But this latter process renders *two* 'reducing divisions' necessary,—that is if the normal number of idants must be reduced to one half.

That there is no such reduction in regular parthenogenesis may be inferred from the large number of idants present in the parthenogenetic eggs of *Artemia salina*, viz. twenty-four or twenty-six. If a diminution to one half of the original number of idants normal for the species took place at each maturation, it is obvious that in each successive generation the idants would be reduced to half, and we should at the present day find only a single one left in *Artemia*. Either this polar division is not a 'reducing division,' or it is preceded by a doubling of the number of idants, just as in ova which require fertilization.

If this latter be true, it follows that in parthenogenesis we meet with a simple retention of the first of the two polar divisions which occur in other ova.

It is unfortunate that direct observation has not hitherto led to an entirely certain decision upon the point. Dr. Otto vom Rath has had the great kindness to examine, with this object in view, many of my old sections[1] of the parthenogenetic ova of *Artemia salina*, in order to find out those parts of them which were most important in this respect. From my earlier researches, conducted upon the same material, I was already aware that the germinal vesicle, after having approached the surface, contains a large number of chromatin granules, which are distributed with almost complete regularity. It was evident that these granules had not yet become the definite chromatosomes or idants, but that they were smaller and more numerous (Fig. IX. 1). In one germinal vesicle I counted 115 of them; in another, which was already changing into a spindle, I also found 115, all lying in the equatorial plane (Fig. IX. 2); in a third, 77; in a fourth, 70; and in a fifth, 57. Now in the equatorial plate of the polar spindle, from 48 to 52 spherical idants are always arranged in a double wreath (Fig. IX. 3 *a*). These must therefore have arisen from the fusion of several of the primary chromatin granules, and the great variation in the number of the latter must depend on the fact that the fusion was

[1] Weismann und Ischikawa, 'Weitere Untersuchungen zum Zahlengesetz der Richtungskörper;' Zoologische Jahrbücher, Bd. III. p. 575, 1888.

much further advanced in some of the germinal vesicles examined than it was in others. Half the number of 48 or 52 idants in the equatorial plate pass to one, and the other half to the other pole. If a diminution in the ids be characteristic of a 'reducing division,' it follows that this term can only be applied to the process which has just been described in *Artemia*, if the whole number of 48–52 idants have arisen directly from the primary chromatin granules: if, on the other hand, only 24–26 idants were so derived, and the equatorial plate was at first composed of a

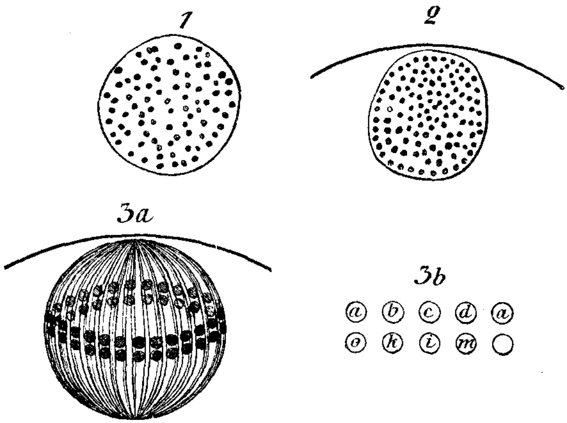

FIG. IX.

Artemia. Germinal vesicle of the parthenogenetic egg before and during polar division: partially diagrammatic, from my own preparations.

1. Numerous chromatin granules scattered through the whole thickness of the germinal vesicle. 2. Numerous chromatin granules (115) collected in the equatorial plane. 3 *a*. The same arranged in a double wreath of 52 idants in the polar spindle. 3 *b*. A part of the double wreath with the separate idants indicated by letters.

single wreath which was subsequently doubled by division of the idants, it would follow that the process would be an 'equal division.' In the latter case, the two idants lying over each other would be identical, i. e. composed of similar ids, and identical idants would pass into each daughter-nucleus. If, however, as in the former supposition, the two adjacent idants were independently derived, and therefore composed of different separate ids (chromatin granules), it is clear that the idioplasmic construction of the two daughter-nuclei must be different.

Inasmuch as we cannot see whether the chromatin granules are made up of similar or different idioplasm, it follows that direct observation cannot conclusively settle whether we are dealing with an 'equal' or a 'reducing division.' Perhaps, however, we may succeed in decisively answering the question by other means, and investigations have already been undertaken with this special object; for the present we must rest content with conclusions based upon probability. Before everything we must make certain that the first division in eggs requiring fertilization is, in all cases, a 'reducing division.' At the present time *Artemia* reproduces sexually in many of its colonies, and hence in parthenogenetic colonies in which the eggs have lost the second polar division but have retained the first, it may be regarded as probable that the latter has kept its original form, i. e. that of a 'reducing division.'

Still further support for the above conclusions is found in the fact that Dr. vom Rath could never find *single* idants in the equatorial plate of the polar spindle of *Artemia*, but only *double* ones, each having the form of two large round bodies lying over each other (Fig. IX. 3 *a*).

If we now further consider that, at the commencement of the change of the germinal vesicle into the spindle, the chromatin granules lie scattered through the whole thickness of the former (Fig. IX. 1), and that they then fuse with one another, arranging themselves as a single layer in the equatorial plane of the spindle, in the form of an oval disc and not that of a simple wreath (Fig. IX. 2), and if we remember that they then pass into the arrangement of a double wreath (Fig. IX. 3 *a*), we are led to conclude that no two idants of this double wreath have arisen from the doubling by division of a single idant, as is the case in the usual 'equal division'; but that the idants of the oval equatorial plate, which arose independently of one another, have subsequently come to place themselves one upon the other in the form of a double wreath. If this conclusion be sound we have to do with a true 'reducing division.'

Hence we are justified in assuming as the most probable conclusion that a 'reducing division' takes place, and furthermore a division which is preceded by a doubling of the idants.

If this be so, we cannot doubt that the effect of the process must be similar to that which follows the corresponding processes in eggs which require fertilization, viz. the arrangement of idants in fresh combinations, as I attempted to show in the first chapter. We are thus led to the view that *in parthenogenetic as well as in sexual eggs a change may take place in the constitution of the germ-plasm during successive generations.*

If we start from that point in phyletic development at which parthenogenesis was first established, each idant in the original egg-cell was at that time composed of a series of different ids. Then, for the first time, these idants were not diminished to half the total number by two polar divisions, but, after being doubled in the egg-mother-cell and again reduced to half by the first polar division, their number in the mature ovum became the same as in the original egg-cell (see Fig. VIII). By this means a fresh combination was rendered possible and indeed unavoidable, unless we assume that the constituents of each pair of similar idants, which arose from the doubling of the previous idants, separated and united with those of the other pairs, forming two exactly similar groups which then respectively entered the two daughter-nuclei. This would be the result of an 'equal division' of the nucleus. Such a division is attained and ensured precisely because the doubling and division of the idants only takes place when they have already become arranged in the equatorial plate; but whenever the doubling has occurred beforehand, as is the case here, the two halves of an idant may indeed be occasionally shared between the two daughter nuclei, but they may also, just as readily, both pass into one and the same daughter-nucleus. From this freedom in the distribution of the idants follow the fresh combinations produced by the 'reducing division;' and the difference between an ordinary nuclear division, and the 'reducing division' which here takes place, depends essentially on the fact that, in the latter, *there is a shifting of the time at which the doubling of the idants occurs.*

Hence, if a species of *Artemia,* which had hitherto reproduced bisexually, were now to become parthenogenetic, then in spite of the cessation, for all future time, of the mingling of the idants of the ovum with those of the spermatozoon, it would by no means follow that the offspring of a female would necessarily become 'identical twins.' With twenty different idants, if there are not the 377 million different combinations which calculation indicates, there would be nevertheless such a vast number of different combinations of idants, that two ova produced by the same mother could only rarely be identical. Among all the possible combinations, that very one might arise which existed in the original egg-cell of the mother herself and became expressed in her somatic cells. Such a combination would contain one idant of every kind, and such an ovum would give rise to an individual 'identical' with the mother, that is, to one similar to the mother in all respects except as regards those modifications of the inherited developmental tendencies, which are called forth by external circumstances.

