt to take this course, and to reconstruct theoretically the gradual appearance of natural death in the Metazoa, I must begin by again alluding to Götte's criticisms in reference to the operation of natural selection.

[1] 'Ursprung des Todes,' p. 29.

I consider death as an adaptation, and believe that it has arisen by the operation of natural selection. Götte [1], however, concludes from this that 'the first origin of hereditary and consequently (for the organization in question) necessary death, is not explained but already assumed.' 'The operation and significance of the principle of utility consists in selecting the fittest from among the structures and processes which are at hand, and not in directly creating new ones. Every new structure arises at first, quite independently of any utility, from certain material causes present in a number of individuals, and when it has proved useful and is transmitted, it extends, according to the laws of the survival of the fittest, in the group of animals in which it appeared. This extension will undergo further increase with every advance in utility which results from further structural changes, until it extends over the whole group. So that usefulness effects the preservation and the distribution of new structures, but has nothing whatever to do with the causes of their primary origin and their consequent transmission to all other individuals. Indeed, on these hereditary causes the necessity of the structures in question depends, so that their usefulness in no way explains their necessity.'

'These conclusions, when applied to the origin of natural death called forth by internal causes, would show that it became inevitable and hereditary in a number of the originally immortal Metazoa, before there could be any question as to the benefits derived from its influence. Such influence must have consisted in the fact that more descendants survived the struggle for existence and were able to enter upon reproduction among the individuals which had inherited the predisposition to die than among the potentially immortal beings which would be damaged in the struggle for existence, and would therefore be exposed to still further injuries. The existing necessity for natural death in all Metazoa might therefore be derived in an unbroken line of descent from the first mortal Metozoan, of which the death became inevitable from internal causes, before the principle of utility could operate in favour of its dissemination.'

In reply to this I would urge: that it has been very often maintained that natural selection can produce nothing new, but can only bring to the front something which existed previously to

[1] l. c., p. 5.

the exercise of choice; but this argument is only true in a very limited sense. The complex world of plants and animals which we see around us contains much that we should call new in comparison with the primitive beings from which, as we believe, everything has developed by means of natural selection. No leaves or flowers, no digestive system, no lungs, legs, wings, bones or muscles were present in the primitive forms, and all these must have arisen from them according to the principle of natural selection. These primitive forms were in a certain sense predestined to develope them, but only as possibilities, and not of necessity; nor were they preformed in them. The course of development, as it actually took place, first became a necessity by the action of natural selection, that is by the choice of various possibilities, according to their usefulness in fitting the organism for its external conditions of life. If we once accept the principle of natural selection, then we must admit that it really can create new structures, instincts, etc., not suddenly or discontinuously, but working by the smallest stages upon the variations that appear. These changes or variations must be looked upon as very insignificant, and are, as I have of late attempted to show [1], quantitative in their nature; and it is only by their accumulation that changes arise which are sufficiently striking to attract our attention, so that we call them 'new' organs, instincts, etc.

These processes may be compared to a man on a journey who proceeds from a certain point on foot by short stages, at any given time, and in any direction. He has then the choice of an infinite number of routes over the whole earth. If such a man begins his wanderings in obedience to the impulse of his own will, his own pleasure or interest,—proceeding forwards, to the right or left, or even backwards, with longer or shorter pauses, and starting at any particular time,—it is obvious that the route taken lies in the man himself and is determined by his own peculiar temperament. His judgment, experience, and inclination will influence his course at each turn of his journey, as new circumstances arise. He will turn aside from a mountain which he considers too lofty to be climbed; he will incline to the right, if this direction appears to afford a better passage over a swollen stream; he will rest when he reaches a pleasant halting-place, and will hurry on when he knows that

[1] See the preceding essay 'On Heredity.'

enemies beset him. And in spite of the perfectly free choice open to him, the course he takes is in fact decided by both the place and time of his starting and by circumstances which—always occurring at every part of the journey—impel him one way or the other; and if all the factors could be ascertained in the minutest detail, his course could be predicted from the beginning.

Such a traveller represents a species, and his route corresponds with the changes which are induced in it by natural selection. The changes are determined by the physical nature of the species, and by the conditions of life by which it is surrounded at any given time. A number of different changes may occur at every point, but only that one will actually develope which is the most useful, under existing external conditions. The species will remain unaltered as long as it is in perfect equilibrium with its surroundings, and as soon as this equilibrium is disturbed it will commence to change. It may also happen that, in spite of all the pressure of competing species, no further change occurs because no one of the innumerable very slight changes, which are alone possible at any one time, can help in the struggle; just as the traveller who is followed by an overpowering enemy, is compelled to succumb when he has been driven down to the sea. A boat alone could save him, without it he must perish; and so it sometimes happens that a species can only be saved from destruction by changes of a conspicuous kind, and these it is unable to produce.

And just as the traveller, in the course of his life, can wander an unlimited distance from his starting-point, and may take the most tortuous and winding route, so the structure of the original organism has undergone manifold changes during its terrestrial life. And just as the traveller at first doubts whether he will ever get beyond the immediate neighbourhood of his starting-point, and yet after some years finds himself very far removed from it—so the insignificant changes which distinguish the first set of generations of an organism lead on through innumerable other sets, to forms which seem totally different from the first, but which have descended from them by the most gradual transition. All this is so obvious that there is hardly any need of a metaphor to explain it, and yet it is frequently misunderstood, as shown by the assertion that natural selection can create nothing new: the fact being that it so adds up and combines the insignificant small deviations presented by natural variation, that it is continually producing something new.

