rejuvenescence being absent, the animal grows old (sénéscence) and finally dies *a natural death.* I do not agree with this interpretation. The significant inner changes which take place during conjugation were obviously prepared some time beforehand, and the micro- and macronuclei of animals which feel impelled to conjugate are already in a state which must sooner or later lead to profound changes of one or both—and this whether conjugation has taken place or not. In either case these changes will be essentially the same,—the destruction of the macro- and division of the micronucleus. One thing alone does not happen,—the coalescence with the nucleus of another individual. But we know that all the products of the micronuclear division disappear except that which gives rise to the reproductive nuclei and that this is always the one lying nearest the connecting bridge which unites the conjugating animals. If then it is the influence of another animal which renders a grand-daughter-nucleus capable of further development, we are led to conclude that such an influence is lost when conjugation does not occur. In this, I believe, lies the cause which leads the vital energies to grow weaker and finally to cease, in the descendants of an animal which has undergone the changes described above. It is the same with the ovum,—the processes of maturation which prepare for fertilization, produce changes which prevent the future life of the egg-cell, unless it be fertilized.

Maupas will reply that it has not yet been proved that such changes appear when conjugation is absent: he has never observed them in the Infusoria which he prevented from conjugating. He did not make the observation because he regarded the changes as phenomena of age. It now remains to follow accurately the alterations which appear in the macro- and micronuclei, when a colony has been prevented from conjugating. The observations will be difficult, because they must extend over many generations; for the end of the period favourable for conjugation cannot be foretold with certainty and, according to Maupas, is not reached in all the animals of a colony at the same time.

My interpretation does not by any means require that the changes in animals prevented from conjugating, should follow precisely the same course and pass through exactly the same stages as those which occur in conjugated animals. This is *a priori* very improbable. We must not forget that the interval between two successive conjugations extends over many generations, and that those inner conditions which prepare for conjugation are gradually built up, reach their highest point, and are then lost. If, when the appropriate period has arrived, conjugation takes place, the long-prepared processes of maturation take their normal course; but if this period is passed by, the whole future development *is abnormal.* The animal increases a hundredfold or more, but development cannot pursue its normal course, the nucleus degenerates,—sometimes the macronucleus being the first, sometimes the micronucleus,—and finally neither assimilation, nor the maintenance of the characteristic body-form can be kept up, and the animals die one after the other. The irregularity in the course of these phenomena, as Maupas describes them, points to the fact that we are concerned with an abnormal process.

Does Natural Death occur in Unicellular Organisms?

Why do some writers regard the process described above as the equivalent of the normal death of Metazoa? Merely because of the traditional dogma which asserts the necessity of normal 'physiological' death. They overlook the fact that *in Infusoria conjugation is a normal process,* the periodical recurrence of which is provided for by nature, and upon which the whole vital mechanism of these animals is, to a certain extent, regulated. Nature must have amphimixis, and brings it about by the internal changes which impel the animals to pair, and by those which gradually render them unable to live when conjugation is artificially prevented. It is, as I have already argued, precisely equivalent to the effects which follow the non-occurrence of fertilization. The spermatozoon which fails to find an ovum, dies. If anyone finds pleasure in bringing confusion into ideas which have just become to some extent clear, he may speak of this as the 'normal death' of the spermatozoon; I call it an accidental death, although I am well aware that this unhappy accident is far more common than the successful attainment of the normal object of a spermatozoon's life. In most animals millions of spermatozoa are lost before a single one attains its object; and these vast numbers are necessary just because the way to the egg is so very precarious. Must we regard this destruction as normal because it is so common? Is not fertilization the normal aim of the vital processes of the spermatozoon? And does not the destruction of those numerous spermatozoa which have missed their aim result from the fact that they are not adapted for a long independent life,—that their vital force is soon expended because no precaution has been taken to renew it by food? But has this lack of food been brought about because it *could* not have been taken however desirable it may have been? I believe that spermatozoa want a mouth, and all other adaptations for the absorption of nutriment, because they do not need them for the attainment of the object for which they exist, and that, were it otherwise, they would have been adapted for living longer. Useless adaptations are never met with. Spermatozoa gone astray are of no further value to the species, and they may just as well disappear. And so it is with those Infusoria which have failed to conjugate; they are useless to the species, since its maintenance requires the periodical crossing of individuals and of this they are no longer capable. If Infusoria were not adapted for this crossing they could live on for ever without amphimixis, just as a parthenogenetic egg and its products live on without it. But those very changes which make an Infusorian capable of conjugation remove all possibility of unending life without it, just as the two 'reducing divisions' withdraw this possibility from the egg. *An even closer parallel can be drawn, for Kupffer and Böhm*[1] have shown, by the case of *Petromyzon*, that there are animal eggs which only undergo the *first* polar division before they come in contact with the spermatozoon, the second following after it has penetrated. Such eggs when unfertilized, contain the quantity of germ-plasm required for embryogeny, but are, nevertheless, incapable of parthenogenetic development. We cannot at present recognize those intimate changes upon which this incapability must depend, but we may conclude that it is a consequence of changes preparatory to amphimixis. The eggs are so completely adapted for this event that their power