We need not consider the unlikely suggestion, that all combinations are equally probable; if only it be conceded that any degree of difference is possible for the combinations of the germ-plasm, remarkable consequences follow. In the first place it appears that, in persistent pure parthenogenesis, the *number of different idants contained in the idioplasm must steadily diminish*, although perhaps at a very slow rate. If the number did not diminish new combinations could never arise, and that of the first parthenogenetic mother (A) would be retained indefinitely,—thus if there were twenty different idants ($a, b, c, d, e \ldots\ldots t$) the whole series would persist unchanged. If, however, another combination arose in the daughter (B), for example $a\ a\ b\ c\ d\ e \ldots\ldots t$, this would be brought about by one of the idants (a in this instance) becoming double, and then inasmuch as the total number of idants must remain the same, it follows that one of the others must be absent (for example l), or the number would be twenty-one instead of twenty. As a result of this the idant l would be wanting in all the descendants of B. If now we suppose that such a new combination, arising in this way by the omission of one idant and the reduplication of another, would not be formed in each generation, but only in every tenth, it follows that at the end of each series of ten generations, a fresh combination will arise by another omission and another reduplication, and so on, so that after a hundred generations the number of *different* idants would have been diminished from twenty to ten, and the whole group would consist of ten pairs, for instance *aa*, *bb*, *cc*, *dd*, *ee*, *ff*, *gg*, *hh*, *ii*, *kk*, the idants in each pair being identical. In the course of later generations the number of different idants might be diminished still further, although more gradually.

We are thus led to believe that, in persistent parthenogenesis unbroken by bisexual reproduction, a great uniformity of germ-plasm will at length arise, and, as a result, a great uniformity of individuals. We cannot doubt this if we consider that each fresh simplification of the germ-plasm, when it has once appeared, is unable to revert towards complexity because fertilization, i. e. the introduction of foreign idants, is excluded. As soon as the 'reducing division' causes a single one out of the twenty maternal idants in the segmentation nucleus of the egg to become double, it has been shown above that one of the other idants must be irretrievably lost not only to the maternal germ-plasm and to the daughter, but also to the descendants of every generation. Among all the numerous possible combinations there is only one which leads to no diminution in the number of different idants, viz. the above-mentioned arrangement *a*, *b*, *c*, *d*, *e*, ... *t*, and this is an exact repetition of the maternal combination. Hence the diminution in the number of different idants is far more probable than the maintenance of the complete series, and this probability will be repeated in each successive generation, until only two kinds of idants remain in the germ-plasm. When, however, this point is reached[1], the reverse becomes true; for the probability that idants *a* alone, or *b* alone, would be left in the egg-nucleus by the 'reducing division' is much less than that both kinds would exist side by side.

This becomes clear if we consider a definite case. Instead of the twenty idants which have been assumed hitherto, let us take only half as many, viz. ten, and let us suppose that they have been already reduced to two different kinds, *a* and *b*. These double themselves in the mother-egg-cell to twenty—ten *a* and ten *b*. The following combinations are then possible for

[1] Even before this point is reached the probability begins to change.—A. W. 1892.

the germ-nucleus[1] of the egg produced by the 'reducing division,'—$10a$; $9a+1b$; $8a+2b$; $7a+3b$; $6a+4b$; $5a+5b$; $4a+6b$; $3a+7b$; $2a+8b$; $1a+9b$; $10b$.

Hence we see that out of eleven possible combinations there are only two which contain one kind of idant alone: all others contain both. In the case of twenty idants there are only two out of forty-one combinations which contain either *a* or *b* alone; with forty idants, only two out of eighty-one.

Naturally this does not imply that the diminution to one kind of idant is improbable, but only that it would always remain largely in the minority, i.e. it would be found in relatively very few cases among the numerous eggs of the same mother. This must, however, change in the course of generations; for only in one out of the eleven combinations are *a* and *b* present in equal numbers, and only in the descendants of this single variety will the germ-plasm be chiefly made up of *a* and *b* in equal proportions: in all the other ten combinations, either *a* or *b* preponderates, and according to the extent of preponderance is the probability of a greater or less number of eggs which contain only *a* or only *b*. We may therefore maintain that, by continued parthenogenesis, the germ-plasm becomes ever simpler as regards its composition out of ids until it comes to consist of only two kinds of idants, but when once this composition has been reached it may be retained through long periods of time, during which there will be a changing majority, sometimes of one and sometimes of the other kind. Among the eggs of such a female there would always be some in which the germ-plasm would contain only one kind of idant.

Observations on Inheritance in Parthenogenesis.

When I developed the idea that the essential meaning of sexual reproduction was to ensure that amount of individual variability which is necessary for the phyletic development of the organic world by means of natural selection, I inferred that uninterrupted parthenogenetic reproduction would prevent the

[1] I have employed Strasburger's term 'germ-nucleus' instead of 'segmentation nucleus' which has been commonly used up to this time, as a general term for the nucleus of the mature egg from which embryonic development proceeds, whether parthenogenetic or amphigonic.

adaptation of a species to new conditions of life [1]. I argued that, the repeated mingling of two individualities being requisite to supply the process of selection with the necessary choice of combinations of individual qualities,—it follows that a choice of sufficient range will not be supplied when one and the same set of combinations are passed on by parthenogenesis, through long series of generations, to an ever increasing number of individuals. A number of 'identical' individuals would thus arise, that is individuals which contain a precisely similar fundamental stock of hereditary predispositions, and which, at most, can only be distinguished by transient peculiarities, viz. by those which are the consequence of external influences of various kinds upon the body during its progress towards maturity or after maturity has been reached. When writing on this subject, I expressed the opinion that 'all species with purely parthenogenetic reproduction are sure to die out; not, indeed, because of any failure in meeting the existing conditions of life, but because they are incapable of transforming themselves into new species, or, in fact, of adapting themselves to any new conditions [2].' I stated this conclusion in the strongest possible way although I thought that it might perhaps require subsequent modification, because, even at that time, I had already considered the possibility that the consequences of sexual reproduction of ancestors might affect their purely parthenogenetic descendants. But whether a simple rearrangement of the ids within the idants would suffice to call forth a fresh combination of individual peculiarities, appeared to me very doubtful; and yet this would have been the only alteration in the germ-plasm which we could have been led to suggest by the state of our knowledge at the time; for a 'reducing division' could not have been supposed to take place in parthenogenetic eggs, because we did not know that the number of the idants doubles before the occurrence of the first polar division, and because a halving of the number of idants, without any previous doubling, would necessarily, in a few generations, diminish their number to one. But now the case is different, and we may affirm that in parthenogenetic

[1] 'Die Bedeutung der sexuellen Fortpflanzung.' Jena, 1886, p. 58. Translated as the fifth essay. See Vol I. p. 298.

[2] See Vol. I. p. 298.

generations, the combination of idants in the different germ-cells of one and the same mother can vary. We can therefore attribute even to parthenogenetic species a certain power of varying, although not to anything like the same extent as in bisexual species.