If we consider the introduction of natural death in connection with the foregoing statements, we may imagine the process as taking place in such a way that,—with the differentiation of Heteroplastids from Homoplastids, and the appearance of division of labour among the homogeneous cell-colonies,—natural selection not only operated upon the physiological peculiarities of feeding, moving, feeling, or reproduction, but also upon the duration of the life of single cells. At this developmental stage there would, at any rate, be no further necessity for maintaining the power of limitless duration. The somatic cells might therefore assume a constitution which excluded the possibility of unending life, provided only that such a constitution was advantageous for them.

It may be objected that cells of which the ancestors possessed the power of living for ever, could not become potentially mortal (that is subject to death from internal causes) either suddenly or gradually, for such a change would contradict the supposition which attributes immortality to their ancestors and to the products of their division. This argument is valid, but it only applies so long as the descendants retain the original constitution. But as soon as the two products of the fission of a potentially immortal cell acquire different constitutions by unequal fission, another possibility arises. Now it is conceivable that one of the products of fission might preserve the physical constitution necessary for immortality, but not the other; just as it is conceivable that such a cell—adapted for unending life—might bud off a small part, which would live a long time without the full capabilities of life possessed by the parent cell; again, it is possible that such a cell might extrude a certain amount of organic matter (a true excretion) which is already dead at the moment it leaves the body. Thus it is possible that true unequal cell-division, in which only one half possesses the condition necessary for increasing, may take place; and in the same way it is conceivable that the constitution of a cell determines the fixed duration of its life, examples of which are before us in the great number of cells in the higher Metazoa, which are destroyed by their functions. The more specialized a cell becomes, or in other words, the more it is intrusted with only one distinct function, the more likely is this to be the case: who then can tell us, whether the limited duration of life was brought about in consequence of the restricted functions of the cell or whether it was determined by other advantages[1]? In either case we must maintain that the disadvantages arising from a limited duration of the cells are more than compensated for by the advantages which result from their highly effective specialized functions. Although no one of the functions of the body is necessarily attended by the limited duration of the cells which perform it, as is proved by the persistence of unicellular forms, yet any or all of them might lead to such a limitation of existence without in any way injuring the species, as is proved by the Metazoa. But the reproductive cells cannot be limited in this way, and they alone are free from it. They could not lose their immortality, if indeed the Metazoa are derived from the immortal Protozoa, for from the very nature of that immortality it cannot be lost. From this point of view the body, or *soma*, appears in a certain sense as a secondary appendage of the real bearer of life,—the reproductive cells.

Just as it was possible for the specific somatic cells to be differentiated from among the chemico-physical variations which presented themselves in the protoplasm, by means of natural selection, until finally each function of the body was performed by its own special kind of cell; so it might be possible for only those variations to persist the constitution of which involved a cessation of activity after a certain fixed time. If this became true of the whole mass of somatic cells, we should then meet with natural death for the first time. Whether we ought to regard this limitation of the life of the specific somatic cells as a mere consequence of their differentiation, or at the same time as a consequence of the powers of natural selection especially directed to such an end,—appears doubtful. But I am myself rather inclined to take the latter view, for if it was advantageous to the somatic cells to preserve the unending life of their ancestors—the unicellular organisms, this end

[1] The problem is very easily solved if we seek assistance from the principle of panmixia developed in the second essay 'On Heredity.' As soon as natural selection ceases to operate upon any character, structural or functional, it begins to disappear. As soon, therefore, as the immortality of somatic cells became useless they would begin to lose this attribute. The process would take place more quickly, as the histological differentiation of the somatic cells became more useful and complete, and thus became less compatible with their everlasting duration.—A.W. 1888.

might have been achieved, just as it was possible at a later period, in the higher Metazoa, to prolong both the duration of life and of reproduction a hundred- or a thousand-fold. At any rate, no reason can be given which would demonstrate the impossibility of such an achievement.

With our inadequate knowledge it is difficult to surmise the immediate causes of such a selective process. Who can point out with any feeling of confidence, the direct advantages in which somatic cells, capable of limited duration, excelled those capable of eternal duration? Perhaps it was in a better performance of their special physiological tasks, perhaps in additional material and energy available for the reproductive cells as a result of this renunciation of the somatic cells; or perhaps such additional power conferred upon the whole organism a greater power of resistance in the struggle for existence, than it would have had, if it had been necessary to regulate all the cells to a corresponding duration.

But we are not at present able to obtain a clear conception of the internal conditions of the organism, especially when we are dealing with the lowest Metazoa, which seem to be very rarely found at the present day, and of which the vital phenomena we only know as they are exhibited by two species, both of doubtful origin. Both species have furthermore lost much of their original nature, both in structure and function, as a result of their parasitic mode of life. Of the Orthonectides and Dicyemidae we know something, but of the reproduction in the single free non-parasitic form, discovered by F. E. Schulze and named by him *Trichoplax adhaerens*, we know nothing whatever, and of its vital phenomena too little to be of any value for the purpose of this essay.