[1] Böhm 'Ueber die Befruchtung des Neunaugen-Eies.' Sitzgsber. d. math.-phys. Klasse d. bayr. Akad. d. Wissensch., Munich, 1887.

of independent development is interfered with by the preliminary changes. But, just as eggs, in which these internal changes have once been carried out, cannot remain indefinitely thus prepared, but very soon change so that they are no longer adapted for fertilization, and finally decay,—so it is with an Infusorian which has passed the time for conjugation; it becomes incapable of conjugating, and finally, of living.

As far as I can see there is only one point of view from which the gradual dissolution of an Infusorian which has not succeeded in conjugating can be rightly regarded as a kind of natural death; viz. if we could prove *that its destruction is dependent on some adaptation especially directed to this end.* Maupas is, naturally enough, very far from accepting this point of view; for he clings to the old belief that death is a universal attribute of life, and is not a phenomenon of adaptation. From my standpoint we might argue as follows:—Conjugation must take place periodically because the crossing of individuals is necessary for the maintenance and development of the species. If it was impossible to ensure the occurrence of crossing in all or the great majority of individuals and colonies, there would be a danger of the uncrossed ones getting the upper hand. To prevent this, the animals which do not conjugate must be prevented from living on indefinitely, in fact natural death must occur, and this was ensured by conferring upon the macronucleus of the animal such a structure that it was used up during assimilation, while the micronucleus was so constructed that it underwent dissolution in consequence of the divisions preparatory to amphimixis, or as we may otherwise imagine it.

I know of no biological principles which are antagonistic to such a view, but I scarcely believe that it is a correct one; analogy with the sexual cells is against it. I do not doubt that nature would be quite capable of bringing about a natural death for those animals which have escaped conjugation, if it were necessary for the maintenance of the species; but their destruction does not appear to be necessary. We should hardly maintain that the dissolution of a spermatozoon which has missed its mark is dependent on the appearance of natural death, especially designed for it. On the contrary, it is obviously destroyed simply because the vital conditions necessary for its continued existence are wanting, viz. fusion with an ovum. The latter also dies for a similar reason when it has not been fertilized. Some years ago I described the different manner in which the eggs of two closely allied species of Crustacea behave when they have no prospect of being fertilized [1]. If a female of *Moina paradoxa*, bearing winter-eggs in the ovary, be separated from the males, it nevertheless deposits its ova in the brood-chamber, but they utterly disintegrate in a few hours and are washed away by the water as it flows through the chamber. It is very different with *Moina rectirostris*; the winter-egg, when ripe and ready to pass into the brood-chamber, almost occupies the entire ovary. When males are absent and fertilization does not occur, the egg is not laid but is retained by the isolated female in her ovary in which it remains apparently unchanged for many days, probably quite capable of being fertilized. Finally it changes in appearance, losing its uniform finely granular look, while the fat-globules and particles of albumen fuse together into great irregular masses which are presently rather rapidly reabsorbed. Instead of winter-eggs the parthenogenetic summer-eggs are now formed, and we may maintain that the material of the former is not lost to the individual or to the species when fertilization is excluded, but is converted into new ova which do not require fertilization. No one can doubt that the habit of laying the winter-egg only after the stimulus provided by fertilization, is an adaptation; but who would explain in this manner the destruction of the unfertilized egg, which remains in the ovary? This destruction is certainly not purposeless; but there are cases of unintended usefulness, and other species of *Moina* prove that this is one of them, for the unfertilized eggs are destroyed in the brood-chamber (where their material *is* lost). The destruction is therefore no adaptation but merely a consequence of the constitution of the egg which is so altered by preparation for the fertilization which should have ensued, that it can neither develope into an embryo nor continue to live. It is just the same, if I mistake not, with Infusoria; the gradual destruction of those animals which do not conjugate is no special adaptation, but rather an inevitable consequence of the necessary internal

[1] Weismann, 'Beiträge zur Naturgeschichte der Daphnoiden,' Leipzig, 1876–79. Abhandlung IV. 'Ueber den Einfluss der Begattung auf die Erzeugung von Wintereiern.'

changes which lead to conjugation, which could perhaps only have been prevented by special means [1].