By the year 1884 I had commenced a series of experiments to decide the question of variability in purely parthenogenetic species. These experiments are still being carried on, and I hope that I may ultimately be able to make a more complete communication upon the subject. I chose for the purpose a species of *Cypris* (Ostracoda), which was characterized by striking and easily seen markings on the shell. I had at my disposal two very differently marked varieties of the species in question (*Cypris reptans*), which had been found in the natural state. The species appears to be purely parthenogenetic in this locality; at any rate I have never found a male, nor a female with spermatozoa in the *receptaculum seminis*[1]. The latter fact conclusively proves the complete absence of males; for in colonies of those species of *Cypris* which possess males, we always find the *receptacula seminis* of mature females filled with spermatozoa. Even if it were a mere coincidence that of the many hundreds of individuals examined, all proved to be females, the presence of spermatozoa in their *receptacula* would still have shown the presence of males, if any had existed in the locality. But the *receptacula* were, without exception, empty, at all times of the year, and under all the external conditions which obtained during my investigation of the colony.

My two sub-species are distinguished as follows (see Fig. X): variety *A* is lighter in colour, and there are only a few dark green spots of small size on the clay yellow ground-colour of the shell. Variety *B* appears dark green because the spots are so much larger that they expose only a little of the clay yellow ground-colour of the shell. In both varieties the spots agree precisely as to number and position; the difference between them is entirely quantitative, but it is considerable, so that the lighter *A* can be distinguished from the darker *B* with the naked eye at the first glance.

The experiment was conducted in the following way: I

[1] Compare my earlier paper 'Parthenogenese bei den Ostracoden;' Zool. Anzeiger, Bd. III. p. 81, 1880. See also Vol. I. p. 301, *note* 2.

placed a solitary individual in a small aquarium, and allowed it to multiply until the whole vessel was full of mature, egg-producing descendants. All the individuals of the colony were then passed in review, and the greater number were killed and preserved, one or more having been selected for breeding, and these were placed separately in fresh aquaria. In this way, in the course of seven years, many thousand individuals have passed through my hands; for the animals breed very rapidly and at all times of the year.

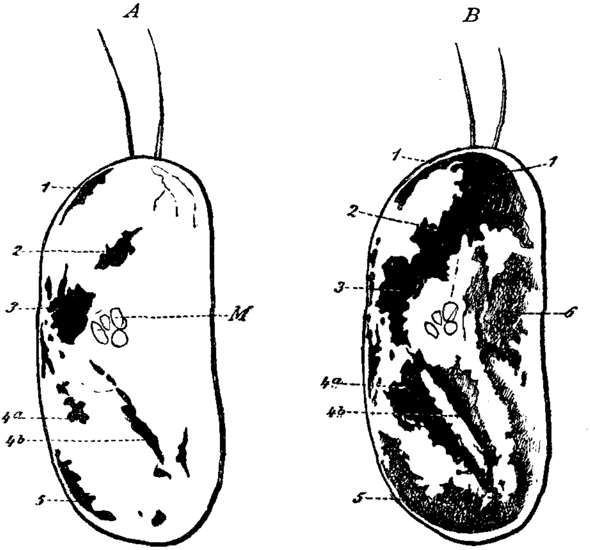

FIG. X.
Cypris reptans, Varieties *A* and *B*.

The first and most remarkable result is *the fact that the descendants of any one individual bear a very close resemblance to each other and to their ancestor.* I was not able to find any individuals which were precisely alike, although at first sight it often seemed that such was the case: minute differences, however, invariably existed as far as my observations reached, although they were often so small as to lead to the doubt whether they were due to different predispositions or to different nutriment, etc. And indeed no two individuals, not even 'identical' human twins, can be exactly alike in this latter respect. Furthermore, as a rule, no changes made their appearance in course of the numerous generations during which the examination lasted, with an exception which will be immediately described. I now possess colonies of *A*, as well as of *B*, which cannot be distinguished from their ancestors in 1884, and which have therefore retained precisely the same markings as those of the original animals. If we reckon six generations to the year,—a number by no means excessive for breeding which took place in a room,—about forty generations will have been passed through since 1884.

I attempted at first to produce the two forms by artificial selection, breeding from the darkest individual of a colony of the variety *A*, and from the lightest of a colony of *B*, in the hope that, perhaps, in the course of generations, one variety might be changed into the other. But I obtained no decisive results, perhaps because I did not make my selection rightly; for the individuals are so very similar that it is often difficult and indeed hardly possible to decide upon those which possess the larger spots: perhaps also I mistook transient differences for inherited ones,—a confusion which, naturally enough, cannot be avoided.

I was therefore all the more astonished to find, in 1887, some individuals of the dark green variety *B* in the same aquarium with the light variety *A*, and therefore side by side with typical, light, clay-coloured individuals. At first I thought, although it was most improbable, that these had been accidentally introduced, but the greatest care had always been exercised in all these experiments. Furthermore, after the most painstaking precautions against such accidents, precautions which prevented all possibility of the eggs being misplaced, there presently appeared another similar case in a different aquarium containing the variety *A*, and, later on, yet another. In this last case it was possible to find in the aquarium intermediate forms between the two varieties, which had been wanting on the previous occasions. Again, in May of the present year, 1891, another case was observed in which a single animal, distinctly belonging to the dark sub-species, suddenly appeared among 540 mature *Cyprides* of the light variety. Five descendants of this individual closely resembled their mother.

For a long time I waited in vain for the converse result, viz. the appearance of light individuals of the variety *A* among those of the dark sub-species *B*, and I was coming to the opinion that the latter was the original form of both varieties, when, in the winter of 1890-91, a few typical individuals of *A* were found in a colony of the sub-species *B*, which had bred true for many years. This colony had arisen from a single dark individual which, in the course of seven years, had produced many hundreds of descendants all of the typical dark variety.

We might perhaps refer to the changing influence of external circumstances as an explanation of these divergences from the type, but any such interpretation is entirely excluded, because both forms made their appearance side by side in the same aquarium and under precisely the same external conditions. These remarkable phenomena must certainly be ascribed to internal causes, viz. to changes in the composition of the germ-plasm. The required explanation is by no means difficult when the subject is studied from the point of view afforded by the theory of idants: in fact these observations seem to me almost a proof of the validity of the opinion expressed above that a 'reducing division' occurs in parthenogenetic development, and that by its means a fresh combination of idants is brought about.

The fact that the variety *A* passes into *B* and conversely, *B* into *A*, leads to the conclusion that both types originated at a time when parthenogenesis was not the exclusive method of reproduction: had this been the case, the ids *a* could not have been included in the germ-plasm of animals of the type *B*, and conversely the ids *b* could not have existed in the type *A*. The explanation of the existence, side by side, of both kinds of ids, is only to be found in sexual reproduction which must have taken place at no very distant time.

Let us assume the simplest possible relationship, viz. that there are only four idants in the germ-plasm, of which three are wholly composed of ids of the type *A*, and one of ids of the type *B*. The four idants, *a a a b*, of the primitive germ-cell become doubled in the mother-germ-cell by longitudinal splitting, and give rise to the eight idants, *a a a a a a b b*. Let us further assume the most favourable case for reversion towards the variety *B*, a reversion which would be possible in an egg in which the 'reducing division' takes place so that the combination of idants, *a a a a*, is removed in the polar body, while the combination, *a a b b*, remains in the germ-nucleus of the ovum. The primitive germ-cells of the next generation contain the same combination, *a a b b*, which is doubled in the mother-germ-cells to *a a a a b b b b*, and it is now clear that a 'reducing division' might occur, which would bring the four idants, *b b b b*, together into the germ-nucleus of an ovum, and from an egg containing germ-plasm with this constitution there must undoubtedly arise an individual of the variety *B*.