At this point it is advisable to return once more to the derivation of death in the Metazoa from the Orthonectides, as Götte endeavoured to derive it, when he overlooked the fact that, according to his theory, natural death is inherited from the Monoplastids and cannot therefore have arisen anew in the Polyplastids. According to this theory, death must necessarily have appeared in the lowest Metazoa as a result of the extrusion of the germ-cells, and by continual repetition must have become hereditary. We must not however forget that, in this case, the cause of death is exclusively external, by which I mean that the somatic cells which remained after the extrusion of the reproductive cells, were unable to feed any longer or at any rate to an adequate extent; and that the cause of their death did not lie in their constitution, but in the unfavourable conditions which surrounded them. This is not so much a process of natural death as of artificial death, regularly appearing in each individual at a corresponding period, because, at a certain time of life, the organism becomes influenced by the same unfavourable conditions. It is just as if the conditions of life invariably led to death by starvation at a certain stage in the life *of a certain* species. *But we know that death arises from purely* internal causes among the higher Metazoa, and that it is anticipated by the whole organisation as the normal end of life. Hence nothing is gained by this explanation founded on the Orthonectides, and we should have to seek further and in a later stage of the development of the Metazoa, for the internal causes of true natural death.

Another theory might be based upon the supposition that natural death has been derived, in the course of time, from an artificial death which always appeared at the same stage of each individual life—as we have supposed to be the case in the Orthonectides. I *cannot agree with this view, because it involves the transmission of* acquired characters, which is at present unproved and must not be assumed to occur until it has been either directly or indirectly demonstrated[1]. I cannot imagine any way in which the somatic cells could communicate this assumed death by starvation to the reproductive cells in such a manner that the somatic cells of the resulting offspring would spontaneously die of hunger in the same manner and at a corresponding time as those of the parent. It would be as impossible to imagine a theoretical conception of such transmission as of the supposed instance of kittens being born without a tail after the parent's tail had been docked; although to make the cases parallel the kittens' tails ought to be lost at the same period of life as that at which the parent lost hers. And in my opinion we do not add to the intelligibility of such an idea by assuming the artificial removal of tails through hundreds of generations. Such changes, and indeed all changes, are, as I think, only conceivable and indeed possible when they arise from within, that is, when they arise from changes in the reproductive

[1] See the preceding essay 'On Heredity.'

cells. But I find no difficulty in believing that variations in these cells took place during the transition from Homoplastids to Heteroplastids, variations which formed the material upon which the unceasing process of natural selection could operate, and thus led to the differentiation of the previously identical cells of the colony into dissimilar ones—some becoming perishable somatic cells, and others the immortal reproductive cells.

It is at any rate a delusion to believe that we have explained natural death, by deriving it from the starvation of the *soma* of the Orthonectides, by the aid of the unproved assumption of the transmission of acquired variations. We must first explain why these organisms produce only a limited number of reproductive cells which are all extruded at once, so that the *soma* is rendered helpless. Why should not the reproductive cells ripen in succession as they do indirectly among the Monoplastides, that is to say in a succession of generations, and as they do directly in great numbers among the Metazoa? There would then be no necessity for the *soma* to die, for a few reproductive cells would always be present, and render the persistence of the individual possible. In fact, the whole arrangement—the formation of reproductive cells at one time only, and their sudden extrusion,—presupposes the mortality of the somatic cells, and is an adaptation to it, just as this mortality itself must be regarded as an adaptation to the simultaneous ripening and sudden extrusion of the generative cells. In short, there is no alternative to the supposition stated above, viz. that the mortality of the somatic cells arose with the differentiation of the originally homogeneous cells of the Polyplastids into the dissimilar cells of the Heteroplastids. And this is the first beginning of natural death.

Probably at first the somatic cells were not more numerous than the reproductive cells, and while this was the case the phenomenon of death was inconspicuous, for that which died was very small. But as the somatic cells relatively increased, the body became of more importance as compared with the reproductive cells, until death seems to affect the whole individual, as in the higher animals, from which our ideas upon the subject are derived. In reality, however, only one part succumbs to natural death, but it is a part which in size far surpasses that which remains and is immortal,—the reproductive cells.

Götte combats the statement that the idea of death necessarily implies the existence of a corpse. Hence he maintains that the cellular sac which is left after the extrusion of the reproductive cells among the Orthonectides, and which ultimately dies, is not a corpse; 'for it does not represent the whole organism, any more than the isolated ectoderm of any other Heteroplastid' (l.c., p. 48). But it is only a popular notion that a corpse must represent the entire organism. In cases of violent death this idea is correct, because then the reproductive cells are also killed. But as soon as we recognise that the reproductive cells on the one side, and the somatic cells on the other, form respectively the immortal and mortal parts of the Metazoan organism, then we must acknowledge that only the latter,—that is, the *soma* without the reproductive cells,—suffers natural death. The fact that all the reproductive cells have not left the body (as sometimes happens) before natural death takes place, does not affect this conception. Among insects, for instance, it may happen that natural death occurs before all the reproductive cells have matured, and these latter then die with the *soma*. But this does not make any difference to their potential immortality, any more than it modifies the scientific conception of a corpse. The idea of natural death involves that of a corpse, which consists of the *soma*, and when the latter happens to contain reproductive cells, these do not succumb to a natural death, which can never apply to them, but to an accidental death. They are killed by the death of the *soma* just as they might be killed by any other accidental cause of death.

The scientific conception of a corpse is not affected, whether the dead *soma* remains whole for some time, or falls to pieces at once. I cannot therefore agree with Götte when he denies that an Orthonectid possesses 'the possibility of becoming a corpse' (in his sense of the word) because 'its death consists in the dissolution of the structure of the organism.' When the young of the Rhabdites form of *Ascaris nigrovenosa* bore through the body-walls of their parent, cause it to disintegrate and finally devour it, the whole organism disappears, and it would be difficult to say whether a corpse exists in the popular sense of the word. But, scientifically speaking, there is certainly a corpse; the real *soma* of the animal dies, and this, however subdivided, must be considered as a corpse. The fact that natural death is so difficult to define without any accurate conception of what is meant by a corpse, proves the necessity for arriving at a scientific idea as to the meaning of the latter. There is no death without a corpse—whether the latter be small or large, whole or in pieces.