Therefore we cannot speak of natural death as an adaptation to prevent unconjugated individuals from gaining the upper hand; and in any case natural death cannot be admitted to obtain among Infusoria *in general*, inasmuch as it only occurs in *those animals which are abnormal in not attaining to conjugation.*

We need not discuss whether the dying out of the unconjugated animals in an Infusorian colony, is an adaptation, specially intended for the removal of these harmful individuals, or whether, as I prefer to assume, it follows as a consequence of those changes which are preparatory to pairing. But even the former assumption affords no support to Maupas; because the natural death presupposed by him is the very reverse of an adaptation, being a fundamental attribute of life itself,—the inherent tendency to wear itself out. According to this view, Infusoria are predestined to death; they can however be rescued by the magic of conjugation, and thus acquire a new span of life.

Such a view does not admit of direct refutation; we can only show *that it has its origin in the old mystic conception of life, and that it is superfluous.*

Conjugation was long spoken of as the 'sexual reproduction' of Infusoria before we had a more intimate knowledge of the nature of the process. The '*tertium comparationis*' was that fusion of two cells into one which occurs at any rate in the original form of both fertilization and conjugation. I have been accustomed for many years to urge, in my lectures, that conjugation is not reproduction, but rather its opposite; for reproduction implies an increase of at least one in the number of individuals, while conjugation leads to a decrease, two individuals fusing into one. It has long been recognized that the processes which take place in conjugation and fertilization *have in themselves nothing to do with reproduction.* Maupas admits this and expresses it quite clearly and correctly when he states that

[1] I am here referring to the interesting facts discovered by R. Hertwig, which he explained as an Infusorian parthenogenesis. The subject is not, however, sufficiently mature for further consideration in this place. See R. Hertwig, 'Ueber die Conjugation der Infusorien.' Munich, 1889.

fertilization in the Metazoa is always associated with reproduction, but that the one process is not necessarily an accompaniment of the other, and that, as a matter of fact, the conjugation of Infusoria has nothing to do with reproduction. The majority of previous writers believed that conjugation revived the exhausted power of multiplying by fission. Maupas shows that this is not the case, that not only is fission deferred for a comparatively long time after the occurrence of conjugation, but that animals which have been prevented from conjugating continue to divide for a considerable period.

The view which Maupas thus overthrows was never a legitimate inference from accurate scientific observations, but was one of those traditional conceptions which gain acceptance after having been consciously or unconsciously derived from other similar conceptions. The supposed vitalizing force of fertilization was looked upon, for a long period of time, as the condition of all development and reproduction. The opposing facts were not at first strong enough to shake the foundation of this idea, and the preconceived notion that the magic of fertilization was the sole vitalizing life-maintaining principle, endured, while the facts of asexual and parthenogenetic reproduction were, by some evasion or other—the influence of fertilization extending over many generations, &c.—forced into the Procrustean bed of the received fundamental conceptions.

Even Maupas remains half buried in these old ideas. Although he has rightly recognized that fertilization and reproduction are two entirely different and even antagonistic processes, that they may be connected, as in the Metazoa, or disconnected, as in the Protozoa, he still holds to the old view of the vitalizing influence of amphimixis; he speaks of it as a 'rajeunissement karyogamique,' and declares it to be a means for the kindling afresh of that life which would, without it, waste away into death. He quite forgets that this view wholly depends upon the facts of fertilization among Metazoa, viz. in the inseparable connection between fertilization and reproduction which we find in these animals, but which *he himself has shown to be absent from the Protozoa.* He overlooks the consequence of this absence, viz. the proof that in this case '*post hoc*' is not '*propter hoc*,' and keeps to the old standpoint which was a right one only so long as we were obliged to believe that new life could not arise without amphimixis, i. e. that reproduction was always associated with fertilization.

As I have already said, I regard the power of living on indefinitely when the vital processes have once begun, as the fundamental peculiarity of living matter. But this principle fails in so many organisms that its very existence was, for a long time, entirely overlooked, and hence the limited duration of life, together with its termination in natural death, were regarded as laws dominating all living beings. Undoubtedly the capability of unending life has been lost in very many organisms of greater or less complexity, and it is, I think, interesting to trace the causes which have led to this loss, and have rendered it necessary and even advantageous.

I will very briefly recall the manner in which the mortality of Metazoa may be explained, for this has been treated in earlier essays, and my views on the point have undergone no essential change. The immortality of Protozoa was carried over to the germ-cells of Metazoa and Metaphyta whether they are sexual, i. e. adapted for amphimixis, or not. In either case they posses potential immortality, i. e. they can, under the conditions imposed upon them by their constitution, continue without limit to exhibit the phenomena of life. The conditions under which the sexually differentiated germ-cells live include the fusion of two in amphimixis, but it is not generally included among the conditions imposed upon agamic or parthenogenetic germ-cells, and, when imposed, it only requires to be fulfilled again after the lapse of a certain period.