In this illustration, which is of course far too simple, reversion to the other variety might happen in the third generation. In those cases, however,—and they are the usual ones,—in which the number of idants is larger, and the proportion of variety *b* much smaller, the exclusive predominance of the latter can only take place far more slowly, and, as a rule, in much fewer cases; for it depends upon the chance of a combination of several idants *b* arising in certain ova, and of the survival to maturity of the individuals which develope from such eggs,—and these naturally must be far rarer than those with a largely predominating number of idants *a*. Furthermore, there is no certainty that, among the eggs produced by such individuals, any with an increased proportion of idants *b* would find a place.

These theoretical considerations harmonize well with the results of experiment. Variety *A* can give rise to descendants belonging to variety *B*, but this does not happen in all broods, and often only after the lapse of numerous generations. And the same is true of variety *B* in relation to the production of variety *A*. In both cases, relatively few individuals change into the other variety, and never all the descendants of one mother. In the aquarium in which such a transformation has occurred numerous individuals of the original form were invariably present,—a proof that it is always a rare exception for such extreme combinations of germ-plasm to be formed. When, however, this combination had once arisen, then such an individual gave rise, in all the cases observed, to offspring of *her own* type. Thus a mother which arose from variety *A*, but has passed over to variety *B*, behaves as though her ancestors had belonged to the latter type. She produces offspring of the variety *B*, and the type is retained for many generations. In the illustration described above the type *B* would be retained indefinitely; for I assumed that only four idants were present, and that all these became of the variety *B*. In reality, however, this would occur but seldom, since the constitution of the germ-plasm must be far more complex: not only are the idants more numerous, but their composition out of ids does not remain entirely the same throughout long periods of time, as I have attempted to show in the first part of this essay.

If the idants are not entirely unchangeable in this respect, if, when they are freshly formed out of ids scattered through the nuclear network, there is an occasional alteration in the arrangement, we might then even assume that, by such displacements, a germ-plasm *a* which contains no purely *b* idants, but only a few ids belonging to the latter variety included within the *a* idants, could, nevertheless, in course of generations, undergo reversion to the variety *B*. But these are niceties, which it is as yet too early to consider; for we are only on the threshold of knowledge concerning hereditary phenomena in parthenogenesis.

But something at any rate has been proved; for we can safely affirm *that in parthenogenesis individual variation exists, which, as in bisexual reproduction, has its foundation in the composition of the germ-plasm itself, and thus depends on heredity, and is itself inheritable.* I thus erred in former times, in believing that purely parthenogenetic species entirely lacked the capability of transformation by means of selection; they do possess this power to a certain extent. I was, however, right upon the main point; for their capability of transformation must be much smaller than in bisexual species, as is evident from the observations described above as well as from theoretical considerations. The latter indicate that, in the course of generations, the constitution of the germ-plasm must ever become simpler; while the observations confirm this suggestion, inasmuch as they prove that a remarkable similarity exists between the descendants throughout numerous generations. The advantages of that complex intermingling of many individual predispositions which was brought about in the amphigonic ancestors of parthenogenetic species become gradually lost, and we may maintain that *purely parthenogenetic species lose the capability of modifying themselves, more completely, the longer the pure parthenogenesis has continued.* So far as we can at present decide, this conclusion is in agreement with facts; inasmuch as no highly developed group of the zoological system, rich in species, is ever entirely composed of purely parthenogenetic species. In the animal kingdom, the Phyllopods and Ostracodes, among the Crustacea, are especially remarkable for the frequency of parthenogenetic reproduction. But *pure* parthenogenesis only occurs in isolated species, as in the above mentioned *Cypris reptans* and many other species of the same genus. Among the Phyllopods I only know of one species, *Limnadia Hermanni*, in which a male has never been found, and it is this very species which seems to have become extremely rare. In the other parthenogenetic species, in addition to the purely parthenogenetic colonies, there are always some which are composed of both sexes, as in *Apus cancriformis*; or else a regular alternation of parthenogenetic with bisexual generations takes place in the colony, as in almost all known species of Daphnids. The rich development of these groups of the zoological system has arisen under the uninterrupted influence of amphigonic reproduction, by means of which variations have been mingled together. It is just the same with the *Aphidae* (plant-lice and bark-lice), and with the *Cynipidae.* All these groups of animals contain a great variety of species, but, in all, a combination of individual characters takes place from time to time through the fertilization of ova, even though, as is often the case, many purely parthenogenetic generations intervene between the bisexual ones.

I believe that we find, in the tenacious retention of amphigonic reproduction by such species as the *Phylloxera,* a strong support of the validity of my theory as to the meaning of sexual reproduction. Those who still recognize in fertilization a renewal of vital strength, a rejuvenescence, do not require this conception of amphigony as an ever springing well of hereditary individual variation in order to understand its remarkable persistence. But those who agree with me in believing that the parthenogenesis of *Cypris reptans* which endures for forty consecutive generations is the refutation of any such idea of rejuvenescence, will hardly find another explanation of this tenacious persistence. Thus, let us call to mind *Phylloxera* and its allies, in which many purely parthenogenetic generations follow one another every year and bring about an immense increase of individuals, to be finally succeeded by a single sexual generation of insignificant wingless males and females without mouth appendages, which have nothing to do but pair immediately after birth in order to produce the fertilized ova. Thus, sexual reproduction is retained in spite of the fact that no increase, but rather a decrease, in the number of individuals is, in these cases, brought about by its means, just as in the conjugation of the lower unicellular organisms. Some great advantage must therefore follow from its retention.

It may, however, be lost, and we cannot at present decide whether the immediate advantages which pure parthenogenesis affords are sufficiently important to justify the disappearance of those arrangements by which the power of increasing variation is guaranteed. We cannot penetrate far enough into the details of the struggle for existence to be able to determine whether a species can in any way fall into so critical a position that its survival can only be brought about by that excessively rapid rate of multiplication which is rendered possible by pure parthenogenesis. In such a case amphigony would have to be abandoned, for the only choice would be that between extinction and parthenogenesis, and the future of the species would be to some extent sacrificed to its temporary maintenance. But I do not by any means wish to imply that this is the only way in which the omission of sexual reproduction can be understood. The question is only opened, and we cannot yet claim to have answered it satisfactorily.

We must now turn our attention for a short time to the vegetable world. Unfortunately, there are not, as far as I am aware, any available observations on plants which give us reliable information as to those processes of maturation of male and female sexual cells which have now been described in the animal kingdom. Certainly Strasburger and others years ago described cell-divisions of mother-cells, both male and female, which resemble the 'reducing divisions' of mother-cells in animals; but whether, in this case also, a doubling of the idants precedes their twice-repeated division into halves, appears to be unknown. If we may assume that such a result is by some means ensured, that the number of ids is halved, and that their fresh grouping is thereby provided for, we cannot at any rate predict whether the process is conducted in precisely the same way as in animals. We ought perhaps rather to expect that some deviation from the reducing methods customary among animals would here be met with, a deviation which would render the meaning and significance of the latter even clearer and more definite.

We are justified, however, in believing that, in the cases of plant parthenogenesis, the amount of variation will diminish, together with the capability of adaptation by the operation of natural selection. Adaptations caused by direct influence on the germ-plasm are naturally conceivable in these as in other cases, but at present we know so little about such changes, whether produced by climatic or nutritive conditions, that it is impossible to determine how much may be implied by them.