If we compare the bodies of the higher Metazoa with those of the lower, we see at once that not only has the structure of the body increased in size and complexity as far as the *soma* is concerned, but we also see that another factor has been introduced, which exercises a most important influence in lengthening the duration of life. This is the replacement of cells by multiplication. Somatic cells have acquired (at any rate in most tissues) the power of multiplying, after the body is completely developed from the reproductive cells. The cells which have undergone histological differentiation can increase by fission, and thus supply the place of those which are being continually destroyed in the course of metabolism. The difference between the higher and lower Metazoa in this respect lies in the fact that there is only one generation of somatic cells in the latter, and these are used up in the process of metabolism at almost the same time that the reproductive cells are extruded, while among the former there are successive generations of somatic cells. I have elsewhere endeavoured to render the duration of life in the animal kingdom intelligible by the application of this principle, and have attempted to show that its varying duration is determined in different species by the varying number of somatic cell-generations [1]. Of course, the varying duration of each cell-generation materially influences the total length of life, and experience teaches us that the duration of cell-generations varies, not only in the lowest Metazoa as compared with the highest, but even in the various kinds of cells in one and the same species of animal.

We must, for the present, leave unanswered the question—upon what changes in the physical constitution of protoplasm does the variation in the capacity for cell-duration depend; and what are the causes which determine the greater or smaller number of cell-generations. I mention this obvious difficulty because it is the custom to meet every attempt to search deeper into the common phenomena of life with the reproach that so much is still left unexplained. If we must wait for the explanation of these

[1] See the first essay on 'The Duration of Life.'

processes until we have ascertained the molecular structure of cells, together with the changes that occur in this structure and the consequences of the changes, we shall probably never understand either the one or the other. The complex processes of life can only be followed by degrees, and we can only hope to solve the great problem by attacking it from all sides.

Therefore it is, in my opinion, an advance if we may assume that length of life is dependent upon the number of generations of somatic cells which can succeed one another in the course of a single life; and, furthermore, that this number, as well as the duration of each single cell-generation, is predestined in the germ itself. This view seems to me to derive support from the obvious fact that the duration of each cell-generation, and also the number of generations, undergo considerable increase as we pass from the lowest to the highest Metazoa.

In an earlier work [1] I have attempted to show how exactly the duration of life is adapted to the conditions by which it is surrounded; how it is lengthened or shortened during the formation of species, according to the conditions of life in each of them; in short, how it is throughout an adaptation to these conditions. A few points however were not touched upon in the work referred to, and these require discussion; their consideration will also throw some light upon the origin of natural death and the forms of life affected by it.

I have above explained the limited duration of the life of somatic cells in the lower Metazoa—Orthonectides—as a phenomenon of adaptation, and have ascribed it to the operation of natural selection, at the same time pointing out that the existence of immortal Metazoan organisms is conceivable. If the Monoplastides are able to multiply by fission, through all time, then their descendants, in which division of labour has induced the antithesis of reproductive and somatic cells, might have done the same. If the Homoplastid cells reproduced their kind uninterruptedly, equal powers of duration must have been possible for the two kinds of Heteroplastid cells; they too might have been immortal so far as immortality only depends upon the capacity for unlimited reproduction.

But the capacity for existence possessed by any species is not only dependent upon the power within it; it is also influenced

[1] See the first essay on 'The Duration of Life.'

by the conditions of the external world, and this renders necessary the process which we call adaptation. Thus it is just as inconceivable that either a homogeneous or a heterogeneous cell-colony possessing the physiological value of a multicellular individual should continue to grow to an unlimited extent by continued cell-division, as it is inconceivable that a unicellular being should increase in size to an unlimited extent. In the latter case the process of cell-division imposes a limit upon the size attained by growth. In the former, the requirements of nutrition, respiration, and movement must prescribe a limit to the growth of the cell-colony which constitutes the individual of the higher species, just as in the case of the unicellular Monoplastides, and it does not affect the argument if we consider this limitation to be governed by the process of natural selection. It would only be possible to regulate the relations of the single cells of the colony to each other by fixing the number of cells within narrow limits. During the development of *Magosphaera*—one of the Homoplastides—the cells arrange themselves in the form of a hollow sphere, lying in a gelatinous envelope. But the fact that reproduction does not follow the simple unvarying rhythm of unicellular organisms is of more importance; for a rhythm of a higher order appears, in which each cell of the colony separates from its neighbours, when it has reached a certain size, and proceeds by very rapid successive divisions to give rise to a certain number of parts which arrange themselves as a new colony. The number of divisions is controlled by the number of cells to which the colony is limited, and at first this number may have been very small. With the introduction of this secondary higher rhythm during reproduction, the first germ of the Polyplastides became evident; for then each process of fission was not, as in unicellular organisms, equivalent to all the others; for in a colony of ten cells the first fission differs from the second, third, or tenth, both in the size of the products of division and also in remoteness from the end of the process. This secondary fission is what we know as segmentation.

It seems to me of little importance whether the first process of segmentation takes place in the water or within a cyst, although it is quite possible that the necessity for some protective structure appeared at a very early period, in order to shield the segmenting cell from danger.