I will not repeat the reasons which, I believe, explain why the Metazoan soma has been permitted to lose, or has been compelled to lose, the power of unending life, and why natural death has made its appearance. I will only call to mind *the fact that, according to the principle of panmixia, every faculty must disappear as soon as it ceases to be necessary.* As soon as differentiation into soma and germ-cells,—viz. the formation of Metazoa and Metaphyta,—took place, this principle began to act, for the species could be maintained without the immortality of single individuals. Whether this immortality is in any way compatible with the high differentiation of the Metazoan body, and if so, whether it would be useful, are questions which may remain unanswered—it is enough that it was unnecessary.

In Protozoa unending life was an inevitable necessity for the maintenance of the species.

Potential immortality is found from the very lowest organisms to the higher Protozoa and to the germ-cells of Metazoa and Metaphyta; but in the latter cases certain conditions are imposed upon it, and these include not only the ordinary conditions of nourishment, and of surrounding circumstance, but, as a rule, the further condition of amphimixis.

The Appearance of Amphimixis in the Organic World.

If we are unable to discover any effect of amphimixis which can render its prevalence intelligible, nothing remains but to accept the rejuvenescence theory. For not only is amphimixis found throughout the whole organic world so far as we know it, but the entire form of the latter has been controlled in a most fundamental manner, and, without amphimixis, would have been utterly different.

It has been shown above that the occurrence of an ontogeny in the Metazoa essentially depends upon the necessity for amphimixis; since this presupposes the concentration of the collective hereditary tendencies of a species in the nucleus of a single cell. But this is not only true of all the varied kinds of direct ontogeny: the complex and changing forms of alternation of generation in animals and plants are also, mainly and in the most important respects, dependent on the necessity for making amphimixis possible. I say 'necessity,' because I hold that everything real is also necessary, and that this is true even of the things we generally call useful; for I believe that in nature the really useful—viz. that which is useful when considered in relation with the whole of its consequences and not by itself alone—is also invariably necessary. *The useful becomes necessary as soon as it is possible.* In this sense we may regard amphimixis as necessary because it obviously involves a deep and essential use.

Its unusually elastic powers of adaptation show how far it is from being necessary, viz. essential to life, in the usual sense of the word.

If amphimixis is truly rejuvenescence, i. e. the hindering of an otherwise inevitable death, we ought to find it as a fundamental process, occurring without a single exception. It is hardly necessary to say that this is not the case. Least of all ought its appearance to depend obviously upon external conditions of life. But this is certainly the case; *the periodicity of its appearance can be proved to depend upon adaptation.*

In many thousands of species of the higher animals amphimixis invariably makes its appearance at the outset of every generation, for no egg can develope without fertilization. This is true of the whole Vertebrate sub-kingdom. Isolated exceptions to this general law suddenly begin to appear in the group of the Arthropods. Certain eggs, in which we should have thought fertilization would be the necessary preliminary to development, have gained the power of developing unaided,—viz. the power of producing males alone (bees), while the same eggs, if fertilized, would produce females. In plant-lice, on the other hand, females emerge from unfertilized ova, and not one generation only, but two, three, and even many, succeed each other before a sexual generation occurs and, with it, amphimixis. How far this latter is from being a process of multiplication, and how superficial is the connexion which usually obtains between amphimixis and multiplication, are shown in the bark-lice, e.g. *Phylloxera.* In these it has already been mentioned that the sexual generation consists of minute animals devoid of mouth and of the power of taking food. The female lays a single egg, so that, as in the primitive form of conjugation, the number of individuals is not increased by reproduction, but diminished by half. Nature could hardly express with greater clearness the stress which she lays on amphimixis; nor could she argue in a more convincing way that increase is distinct from amphimixis, and that the quickening of new germs need not be dependent upon the latter.

If amphimixis were a process of rejuvenescence we could hardly believe that its occurrence in the life of a species would be so excessively fluctuating,—sometimes taking place in each generation, sometimes recurring after a lapse of two, three, or even as many as ten generations, sometimes being absent for forty generations, as I have proved to be the case in *Cypris reptans.* It might be suggested that the recurrence of amphimixis does not depend on the number of generations of individuals, but on the number of cell-generations, and that continuous life is rendered possible by the reappearance of amphimixis after each million or hundred thousand generations of cells. We might also—as I have already mentioned—compare the 'agamic' cell-generations of Infusoria, which follow each other between two periods of conjugation, with the collection of cells composing the person of a Metazoon, and regard the ontogenetic cell-series, as a whole, as the equivalent of the millions of individuals which make up an Infusorian colony. In both these cases the rejuvenating and quickening influence of amphimixis may be supposed to endure for a certain number of cell-generations. I must admit that I consider such reasoning to be bad 'philosophy of nature,' i.e. playing with words which convey no distinct meaning. It is contradicted by the fact that the cell-cycle of ontogeny in the lowest representative of the Vertebrata, the Amphioxus, cannot be compared as to length with that of the higher members of the group; it is equally disproved by the phenomena of cyclical development, showing that in one case the effects of fertilization may extend through one ontogeny, in another through two, three, six, or even ten ontogenies, not to mention the case in which forty generations have elapsed without the occurrence of amphimixis.