Ten years ago parthenogenesis was doubted by botanists, or at any rate was regarded as very rare, and only to be found in cultivated plants, such as *Pteris eretica*, in which a certain tendency to degenerate was recognizable, or, at any rate, in which the structural and functional arrangements were no longer subject to the operation of natural selection. But we now recognize that a whole group of fungi, the Saprolegniae, 'including several genera and many species, are parthenogenetic.' Among the Ascomycetes 'it is admitted that many genera and species . . . are certainly asexual.' Amphigonic reproduction in the Æcidiomycetes is 'extremely doubtful,' while the Basidiomycetes 'afford an example of a vast family of plants, of the most varied form and habit, including hundreds of genera and species, in which, so far as minute and long-continued investigation has shown, there is not, and probably never has been, any trace of a sexual process[1].'

If the last statement be correct, it is impossible to maintain the existence of parthenogenesis in the Basidiomycetes; for this method implies the sexual reproduction of ancestors as its origin. Parthenogenesis is virgin reproduction, and signifies a power of development without fertilization possessed by female germ-cells. Parthenogenesis has arisen from bisexual reproduction by the elimination of the male and

[1] See Vines in 'Nature,' 1889 (Oct. 24), p. 626.

the male germ-cells; with the knowledge we now possess there can be no doubt upon this question. Not every unicellular *germ is phyletically an ovum. We ought to recognize and* apply to the botanical world the difference between parthenogenesis and asexual reproduction from unicellular germs. This distinction has not been made with any completeness, as we see in the passages quoted above from Professor Vines, and hence it is impossible to draw any safe conclusions from the asexual reproduction of the above-named fungi and from the fact of the phyletic development of numerous genera and species,—as to the amount of variation provided by heredity in parthenogenetic reproduction. The conditions of life among fungi are well known to differ markedly from those of most other plants, and it is not inconceivable that these may be associated with the disappearance or absence of amphigony; for the peculiar conditions of life may exercise an unusually strong direct influence upon the germ-plasm, and may thus render it variable. We know that variability is induced in other plants when they are submitted to very favourable nutritive conditions. But the researches of botanists must not be anticipated by these conjectures.

The Origin of Parthenogenetic Eggs from those which require Fertilization.

As I have already stated, parthenogenesis must have arisen from sexual reproduction. Those cells which develope parthenogenetically *are female germ-cells which have gained the power* of producing new organisms without fertilization. We must now enquire how this change has been brought about.

I must first allude to the gonoplastid theory, of which the principle has been proved to be untenable, but which is nevertheless correct in certain aspects, at least in the form in which Balfour conceived it. This thoughtful writer expressed the idea that the arrangement of polar bodies might have been brought about by nature, *in order to prevent parthenogenesis.* He therefore imagined that parthenogenetic development would ensue if the polar bodies, containing the supposed 'male principle,' remained in the egg. If, however, the facts are somewhat different, in so far as the polar divisions of the egg have been from the first an adaptation to fertilization, they have at any rate the effect of checking the power of development in the egg, so that, in a certain sense, we may maintain that their expulsion prevents parthenogenesis. On the other hand, we are now aware that a polar body is expelled from the parthenogenetic egg, while the difference between this and the egg requiring fertilization lies in the fact that a second polar body is expelled from the latter; but the correct idea nevertheless remains that something indispensable for the power of development is removed from the egg. According to our present views this is not the unknown 'male principle,' but a certain quantity of germ-plasm.

When we begin to enquire into the manner in which the power of parthenogenetic development was gained by an egg which required fertilization from the most remote time at which multicellular beings existed, the first thought that strikes us is, —*might not this have been brought about by the suppression of the second polar division?* If this happened, the first polar division would cause a diminution to the normal number of the previously doubled idants, and the second polar division being absent, the egg-cell would retain precisely as much nuclear material as it would have contained if fertilization had followed the expulsion of the second polar body. Since, then, regular parthenogenetic eggs invariably possess only one polar body, this supposition attains a high degree of probability. There are, however, facts which show that parthenogenesis may be acquired in another way.

Blochmann has observed, as is well known, that when the egg of the queen-bee is deposited in the cell of a drone, the same course of maturation is pursued as when it is laid in a female cell. In both cases two polar nuclei are formed, in both the nuclear substance is halved twice successively. In the case of the unfertilized male egg, the nucleus which remains after the second division possesses the power of becoming the germ-nucleus, and of developing; while the female egg is only able to enter upon embryogeny after the fusion of its nucleus with that of the fertilizing spermatozoon.

The eggs of Lepidoptera behave in a somewhat similar way; in the great majority of cases they require fertilization, but some can develope parthenogenetically. In the case of *Liparis dispar*, Platner found that such parthenogenetic eggs, like those which require fertilization, expel two primary polar bodies.

From this it is clear that parthenogenesis is possible, even when the quantity of germ-plasm in the egg has been reduced to half. Rolph, in his day, attributed parthenogenesis to better nourishment; Strasburger surmised, in adapting these thoughts to the significance of nuclear substance, which had in the meantime been recognized, that 'favourable conditions of nutrition counterbalanced the deficiency of nuclear idioplasm.' He assumed that the nucleoplasm was reduced to half, even in parthenogenetic eggs, and that 'the egg-nucleus after its reduction to half was unable to initiate the processes of development in the cell-body.' It was in these very cases of exceptional parthenogenesis in single ova that I expressed the definite opinion that the difference between eggs which are capable of parthenogenetic development and those which are not, must be quantitative and not qualitative [1]. I concluded from the facts connected with exceptional parthenogenesis, that a *certain amount of germ-plasm* must be contained in the egg-nucleus if it is to be in the position of entering upon embryogeny, and of completing it, and that, in these exceptional cases of parthenogenetic development, the germ-plasm in the egg, after having been reduced to half its normal amount, possesses, in some unusual way, the power of increasing to double. I am well aware that many facts subsequently discovered appear to be opposed to this suggestion, but I believe they only appear to be so. For example, my views as to the two varieties of *Ascaris megalocephala* might be cited in opposition; of these varieties one possesses two idants in the segmentation nucleus, the other four. We might conclude from this that the *amount* of nuclear matter does not control entrance upon development, but some other cause,—perhaps those 'spheres of attraction' and the central-bodies which E. van Beneden discovered lying in them, and which Boveri has called the centrosomata. I do not dispute the significance of these remarkable bodies in relation to the commencement of nuclear division, but do we know whence they come, and whether they are not perhaps, on their part, controlled by the nuclear idioplasm (germ-plasm)?

[1] 'Continuity of Germ-plasm.' Jena, 1885, p. 90. Translated as the fourth essay; see Vol. I. p. 231.

I hold that this is not only possible, but even probable. The difference between the embryogenies of two allied species not only depends upon the characteristic differentiation of the single cells which compose the body, but also equally upon their number, both relatively and absolutely, in all parts of the body. One and the same part of the body may be long in one species, and short in another : more cells will be required for the construction of the former than for the latter, or, in other words, the earliest embryonic cells of this part of the body must multiply more rapidly in one species than the other. If now this mode of cell-division is determined by the specific nature of the above-named centrosomata of such cells, it follows that embyrogeny must be essentially controlled by the centrosoma, i.e. by a part which lies in the cell-body, and which we have hitherto regarded as a part of it.