It is impossible to accept Götte's conception of the germ (Keim), and at this point the question arises as to its true meaning. I should propose to include under this term every cell, cytode, or group of cells which, while not possessing the structure of the mature individual of the species, possesses the power of developing into it under certain circumstances. The emphasis is now laid upon the expression development, which is something opposed to simple growth, without change of form. A cell which becomes a complete individual by growth alone is not a germ but an individual, although a very small one. For example, the small encapsuled Heliozoon, which arises as the product of multiple fission, is not a germ in our sense of the word. It is an individual, provided with all the characteristic marks of its species, and it has only to protrude the retracted processes (pseudopodia) and to take in the expelled water (formation of vacuoles) in order to become capable of living in a free state. In this sense of the word, germs are not confined to the Polyplastides, but are found in many Monoplastides. There is nevertheless, in my opinion, a profound and significant difference between the germs of these two groups. And this lies not so much in the morphological as in the developmental significance of these structures. As far as I have been able to compare the facts, I may state that the germs of the Monoplastides are entirely of secondary origin, and have never formed the phyletic origin of the species in which they are found. For instance, the spore-formation of the Gregarines resulted from a gradually increasing process of division, which was concentrated into the period of encystment; and it was induced by a necessity for rapid multiplication due to the parasitic life and unfavourable surroundings of these animals. If Gregarines were free-living animals, they would not need this method of reproduction. The encysted animal would probably divide into eight, four, or two parts, or perhaps, like many Infusoria [1], it would not divide at all,

[1] These assumptions can be authenticated among the Infusoria. The encysted *Colpoda cucullus*, Ehrbg. divides into two, four, eight, or sixteen parts; *Otostoma Carteri*, into two, four, or eight; *Tillina magna*, Gruber, into four or five; *Lagynus* sp. Gruber, into two; *Amphileptus meleagris*, Ehrbg. into two or four. The last two species and many others frequently do not divide at all during the encysted condition. But while any further increase in the number of divisions within the cyst does not occur in free-swimming Infusoria, the interesting case of *Ichthyophthirius multifiliis*, Fouquet, shows that parasitic habits call forth a remarkable increase in

so that the whole reproduction would depend on simple fission alone during the free state.

The original mode of reproduction among the Monoplastides was undoubtedly simple fission. This became connected with encystment, which originally took place without multiplication; and only when the divisions in the cyst became excessively numerous did such minute plastids appear that a genuine process of development had to be undergone in order to produce complete individuals. Here we have the general conception of the germ as I defined it. Its limitations are naturally not very sharply defined, for it is impossible to draw an absolute distinction between simple growth and true development accompanied by changes in form and structure. For instance, Häckel's *Protomyxa aurantiaca* divides within its cyst into numerous plastids, which might be spoken of as germs. But the changes of form which they undergo before they become young *Protomyxae* are very small, and for the most part depend upon the expansion of the body, which existed in the capsule as a contracted pear-shaped mass. It is therefore more correct to speak only of the simple growth of the products of the fission of the parent organism, and to look upon these products as young *Protomyxae* rather than germs. On the other hand, the young animals which creep out of the germs (the 'spores') of *Gregarina gigantea*, described by E. van Beneden, differ essentially from the adult, and pass through a series of developmental stages before they assume the characteristic form of a Gregarine.

This is true development [1]. But such a method of germ-formation and development are found most frequently, although not exclusively, among the parasitic Monoplastides, and this fact alone serves to indicate their secondary origin. It is a form of ontogenetic development differing from that of the Polyplastides in that it does not revert to a phyletically primitive condition of the species, but, on the contrary, exhibits stages which first appear in the phyletic

the number of divisions. This animal divides into at least a thousand daughter individuals.

[1] True development also takes place in the above-mentioned *Ichthyophthirius*. While in other Infusoria the products of fission exactly resemble the parent, in *Ichthyophthirius* they have a different form; the sucking mouth is wanting while provisional clasping cilia are at first present. In this case therefore the word germ may be rightly applied, and *Ichthyophthirius* affords an interesting example of the phyletic origin of germs among the lower Flagellata and Gregarines. Cf. Fouquet, 'Arch. Zool. Expérimentale,' Tom. V. p. 159. 1876.

development of the specific form. The Psorosperms were only formed after the Gregarines had become established as a group. The amoeboid organisms which creep out of them are in no way to be regarded as the primitive forms of the Gregarines, even if the latter may have resembled them, but they are coenogenetic forms produced by the necessity for a production of numerous and very minute germs. The necessity for a process of genuine development perhaps depends upon the small amount of material contained in one of these germs, and on other conditions, such as change of host, change of medium, etc. It therefore results that the fundamental law of biogenesis *does not apply to the Monoplastides; for these forms are either entirely without a genuine ontogeny and only possess the possibility of growth, or else they are only endowed with a coenogenetic ontogeny* [1].

Some authorities may be inclined to limit the above proposition, and to maintain that we must admit the possibility that we are likely to occasionally meet with an ontogeny of which the stages largely correspond with the most important stages in the phyletic development of the species, and that the ontogenetic repetition of the phylogeny, although not the rule, may *still* occur as a rare exception in the Protozoa.