If we regard amphimixis as an adaptation of the highest importance, the phenomena can be explained in a simple way. I only assume that amphimixis is of advantage in the phyletic development of life, and furthermore that it is beneficial in maintaining the level of adaptation, which has been once attained, in every single organism; for this is as dependent upon the continuous activity of natural selection as the coining of new species. According to the frequency with which amphimixis recurs in the life of a species, is the efficiency with which the species is maintained; since so much the more easily will it adapt itself to new conditions of life, and thus become modified.

Amphimixis must first have appeared among unicellular organisms in the form in which we now find it in most Protozoa (Flagellata, Sporozoa, Rhizopoda)—namely, as the complete fusion of two entire animals[1].

[1] Maupas (op. cit. p. 492) attributes to me the view that conjugation bears a different significance in the lower Protozoa from that which it possesses in the higher, and he describes this 'manière de voir' as

Since this process is in direct antagonism to reproduction, i.e. increase, it can only be repeated after long intervals, lest it should prevent the sufficient increase of a colony of such animals. Hence we find that conjugation recurs periodically among the Protozoa; and indeed—as Maupas has taught us in the Infusoria—only repeats itself after a great many (120-300) generations.

Amphimixis, as we have seen, only became possible among Metazoa by concentrating or packing all the predispositions into the restricted area supplied by the nuclear substance of a single cell,—and this must happen even when the adult body is composed of millions of cells, differentiated in the most diverse directions, and combined to form tissues, organs, and systems. The result of this arrangement is seen in a highly complex ontogeny; and it is obvious that many conditions of life may arise which render it advantageous that the increase of the species should not proceed exclusively by this long and intricate, and therefore dangerous road, and that accordingly the origin of each new individual should not be necessarily bound up with amphimixis. In this way we are able to understand the wide distribution and diverse forms of asexual reproduction among the lower Metazoa and in plants.

There is, however, another factor,—the appearance, in the two last-mentioned groups, of that complex form of individuality known as the stock. This is brought about by the budding or division of the person, a form of increase which renders possible a continuity of the persons proceeding from one another. Such increase is not associated with amphimixis, because the indis-

'superficielle,' etc. I have never held such a view; the only passage in my writings which can have given rise to such a misapprehension deals with the phyletic origin of conjugation ('Bedeutung der sexuellen Fortpflanzung, p. 52, translated in vol. i, see pp. 293–294). Anyone who refers to this passage will find a hypothesis, expressed with all reserve, suggesting the original significance of the fusion of two unicellular organisms. Conjugation must have had some beginning, and although I believe that in its present form it signifies a source of variability, it must originally have had some other meaning, for two Monera would scarcely coalesce in order to ensure variability in their descendants. A change of function must have taken place, or, as Dohrn has very clearly expressed it, a secondary effect associated with the original main effect has, at a later date, usurped the place of the latter. Maupas accepts conjugation in the form in which it exists, and makes no attempt to understand how it originated. I do not blame him for this, but is it really so superficial to investigate the origin of any phenomenon?

pensable mechanical conditions are wanting. Hence, in the formation of stocks, amphimixis does not appear in every generation of persons, but only periodically in certain generations, and from this follows an alternation between two methods of increase, viz. with and without amphimixis, or, as it is called, an alternation of generation. Many principles come into action in this mode of development, which we cannot stop to consider, above all the gradual development of high individualisation in the stock, through the differentiation of its persons on the principle of division of labour, as was expounded many years ago, in a most convincing manner, by Rudolph Leuckart.

We can furthermore understand why a longer or shorter series of generations elapses before amphimixis becomes associated with increase: a long interval is the necessary consequence of the formation of highly differentiated animal stocks.

I need hardly say that I do not, by any means, intend to imply that no change in the method of reproduction can have arisen without stock-formation. In the groups of polypes and medusae, among which the above-mentioned alternation of generation is so widely spread, we find species which do not form stocks, and which, after passing through a series of generations by fission or budding, return to the method of sexual reproduction. It is clear that in such cases, the omission of a detailed and dangerous embryogeny, together with the more rapid multiplication which accompanies the omission, has been the efficient cause which has limited amphimixis to certain generations. The fresh-water polype, Hydra, is an example of this. The duration of the 'agamic' period is so regulated by the external conditions of life that the concentration of the collective predispositions of the species in a single cell, which is associated with amphimixis, is at the same time made use of to form a resting-egg, which carries the species over the unfavourable seasons.