We do not however know that this is really the case; possibly the centrosoma may have been originally derived from the nucleus. But even if we admit that it is, not only in position but also in origin, a part of the cell-body, we must nevertheless believe that its activity is dependent on the nucleus and nuclear substance. The centrosomata form the active, and thus the chief part of that remarkable mechanism which controls nuclear division. If this mechanism is once set in motion, it completes the division in the manner described above, just as a spinning machine twists its numerous threads, but that the apparatus is put in motion, does not depend upon itself, but obviously upon the internal conditions of the cell, which react upon the mechanism for division, so that it is compelled to enter upon activity. How can we otherwise understand Flemming's recent discovery that the centrosoma is always present in the cell-body, but only periodically initiates the nuclear division? Now the internal condition of the cell is, as we are aware, primarily determined, in all its qualities, by the nuclear substance, and consequently the centrosoma and the dependent mechanism for division are ultimately controlled by the nuclear substance, which regulates the rhythm of cell-division and dominates the whole structure of the organism. If it were otherwise, this nuclear material could not be the hereditary substance—the material basis of hereditary qualities[1].

[1] Fol's recent observation that the centrosomata of ovum and spermato-

We know little at present about the detail of processes going on in the cell, and mediating between nucleus and cell-body and between this latter and the centrosoma; but I believe that this at any rate may be regarded as certain, viz. that everything which occurs in the cell, including the rhythm and the manner of its multiplication, depends upon the nuclear substance. But if this be so we cannot neglect its quantity: *there must be a minimum amount of nuclear substance below which the control over the vital processes of the cell cannot be completely exercised.* If this be correct, we shall be justified in explaining the cases of exceptional parthenogenesis by the assumption, that the nucleoplasm of certain eggs possesses a greater power of growth than that of the majority of eggs of the same species; while in the case of the bee, every ovum possesses a power of growth sufficient to double its nuclear substance, after reduction to half,—that is, when it is not raised to the full amount by means of fertilization.

This explanation, so far as I can see, is in complete agreement with all the facts of the case, and especially with the observations by which various investigators were, in earlier times, enabled to show that the unfertilized eggs of various species of animals, e.g. the silk-worm moth (*Bombyx mori*), frequently enter upon an embryonic development which is never completed, but is arrested at an earlier or later stage. This becomes intelligible if we suppose that the cell is controlled by the *quantity* of nucleoplasm. According as the germ-plasm, diminished to half by expulsion of the two polar bodies, possesses a weaker or stronger power of growth, it will follow that its quantity will be sufficient to bring about the first divisions of the ovum, but not to complete the whole em-

zoon divide during fertilization, and that the halves fuse together to form the two pole-bodies of the first segmentation spindle, agrees well with this view. Fol, 'La Quadrille des Centres,' Genève, 1891. Moreover this observation does not include anything which need surprise us, because nothing takes place except that which precedes every nuclear division, viz. the doubling of the centrosoma. The two sexual nuclei behave exactly like any other nuclei: even as regards outward appearance they may retain their independence for a long time in certain species, and fusion into a single nucleus only occurs at a later stage of segmentation. The evidence for this statement is afforded by observations upon *Cyclopidae* by Dr. Ischikawa, communicated to me in letters, and independently by the researches of my assistant, Dr. Häcker, upon the same animals.

bryogeny, or, on the other hand, will suffice to bring it to completion. In an earlier work I have endeavoured to render this theoretically intelligible and must here refer to that attempt[1]. But I should wish to add in this place that I have, since then, convinced myself that the view which I urged is correct. In conjunction with Dr. Ischikawa, I have examined the eggs of many Lepidoptera as to the power of development without fertilization: we observed that, as a matter of fact, some eggs entered upon embryogeny, which was, however, sooner or later arrested in most of them, only a very few reaching the caterpillar stage. Out of about a hundred unfertilized ova of *Aglia tau*, we obtained only a single fully developed caterpillar, many eggs shrivelled after a few days, while others remained plump: in most of the latter the yolk contained a large number of blastoderm cells; for a whole month these eggs developed very slowly and irregularly[2], but they finally shrivelled and decayed. The ova of one and the same female vary in respect to their powers of parthenogenetic development, and such individual differences cannot lie in the yolk, inasmuch as this nutritive material is distributed in the same manner and in equal amount in all eggs: they must rather be referred to differences in the rate of growth of the germ-plasm; at any rate, I cannot imagine any other cause which might account for them.

But this conclusion does not carry the implication that parthenogenesis could not have arisen by the method which was first indicated, viz. by the suppression of the second polar body. Indeed, I am inclined to believe that regular parthenogenesis has invariably arisen in this way; for otherwise the absence of the second polar body would not be so common, nor would it be without exception. This method cannot however obtain in facultative parthenogenesis, because that very egg which is capable of parthenogenetic development must also remain capable of fertilization. But this latter capability involves that reduction of the germ-plasm which occurs by means of the second polar division. In those cases in which parthenogenesis became necessary, and at the same time the capacity for fertili-

[1] Continuity of Germ-plasm.' Jena, 1885, pp. 92 et seqq. Translated as the fourth essay; see Vol. I. pp. 231 et seqq.

[2] The observations were not directed to the details of embryogeny.

zation had to be retained, there remained nothing except to strengthen the ordinary process of egg-maturation and thus to endow the retained half of the germ-plasm with increased powers of growth.

III. Amphimixis as the Significance of Conjugation and Fertilization.

The Facts of Conjugation.

Biologists have been, for some time, in the habit of comparing the conjugation of unicellular organisms with the sexual reproduction of multicellular forms of life, and of regarding them as to some extent equivalent. There was an obvious comparison between the more or less complete fusion of two of the former, and the coalescence of the two sexual cells of the latter; and this conception was strengthened when observation appeared to prove that the reproduction of unicellular beings by means of fission could not continue indefinitely, unless conjugation took place from time to time. Conjugation was looked upon as a 'fertilizing' process which endowed the organism anew with the capacity for fission, not once only but repeatedly, just as fertilization in multicellular beings renders possible the production of numerous cell-generations, constituting embryogeny. The cell material which, in the latter case, is made use of in building up the multicellular organism, appears in the former as a succession of many generations of unicellular beings; but, in both cases, the capacity for such cell multiplication depends upon the previous occurrence of a fusion of cells, thus originating the life-giving force which renders reproduction possible.

The above sentences form an approximate statement of the views which, with some individual differences, have obtained among biologists during the decade before the last. Even the remarkable discoveries of Bütschli on the conjugation of Infusoria led to no essential modification, although they taught us to recognize the mysterious nuclear changes, the analogy of which to the processes of fertilization was then unknown.

However, mainly in consequence of the observations of the brothers Hertwig, of Fol and of E. van Beneden, this analogy is now recognized, and we may admit that the connection between conjugation and fertilization is firmly established, more especially since the investigations on the conjugation of Infusoria, begun by Bütschli, have been carried to a high degree of completeness by the work of Balbiani, Engelmann, Gruber, R. Hertwig, and above all by the exhaustive and wonderful investigations of Maupas [1].

But even if we may at length regard the agreement between the processes of reproduction and conjugation as firmly established, and the ideas of an earlier date confirmed, we cannot, in my opinion, retain the former conceptions as to the deeper significance of these two processes. Both conjugation and fertilization appear in an entirely new light if,—leaving behind all ancient prejudices, and without bias—we examine and compare them from the standpoint of our present knowledge. Each process throws light upon the other, and the true meaning of both is thus made clear.