A careful consideration of the subject indicates, however, that the occurrence of such an exception is very improbable. Such an ontogeny would, for instance, occur if one of the lowest Monoplastides, such as a Moneron, were to develope into a higher form, such as one of the Flagellata, with mouth, eye-spot, and cortical layer, under such external conditions that it would be advantageous for the existence of its species that it should no longer reproduce itself by simple fission, but that the periodical formation of a cyst (which was perhaps previously part of the life-history) should be associated with the occurrence of numerous divisions within the cyst itself, and with the formation of germs. We must suppose either that these germs were so minute that the young animals could not

[1] Bütschli, long ago, doubted the application of the fundamental law of biogenesis to the Protozoa (cf. 'Ueber die Entstehung der Schwärmsprösslings der *Podophrya quadripartita*,' Jen. Zeit. f. Med. u. Naturw. Bd. X. p. 19, Note). Gruber has more recently expressed similar views, and in fact denies the presence of development in the Protozoa, and only recognizes growth ('*Dimorpha mutans*, Z. f. W. Z.' Bd. XXXVII. p. 445). This proposition must however be restricted, inasmuch as a development certainly occurs, although one which is coenogenetic and not palingenetic.

become Flagellata directly, or that it was advantageous for them to move and feed as Monera at an early period, and to assume the more complex structure of the parent by gradual stages. In other words, the phyletic development would proceed hand in hand with the ontogeny corresponding to it, although not from any internal cause, but as an adaptation to the existing conditions of life. But the supposed transformation of the species also depended upon these same conditions of life, which must therefore have been of such a nature as to bring about simultaneously, by an intercalation of germs and by a genuine development, the evolution of the form in question in the last stage of its ontogeny, and the maintenance of its original condition during the initial stage. Such a combination of circumstances can have scarcely ever happened. Against the occurrence of such a transformation as we have supposed, it might be argued, indeed, that the assumed production of very numerous germs does not occur among free-living Monoplastides. Those which have acquired parasitic habits must be younger phyletic forms, for their first host—whether a lowly or a highly organized Metazoon—must have appeared before they could gain access to it and adapt themselves to the conditions of a parasitic life, and by this time the Flagellate Infusoria were already established. It is by far less probable that the persistence or rather the intercalation of the ancestral form would occur in an ontogenetic cycle, consisting of a series of stages, and not of two only, as in our example. For as soon as reproduction can be effected by the simple fission of the adult, not only is there no reason why the earlier phyletic stages should be again and again repeated, but such recapitulation is simply impossible. We cannot, therefore, conclude that the anomalous early stages of a Monoplastid such as *Acineta* correspond with an early form of phyletic development.

Supposing, for instance, that the Acinetaria were derived from the Ciliata, then this transformation must have taken place in the course of the continued division of the ciliate ancestor—partially connected with encystment, but for the most part independently of it. Of the myriads of generations which such a process of development may have occupied, perhaps the first set moved with suctorial processes, while the second gradually adopted sedentary habits, and throughout the whole of the long series, each succeeding generation must have been almost exactly like its predecessor, and must always have consisted of individuals which possessed the characters of the species.

This does not exclude the possibility that in spite of an assumed sedentary mode of life, the need for locomotion and for obtaining food in fresh places may have arisen at some period of life. But whenever formation of swarm-spores takes place instead of simple fission, this does not depend upon the persistence of an ancestral form in the ontogenetic cycle, but is due to the intercalation of an entirely new ontogenetic stage, which happens to resemble an ancestral form, in the possession of cilia, etc.

I imagine that I have now sufficiently explained the above proposition, that the repetition of the phylogeny in the ontogeny does not and cannot occur among unicellular organisms.

With the Polyplastides the opposite is the case. There is no species, as far as we know, which does not—either in each individual, or after long cycles which comprise many individuals (alternation of generations)—invariably revert to the Monoplastid state. This applies from the lowest forms, such as *Magosphaera* and the Orthonectides, up to the very highest. In the latter a great number of intermediate phyletic stages always occur, although some have been omitted as the result of concentration in the ontogeny, while others have sometimes been intercalated.

Sexual reproduction is the obvious cause of this very important arrangement. Even if this is an hypothesis rather than a fact we must nevertheless accept it unconditionally, because it is a method of reproduction found everywhere. It is the rule in every group of the animal kingdom, and is only absent in a few species in which it is replaced by parthenogenesis. In these latter instances sexual reproduction may be local, and entirely absent in certain districts only (*Apus*), or it may be only apparently wanting; in some cases where it is undoubtedly absent, it is equally certain that it was present at an earlier period (*Limnadia Hermanni*). We cannot as yet determine whether its loss will not involve the degeneration and ultimate extinction of the species in question.

If the essential nature of sexual reproduction depends upon the conjugation of two equivalent but dissimilar morphological elements, then we can understand that a multicellular being can only attain sexual reproduction when a unicellular stage is present in its development; for the coalescence of entire multicellular organisms in such a manner that fusion would only take place between equivalent cells, would seem to be impracticable. In the necessity for sexual reproduction, there is therefore also implied the necessity for reverting to the original condition of the Polyplastides—that of a single cell—and upon this alone depends the fundamental law of biogenesis. This law is therefore confined to the Polyplastides, and does not apply to the Monoplastides; and Götte's suggestion that the latter fall back into the primitive condition of the organism during their encystment (rejuvenescence), finds no support in this aspect of the question.

I have on a previous occasion [1] referred the utility of death to the ultimate fact that the unending life of the Metazoan body would be a useless luxury, and to the fact that the individuals would necessarily become injured in the course of time, and would be therefore 'not only valueless to the species, but . . . even harmful, for they take the place of those which are sound' (l. c., p. 24). I might also have said that such damaged individuals would sooner or later fall victims to some accidental death, so that there would be no possibility of real immortality. I now propose to examine this statement a little more closely, and to return to a question which has already been alluded to before.