The adoption of entirely different methods by closely allied animals shows how little the existence and duration of the periods of asexual reproduction have to do with the number of cells composing a single individual. In one and the same group of Hydromedusae we find species with long periods of asexual reproduction side by side with others in which it has entirely disappeared, so that every generation proceeds from fertilized eggs, and is therefore under the direct influence of amphimixis. It is well known that some Medusae are budded off from a polype-stock, and constitute the sexual generation of the latter, marking the end of a series of asexual generations; while other Medusae invariably arise from fertilized ova, and always produce eggs requiring fertilization, or, in other words, adapted for amphimixis.

The degree of organisation is, in yet another way, associated with the alternation of asexual with sexual generations, and thus with the periodicity of amphimixis. This new relationship between organisation and the recurrence of amphimixis, depends upon the fact that the asexual methods of reproduction by fission or budding are not possible in the highest and most complex Metazoa. They are only found in the lower groups of Metazoa, —the Coelenterates, Worms, and Echinoderms; disappearing in the Arthropods, Molluscs, and Vertebrates.

In these latter, we might well suppose that every act of increase would be connected with amphimixis; for,—since the structural complexity of the animals in question has rendered fission and budding impracticable and has therefore compelled a reversion to the unicellular germ and the occurrence of a detailed ontogeny in every generation,—it might seem probable that nature would not lose the advantage of connecting amphimixis with such a method of reproduction. We might therefore expect to find no exception to the occurrence of sexual reproduction in these groups. In this anticipation we should be deceived, inasmuch as it only appears in the great majority of cases. In the minority, amphimixis is very far from universal, in spite of a development from unicellular germs which would so easily have permitted it: furthermore, in this minority it was formerly connected with reproduction, and has been abandoned in different degrees. These cases of development from parthenogenetic eggs are, above all others, fitted to prove the importance of the principle of utility. The transformation of female sexual cells, at first directly adapted for amphimixis, into germs no longer requiring fertilization, is an artifice by which nature has contrived to avoid amphimixis when a high degree of structural complexity has prevented reproduction by fission and budding.

It may be remarked here that this suggestion supplies the answer to a difficulty which I was, for a long time, unable to solve—namely, *the remarkable limitation of parthenogenesis to a few definite groups.* It is only found in Crustacea, Insecta, and Rotifers, and not among Vermes, Coelenterates, and Echinoderms[1]: furthermore, it does not exist in the two higher groups of Molluscs and Vertebrates. The solution to the problem is found in the suggestion that the lower groups of animals dispense with parthenogenesis, because it is unnecessary to them. Whenever increase without amphimixis became advantageous, it was more readily and better supplied by fission and budding. The absence of parthenogenesis in the higher groups of animals may probably be explained on the supposition that no force has appeared which would render it advantageous for amphimixis to be separated from the existing method of increase. This is especially clear when we investigate the grounds on which it must have become advantageous among the Arthropods.

The periodical occurrence of unfavourable conditions of life has often been suggested as the cause of the appearance of parthenogenesis in Arthropods and Rotifers. I need only refer to my already quoted work on *Daphnidae*, in which this question is considered at length. Whenever a species lives scattered over a small area subject to rapidly changing external conditions which are, for a short time, favourable to life and multiplication, and then suddenly become unfavourable or even destructive,—it must be a great advantage for the increase of individuals to take place with the greatest possible rapidity during the favourable periods. As indicated in my former work, the advantage of parthenogenesis in such cases lies in the fact that multiplication must become many times more effective when every individual is a female, or, to express the thought in more general terms, when every single germ-cell can produce a new animal. A further acceleration ensues from the omission of that retardation of development which is implied by the occurrence of copulation and fertilization.

From this point of view we can not only explain the appearance of parthenogenesis in general, but also its special form in

[1] I am aware that it is believed to occur in some Coelenterates, but it seems to me doubtful whether any true parthenogenesis takes place. And, in any case, isolated exceptions do not invalidate the significance of the rule.