I will first briefly recapitulate the facts of conjugation as established by Maupas and ably confirmed and extended by R. Hertwig, and I have therefore appended in Fig. XI. a free rendering of Maupas' figures, which illustrate the changes in the nucleus accompanying the conjugation of *Paramaecium caudatum*. *M* indicates the macronucleus, *m* the micronucleus; m^1 and m^2, in figure 3, signify the two daughter-nuclei which arise from the first division of the micronucleus; m^1—m^4, in figure 4, the four grand-daughter-nuclei of the same, derived from the fission of the daughter-nuclei. In figure 5, three of these, m^1—m^3, are already disintegrating, while the fourth, m^4, is drawn out into a spindle preparatory to division, and the consequent formation of the two reproductive nuclei, Cop^1 and Cop^2. Figure 6 shows the reciprocal transference of the male reproductive nucleus from each animal into the other; and

[1] We should read the admirable work of Maupas with even greater satisfaction if it contained fewer reflexions upon those who have worked in the same field. Maupas should not have forgotten that even the ablest cannot avoid error, and that it is the fate of all work, even the most excellent, to be in time surpassed;—for upon this the whole advance of science depends. We may correct the mistakes of our predecessors without forgetting that we stand on their shoulders. The very power we possess of improving on them is largely due to the fact that they have placed their successors upon a higher level than that from which they started themselves, and it is but a poor return for this to label their work 'superficial,' 'inaccurate,' &c., &c.

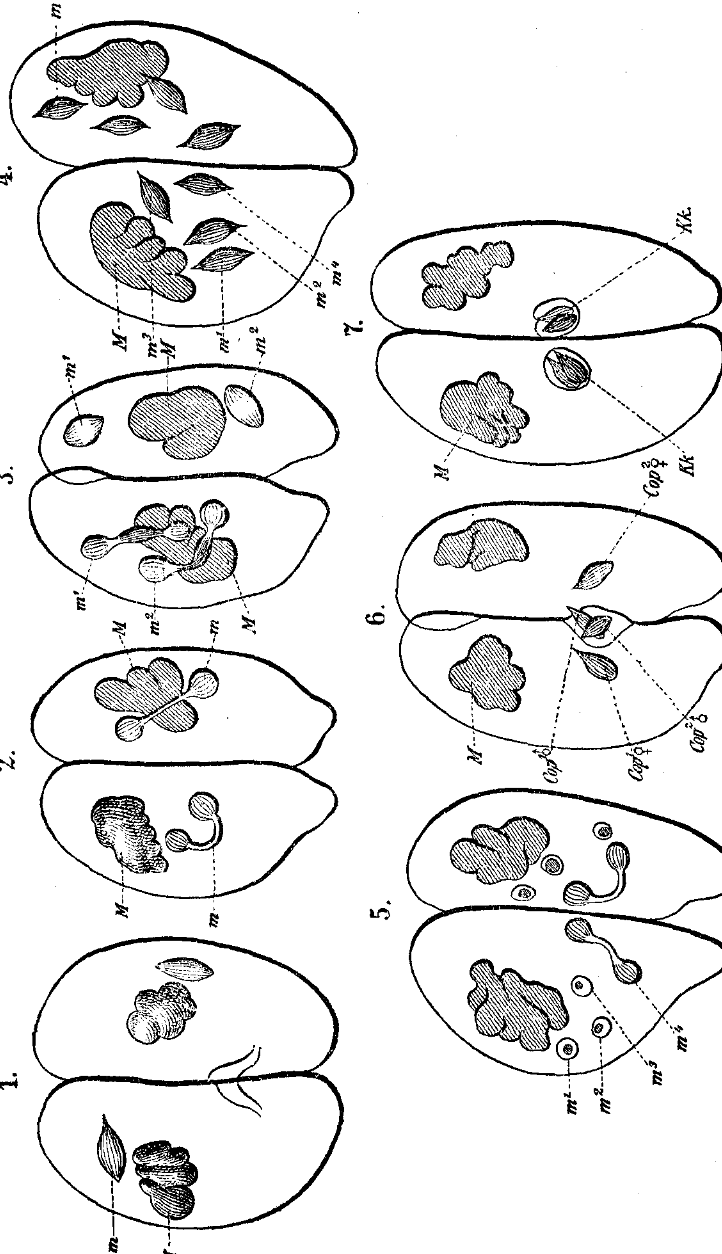

FIG. XI. The conjugation of *Paramaecium caudatum* (modified from Maupas). *M*—Macronucleus. *m*—micronucleus.

figure 7, the fusion of the male and female nuclei to form the germ-nucleus, *Kk*.

The essential part of this process is shown even more clearly in the annexed diagrammatic representation of the changes undergone by the micronucleus, which Maupas has constructed for *Colpidium truncatum*. Fig. XII. illustrates diagrammatically the nuclear changes of two conjugating individuals of this species. The black spheres represent the persistent nuclei, while the circles stand for those which disintegrate and disappear. Similar processes take place in each individual of the conjugating pair. The micronucleus first grows from its previous small size, A^1, to a considerable bulk, and it is shown in A^2 as ready for the first fission, producing the two nuclei (*B*). Each of these daughter-nuclei again divides, and thus the four grand-daughter-nuclei arise (*C*). Three of these disintegrate and disappear, while one divides and produces two nuclei (*D*) comparable with the sperm- and egg-nuclei of Metazoa. We may call these the male and female reproductive nuclei, and may regard that as the male which leaves the animal in which it had its birth and enters the other organism in order to fuse with its female reproductive nucleus. This fusion, represented at *E* in the diagram, leads to the production of the 'combination nucleus [1],' the analogue of the 'germ-nucleus' of fertilization.

The old macronucleus disintegrates and is absorbed, but by the double division of the 'combination-nucleus' two new macro- and two new micronuclei arise, preliminary to the first fission of the whole animal which now commences.

The essential part of the whole process is the fusion of two equal amounts of nuclear substance, the one derived from one animal and the other from another, and the formation from this nuclear substance, thus derived from two individuals, of the nuclei which dominate the animals after conjugation. This harmonizes with the process of fertilization in that here also two equal masses of nuclear substance, derived from two different individuals, unite to form the new germ-nucleus. Now that we at length recognize that the 'nuclear substance' is the ruling principle of the cell, that Nägeli's 'idioplasm' is the

[1] By this term I mean a nucleus which has arisen by amphimixis, and consists of equal amounts of idioplasm from two individuals.

hereditary substance, we are enabled to state that the essence of both conjugation and fertilization is nothing more than a *mingling of the hereditary substances of two individuals.* I pro-

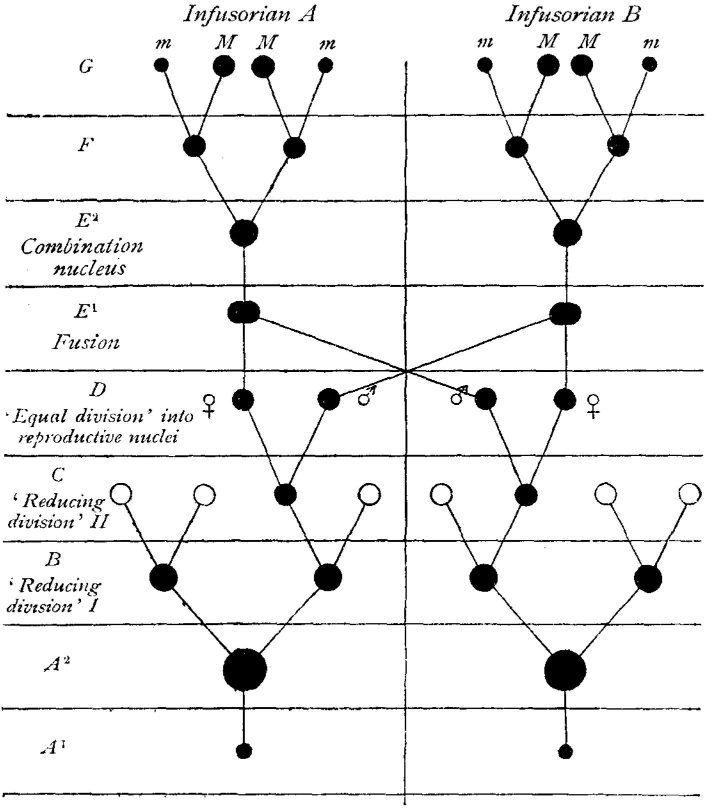

FIG. XII.