It is obvious that the advantages above set forth did not form the motive which impelled natural selection to convert the immortal life of the Monoplastides into the life of limited duration possessed by the Heteroplastides, or more correctly, which led to the restriction of potential immortality to the reproductive cells of the latter. It is at any rate theoretically conceivable that a struggle might arise between the mortal and immortal individuals of a certain Metazoan species, and that natural selection might secure the success of the former, because the longer the immortal individuals lived, the more defective they became, and as a result gave rise to weaker offspring in diminished numbers. Probably no one would be bold enough to suggest such a crude example of natural selection. And yet I venture to think that the principle of natural selection is here also to be taken into account, and even plays, although in a negative rather than a positive way, a very essential part in determining the duration of life in the Metazoa.

[1] See the first essay on 'The Duration of Life,' p. 23 *et seq.*

When the somatic cells of the first Heteroplastides ceased to be immortal, such a loss would not in any way have precluded them from regaining this condition. Just as, with the differentiation of the first somatic cells of the lowest Heteroplastides, their duration was limited to that of a single cell-generation,—so it must have been possible for them, at a later period and if the necessity arose, to lengthen their duration over two, three, or more generations. And if my theory of the duration of life in the Metazoa is well founded, these cells have as a matter of fact increased their duration, to an extent about equal to that of the organism to which they belong. There is no ground whatever for the assumption that it is impossible to fix the number of cell-generations at infinity,—as actually happens in the case of the reproductive cells,—but on the other hand it has already been shown to be obvious that such an extension is opposed to the principle of utility. It could never be to the advantage of a species to produce crippled individuals, and therefore the infinite duration of individuals has never reappeared among the Metazoa. So far the limited duration of Metazoan life may be attributed to the worthlessness or even the injurious nature of individuals, which although immortal, were nevertheless liable to wear and tear. This fact explains why immortality has never reappeared, it explains the predominance of death, but it was not the single primary cause of this phenomenon. The perishable and vulnerable nature of the *soma* was the reason why nature made no effort to endow this part of the individual with a life of unlimited length.

Götte considers that death is inherent in reproduction, and in a certain sense this is true, but not in the general way supposed by him.

I have endeavoured to show above that it is most advantageous for the preservation of the species among the lowest Metazoa, that the body should consist of a relatively small number of cells, and that the reproductive cells should ripen simultaneously and all escape together. If this conclusion be accepted, the uselessness of a prolonged life to the somatic cells is obvious, and the occurrence of death at the time of the extrusion of the reproductive cells is explained. In this manner death (of the *soma*) and reproduction are here made to coincide.

This relation of reproduction to death still exists in a great number of the higher animals. But such an association, together with the simultaneous ripening of the reproductive cells, has not been maintained continuously in the past. As the *soma* becomes larger and more highly organized, it is able to withstand more injuries, and its average duration of life will extend: *pari passu* with these changes it will become increasingly advantageous not only for the number of reproductive cells to be multiplied, but also for the time during which they are produced to be prolonged. In this manner a lengthening of the reproductive period arises, at first continuously and then periodically. It is beyond my present purpose to consider in detail the conditions upon which this lengthening depends, but I would emphasize the fact that a lengthening of life is connected with the increase in the duration of reproduction, while on the other hand there is no reason to expect life to be prolonged beyond the reproductive period; so that the end of this period is usually more or less coincident with death.

A further prolongation of life could only take place when the parent begins to undertake the duty of rearing the young. The most primitive form of this is found among those animals, which do not expel their reproductive cells as soon as they are ripe but retain them within their bodies, so that the early stages of development take place under the shelter of the parent organism. Associated with such a process there is frequently a necessity for the germs to reach a certain spot, where alone their further development can take place. Thus a segment of a tapeworm lives until it has brought the embryos into a position which affords the possibility of their passive transference to the stomach of their special host. But the duration of life is first materially lengthened when the offspring begin to be really tended, and as a general rule the increase in length is exactly proportional to the time which is demanded by the care of the young. Accurately conducted observations are wanting upon this precise point, but the general tendency of the facts, as a whole, cannot be doubted. Those insects of which the care for their offspring terminates with the deposition of eggs at the appropriate time, place, etc., do not survive this act; and the duration of life in such imagos is shorter or longer according as the eggs are laid simultaneously or ripen gradually. On the other hand, insects—such as bees and ants—which tend their young, have a life which is prolonged for years.

But the lengthening of the reproductive period alone may result in a marked increase in the length of life, as is proved by the queen-bee. In all these cases it is easy to imagine the operation of natural selection in producing such alterations in the duration of life, and indeed we might accurately calculate the amount of increase which would be produced in any given case if the necessary data were available, viz. the physiological strength of the body, and its relations to the external world, such as, for instance, the power of obtaining food at various periods of life, the expenditure of energy necessary for this end, and the statistics of destruction, that is, the probabilities in favour of the accidental death of a single individual at any given time. These statistics must be known both for the imagos, larvae, and eggs; for the lower they are for the imagos, and the higher for the larvae and eggs, the more advantageous will it be, *ceteris paribus*, for the number of eggs produced by the imago to be increased, and the more probable it would therefore be that a long reproductive period, involving a lengthening of the life of the imago, would be introduced. But we are still far from being able to apply mathematics to the phenomena of life; the factors are too numerous, and no attempt has been made as yet to determine them with accuracy.