particular cases. In those Daphnids which, like the species of *Moina*, inhabit small rapidly filled, but also rapidly drying pools, the number of purely parthenogenetic generations which succeed one another after the foundation of the colony, is small. In *Moina paradoxa* and *M. rectirostris* males appear in the second generation, and some of the females produce resting-eggs which require fertilization. If this did not occur, if sexual reproduction, viz. multiplication associated with amphimixis, did not take place very soon after the foundation of the colony, it would frequently happen that the latter would be destroyed by sudden drought, without the formation of resting-eggs to carry life in a latent condition over an unfavourable period, and the colony would simply perish. It may be urged that parthenogenetic eggs might have been provided with resting shells like those which are, as a matter of fact, found in other Phyllopods, for example *Apus*. But clearly the object is to confer upon the species the advantage of periodically repeated amphimixis, and this is therefore connected with the formation of resting-eggs, and reproduction is so regulated that the number of parthenogenetic generations is determined by the average duration of the favourable periods of life. Thus, among the marsh-dwelling Daphnids numerous purely parthenogenetic generations succeed each other before a sexual generation appears, while in those which inhabit lakes and are subject to uniform conditions of life interrupted only by the cold of winter, the cycle is still longer. In some species amphimixis may be entirely abandoned, and this seems to occur most readily in those which produce but one kind of egg, which must naturally be provided with a protective resting shell, rather than in those forming two kinds of eggs, of which only one is a resting-egg and requires fertilization. Thus it is well known that most of the colonies of the common *Apus cancriformis* are purely parthenogenetic, and the same is true of the greater number of fresh-water Ostracodes.

Ten years ago, when I first directed my attention to the parthenogenesis of these minute Crustacea[1], I was able to distinguish three stages of reproduction,—the first was found in

[1] Zoologischer Anzeiger, 1880, p. 72. 'Parthenogenese bei Ostracoden.'

such species as *Cyprois monacha*, of which every generation reproduces sexually; the second was found in those species in which numerous parthenogenetic generations alternate with a sexual one; and finally the third included species in which males have not yet been found: in one such species (*Cypris reptans*), forty consecutive purely parthenogenetic generations have been observed.

We cannot yet decide why the advantages of amphimixis have been entirely given up in this and other cases. We cannot at present solve, or even profitably discuss, every biological problem. But it is probable that we are dealing not with adaptation alone, but perhaps with a suppression of amphimixis by means of parthenogenesis. Everything which is desirable is not possible; and after parthenogenesis has once been incorporated in the hereditary tendencies of a species, circumstances may arise in consequence of which it may be transferred, by the power of heredity, to the remaining sexual generations also, without the possibility of any interference on the part of natural selection. Whether this explanation is in the right direction or not, it is at any rate clear, as regards the question under discussion (viz. the true significance of amphimixis), that the loss of an *advantage* may be intelligible in many ways, while the loss of a *process of vital rejuvenescence* must stand in direct opposition to the continuance of life.

It would be of the highest interest to consider more closely the various cases of parthenogenesis, from this point of view: we do not, however, possess sufficiently accurate knowledge of the vital relations of the animals in question to enable us to estimate the advantages conferred by the disappearance of amphimixis, or rather the introduction of parthenogenesis, in a larger or smaller number of generations. I may, nevertheless, be permitted to afford some indication of the line of argument.

Parthenogenesis plays an important part in the group of plant-lice and bark-lice, containing very numerous species. The ova may be deposited or may undergo embryonic development within the body of the mother. In either case the advantage of parthenogenesis depends, as in the Daphnids, on the extraordinary rate of multiplication, which naturally reaches the highest point in the viviparous *Aphidae*, because the offspring actually produce embryoes within their own bodies before they are born. But here we have to do, not so much with the sudden termination of a limited and changeful developmental period, as with the greatest possible use of the opportunities afforded by an extremely rich nutriment of vegetable juices. The excessively rapid multiplication ensures the colony, and therefore the species, from destruction at the hands of its numerous foes, which, just on account of the abundance of food provided by the vast increase of their prey, become themselves still more numerous, so that the multiplication of these plant parasites must be carried on at the highest possible rate. Hence we find that many purely parthenogenetic generations succeed each other, while amphimixis is ensured by a single generation of males and females, appearing towards the close of the period in which the richest nutriment is supplied.

On the other hand, we find that in many *Cynipidae* a parthenogenetic alternates with a sexual generation, and it generally happens that the latter appears in the summer, and the former in spring or even winter. The often considerable structural divergence between these two generations depends upon the very divergent conditions of life to which they are respectively exposed, and above all upon the fact that the eggs are laid in various, differently formed parts of plants, necessitating therefore a corresponding difference in the ovipositing apparatus. But such considerations need not detain us here. The benefits conferred by the absence of amphimixis from the winter generation appear to me to follow from the exceptionally unfavourable conditions of life by which it is beset. Many of these small Hymenoptera, e. g. *Biorhiza aptera*, emerge in the very middle of winter, on warm days in December or January, and creep upon the oak-trees, laying their eggs in the heart of the winter buds, having laboriously bored through the hard protective scales with the ovipositor. Without taking food, and frequently interrupted by cold and the long nights, they carry on this work until all their eggs are safely deposited or until death from snow or cold puts an end to their labours. It is clear that such hard conditions must prove fatal to many of these insects before they have fulfilled their task, and it must conduce greatly towards the maintenance of the species, not only for all the time occupied in selection by the sexes and in fertilization to be saved, but also for every survivor in the struggle to be capable of laying eggs with the power of developing unaided, in other words for every such animal to be a female.