But we must at least admit the principle that both the lengthening and shortening of life are possible by means of natural selection, and that this process is alone able to render intelligible the exact adaptation of the length of life to the conditions of existence.

A shortening of the normal duration of life is also possible; this is shown in every case of sudden death, after the deposition of the whole of the eggs at a single time. This occurs among certain insects, while nearly allied forms of which the oviposition lasts over many days therefore possess a correspondingly long imago-life. The *Ephemeridae* and Lepidoptera afford many examples of this, and in an earlier work I have collected some of them[1]. The humming-bird hawk-moth flies about for weeks laying an egg here and there, and, like the allied poplar hawk-moth and lime hawk-moth, probably dies when it has deposited all the eggs which can be matured with the amount of nutriment at its disposal. Many other Lepidoptera, such as the majority of butterflies, fly about for weeks depositing their eggs, but others, such as the emperor-moths and lappet-

[1] See Appendix to the first essay on 'The Duration of Life,' pp. 43–46.

moths, lay their eggs one after another and then die. The eggs of the parthenogenetic *Psychidae* are laid directly after the imago has left the cocoon, and death ensues immediately, so that the whole life of the imago only lasts for a few hours. No one could look upon this brief life as a primitive arrangement among Lepidoptera, any more than we do upon the absence of wings in the female *Psychidae*; shortening of life here is therefore clearly explicable.

In such cases have we any right to speak of the fatal effect of reproduction? We may certainly say that these insects die of exhaustion; their vital strength is used up in the last effort of laying eggs, and in the case of the males, in the act of copulation. Reproduction is here certainly the most apparent cause of death, but a more remote and deeper cause is to be found in the limitation of vital strength to the length and the necessary duties of the reproductive period. The fact that there are female Lepidoptera which, like the emperor-moths, do not feed in the imago-state, proves the truth of this statement. They still possess a mouth and a complete alimentary canal, but they have no spiral 'tongue,' and do not take food of any kind, not even a drop of water. They live in a torpid condition for days or weeks until fertilization is accomplished, and then they lay their eggs and die. The habit of extracting honey from flowers—common to most hawk-moths and butterflies—would not have thus fallen into disuse, if the store of nutriment, accumulated in the form of the fat-bodies, during the life of the caterpillar, had not been exactly sufficient to maintain life until the completion of oviposition. The fact that the habit of taking food has been thus abandoned is a proof that the duration of life beyond the reproductive period would not be to the advantage of the species.

The protraction of existence into old age among the higher Metazoa proves that death is not a necessary consequence of reproduction. It seems to me that Götte's statement 'that the appearances of senility must not be regarded as the general cause of death' is not in opposition to my opinions but rather to those which receive general acceptance. I have myself pointed out that 'death is not always preceded by senility or a period of old age[1].'

The materials are wanting for a comprehensive investigation of

[1] See the first essay on 'The Duration of Life,' p. 21.

the causes which first introduced this period among the higher Metazoa; in fact the most fundamental data are absent, for we do not even know the part of the animal kingdom in which it first appeared: we cannot even state the amount by which the duration of life exceeds that of the period of reproduction, or what is the value to the species of this last stage in the life of the individual.

It is in these general directions that we must seek for the significance of old age. It is obviously of use to man, for it enables the old to care for their children, and is also advantageous in enabling the older individuals to participate in human affairs and to exercise an influence upon the advancement of intellectual powers, and thus to influence indirectly the maintenance of the race. But as soon as we descend a step lower, if only as far as the apes, accurate facts are wanting, for we are, and shall probably long be, ignorant of the total duration of their life, and the point at which the period of reproduction ceases.

I must here break off in the midst of these considerations, rather than conclude them, for much still remains to be said. I hope, nevertheless, that I have thrown new light upon some important points, and I now propose to conclude with the following short abstract of the results of my enquiry.

I. Natural death occurs only among multicellular beings; it is not found among unicellular organisms. The process of encystment in the latter is in no way comparable with death.

II. Natural death first appears among the lowest Heteroplastid Metazoa, in the limitation of all the cells collectively to one generation, and of the somatic or body-cells proper to a restricted period: the somatic cells afterwards in the higher Metazoa came to last several and even many generations, and life was lengthened to a corresponding degree.

III. This limitation went hand in hand with a *differentiation* of the cells of the organism into reproductive and somatic cells, in accordance with the principle of division of labour. This differentiation took place by the operation of natural selection.

IV. The fundamental biogenetic law applies only to multicellular beings; it does not apply to unicellular forms of life. This depends on the one hand upon the mode of reproduction by fission which obtains among the Monoplastides (unicellular organisms), and on the other upon the necessity, induced by sexual reproduction, for the maintenance of a unicellular stage in the development of the Polyplastides (multicellular organisms).

V. Death itself, and the longer or shorter duration of life, both depend entirely on adaptation. Death is not an essential attribute of living matter; it is neither necessarily associated with reproduction, nor a necessary consequence of it.

In conclusion, I should wish to call attention to an idea which is rather implied than expressed in this essay:—it is, that reproduction did not first make its appearance coincidently with death. Reproduction is in truth an essential attribute of living matter, just as is the growth which gives rise to it. It is as impossible to imagine life enduring without reproduction as it would be to conceive life lasting without the capacity for absorption of food and without the power of metabolism. Life is continuous and not periodically interrupted: ever since its first appearance upon the earth, in the lowest organisms, it has continued without break; the forms in which it is manifested have alone undergone change. Every individual alive to day—even the very highest—is to be derived in an unbroken line from the first and lowest forms.