Much might still be said as to the causes of the omission of amphimixis from one or more generations, but a few words will suffice to show that the appearance of parthenogenesis depends upon adaptation to the conditions of life,—*that reproduction without amphimixis has invariably originated from sexual reproduction, whenever it was required in order to gain some distinct advantage in the effort to maintain the species.* We may well assume that the advantages which the appearance of parthenogenesis must confer, outweigh the disadvantages involved in the giving up of amphimixis. Our estimate as to the effects of the latter is far less certain and precise than of the former. If, however, I am not mistaken in my views on the significance of amphimixis as the source of individual variation, it follows that its omission from a single generation or even from a series of generations may be easily compensated; for it always reappears, and mingles afresh the complex individual predispositions into new combinations. The injury caused by its withdrawal would be less as the fertility of the species was greater; with this is connected the fact that *parthenogenesis is chiefly found in very prolific species.* Those individuals which sink below the level of organization characteristic of the species could the more easily be eliminated in the struggle for existence without in any way endangering the life of the species. Perhaps this explains why, in some few species of Crustacea (*Cypris*) and of Insecta (*Rhodites rosae*), amphimixis has utterly vanished without having caused, up to the present time, any trace of degeneration in the species.

We may safely assume that the entire absence of amphimixis is to be primarily explained as an adaptation, and that the alternation between sexual and asexual multiplication met with in Hydromedusae, Cestoda, &c., has arisen from the demands made by the conditions of life,—demands similar to those which have determined the alternation between monosexual and bisexual generations found in Insecta, Crustacea, &c. In both classes of cases amphimixis has been restricted to certain generations because it was not necessary in all of them, and because such restriction was a great advantage, The means by which this limitation is exercised are different in the two classes, not by any means because parthenogenesis could not have been introduced among the lower Metazoa, but because nature did not require it, but resorted to the far more practicable and flexible methods of fission and budding. When these ceased to be available, she was compelled to alter the sexual cells in such a way that their powers of development were no longer connected with amphimixis.

There are indeed no plants wholly devoid of the power of reproduction by buds. Not only the formation of stocks but also the copious increase of persons and stocks[1] by means of buds is everywhere at the disposal of nature, and she has made a lavish use of them. With this is probably connected the fact that parthenogenesis is unusually rare in plants and only occurs in a few groups. I must leave it to abler botanists to investigate the grounds upon which unicellular germs, originally adapted for amphimixis, have been, in certain exceptional cases, afterwards transformed into parthenogenetic germs. The alternation of generation, so prevalent among the lower classes of plants, takes a form somewhat different from that found in the lower groups of animals, inasmuch as, not only the multiplication which is associated with amphimixis, but also that which is without, viz. agamic, depends upon unicellular germs. Ferns, Mosses, and Lycopodiums produce vast quantities of spores, the unicellular nature of which certainly does not follow from any former connexion with amphimixis in remote ancestors. It is far more probable that the unicellular condition has proved necessary in order to confer other advantages which, as has been suggested above, depend upon a minute size:—the lightness which facilitates transport by wind and water, and the possibility of production in enormous numbers.

In conclusion, it has been shown that amphimixis is everywhere present among the vital phenomena of a species when its existence is without injury to other vital interests,—that it appears, in the Protozoa, independently of reproduction, when a connexion with the latter was possible but unnecessary,—and that, in the Metazoa, it is bound up with reproduction, inasmuch as its existence only thus became possible. It has

[1] For a definition of this term see page 213.

further been shown that its occurrence in the life of a species becomes more frequent according as its admission by the vital conditions does not entail other disadvantages. When neither the formation of stocks nor the most rapid multiplication of individuals in the shortest time is required, we find amphimixis connected with the origin of every new individual ; but whenever the existence of the species would be endangered if new generations could not arise from the old in the most rapid succession and without any interval, we find that amphimixis is not inseparably associated with every act of reproduction, but makes its appearance only in certain generations. All this clearly points to the conclusion that amphimixis is no indispensable vital condition, no renewal of life or 'rejuvenescence,' but a process which has indeed a deep significance, although it is not inseparable from the continuance of vital processes. This conclusion becomes even more evident when we recognize how precisely, in the alternation of agamic and sexual reproduction, the number of agamic generations is regulated so as to correspond with the conditions of the species. *The rare or frequent repetition of amphimixis in the life-history of a species is not determined by its physical nature but by the conditions of life.* Its regulation depends upon adaptation ; it may be entirely excluded and the life of the species still continues. I do not know of any facts which lead us, after recognizing all this, to assume that amphimixis is anything more than an essential advantage in the maintenance and modification of species.