Diagram of the changes undergone by the micronucleus during the conjugation of a Ciliate Infusorian; (after the diagram given by Maupas in the case of *Colpidium truncatum*).

pose to introduce the term *Amphimixis* to indicate such a process of mingling of the idioplasm from two individuals. The usefulness and indeed the necessity for some such special term will soon be apparent. If we next consider the phenomena which have been directly observed, we find that, in spite of the already mentioned fundamental agreement between the two forms of amphimixis (conjugation and fertilization), there are some not unimportant differences between them.

This is partly due to the fact that those Infusoria which have supplied the most familiar examples of conjugation, possess two kinds of nuclei, the macronucleus and the micronucleus. To the former is attributed the vegetative functions, while the latter has been termed the 'generative nucleus.' It is certain that both nuclei proceed from the same material, viz. from the combination-nucleus of the animals after conjugation, that is, from a germ-nucleus. It is thus established that their differentiation depends on the principle of division of labour, and Maupas probably comes near the truth when he attributes to the macronucleus a 'bon fonctionnement des organes de la vie végétative et à la forme individuelle,'—a conception which does not precisely coincide with that of Bütschli, Gruber, and Hertwig, who regard it as an 'assimilative nucleus' only. Ascertained facts indicate that the micronucleus, in the first place, sub-serves amphimixis; for it and it alone produces the reproductive nuclei. But we must beware of restricting its activity to this single function. Numerous facts tend to show that it has another function, in addition to that which relates to the periods of conjugation. In many species there is not one micronucleus, but two of them, which are found regularly through the whole period of fission, although only one takes part in conjugation, while the other disintegrates. In other species numerous micronuclei exist, and in *Stentor Roeselii* there are eight-and-twenty regularly distributed through the whole animal. This indicates that during the period of multiplication of the Infusorian its mass of idioplasm must be greater than during the period of conjugation, and this again points to some special activity during the former period. I do not know of what kind this activity is, and do not care to speculate, since the question has no bearing upon our present subject. This much, however, is determined, that as regards conjugation, the micronuclei bring about *the continuity of the germ-plasm.* Among the Metazoa this continuity is not, in many cases, effected so directly and visibly, but it is brought about, as I believe, by minute invisible masses of germ-plasm, which arise from the egg and are afterwards carried on, mingled with the contents of certain somatic cells. In these cases the origin of such masses in the egg can only be conjectured, but in conjugation observation shows that a part of the idioplasm is, as a matter of fact, set apart in the form of micronuclei for the use of the next generation. The nuclear substance of the micronucleus alone is undying, and continues the vital processes without limit, while the macronucleus behaves, in this respect, in an entirely different manner.

In the Metazoa the whole cellular structure of the body—the soma—is worn out by the processes of life, and suffers natural death: in just the same way the Infusorian macronucleus cannot continue its functions for unlimited generations, but must be renewed from time to time; and indeed, as we have already seen, it is formed anew from the combination nucleus which originates in the amphimixis of the two reproductive nuclei. During the formation of the new macronucleus the old one is destroyed and disappears. These are processes which have no analogy with fertilization: I shall return to their deeper significance later on.

A further difference between fertilization and conjugation lies in the fact that the reproductive nuclei of Infusoria arise from the thrice-repeated nuclear division of the micronucleus, while the nuclei of the egg- and sperm-cells of Metazoa are derived from the twice-repeated division of the mother-cell.

Meaning of the Phenomena.

It may appear decidedly premature to attempt an explanation of the above-mentioned differences and resemblances between the two forms of amphimixis; but I am willing to undertake this responsibility, if only to give a fixed direction to further investigation. If I abandon all the theoretical conceptions of fertilization and heredity developed in my earlier writings, I do not believe that we need, on this account, give up all views upon the processes of conjugation as they are known to-day, but rather that future research will be more profitable if we endeavour to test some settled theory, instead of making observations with no object in view.

The preparatory divisions of the micronucleus have been frequently compared to the formation of polar bodies in the animal egg. If we consider the physiological significance of the two processes, this comparison is certainly striking, but it is incorrect to push it so far as the attempt to homologize the separate phases[1] and to explain them as morphologically equivalent; for all homology between two living forms depends upon their similar origin, and no one can believe that the higher animals have originated from the Ciliate Infusoria. *The kind of conjugation exhibited by the latter is widely removed from its simplest form*, occurring among the lower Protozoa, and any direct connection between the conjugation of Ciliata and the sexual reproduction of Metazoa cannot be assumed. Hence any attempt to homologize the *separate phases* of these two kinds of amphimixis must fail, although the processes are *in their essence* certainly homologous; for both have sprung from the same root,—the conjugation of the lowest forms of living beings.

I shall, however, attempt to show that many of the details of the two processes possess *a corresponding significance*, which must therefore be very deeply rooted, inasmuch as similar events have not been called forth by a common origin but by physiological necessity; just as the eyes discovered by Semper[2] on the back of certain slug-like Molluscs (*Oncidium*) resemble Vertebrate eyes, not because the Molluscs have been derived from Vertebrates, or *vice versa*, but because the necessity for eyes has called forth such a structure out of the foundation provided by the fundamental nature of light and the histological details of the *Oncidium's* dorsal surface.

I find the foundation of my explanation of the nuclear divisions accompanying amphimixis in the fact that *the micronucleus of Infusoria possesses nuclear rods or idants*, the proof of which we owe to the researches of Pfitzner[3], R. Bergh[4], Maupas, and Balbiani[5]. This fact indicates that the structure of the idio-

[1] A. Giard, 'Sur les globules polaires et les Homologues de ces éléments chez les infusoires ciliés.' Paris, 1890.

[2] C. Semper, 'Ueber Schneckenaugen vom Wirbelthiertypus.'

[3] *Pfitzner, 'Zur Kenntniss der Kerntheilung von Opalina ranarum.'* Morph. Jahrbuch, Bd. XI. p. 454; 1886.

[4] R. Bergh, 'Recherches sur les noyaux de l'Urostyla.' Liège, 1889.

[5] Balbiani, 'Sur la structure intime du noyau de *Loxophyllum meleagris*.' Zool. Anzeiger, No. 329 and 330; 1890.

plasm in Infusoria corresponds with that in Metazoa, and we are justified in transferring to these Protozoa the conceptions at which we have arrived as to the relation and significance of the Metazoan idioplasm, and, above all, the conception of *the individual difference of nuclear idants.*

R. Bergh's researches upon *Urostyla grandis* prove that the spindle of the micronucleus contains, during division, nine rod-like idants (see his fig. 9). Since, however, only one side of the spindle is represented in the drawing, the total number of idants must be eighteen. All who have observed the phenomena of conjugation agree that the first preparatory change in the micronucleus consists in a *considerable enlargement*[1]. Maupas[2] gives a series of fourteen figures illustrating this increase in the size of the micronucleus and its conversion into a spindle, and he calculates that, during this period, its original mass is multiplied eight-fold.

Richard Hertwig[3], who has directed special attention to this point, found that the micronucleus of a *Paramaecium*, immediately after division, was extremely small,—less than three microns[4] in diameter, while that of the micronucleus of an animal previous to conjugation was about seventy-five microns.

This enormous increase in size largely depends on the growth of the achromatin substance which plays a most essential and remarkable part in the subsequent divisions, but it does not therefore follow that there is no simultaneous increase in the idioplasm. I assume that the increase of the micronucleus is connected with *a doubling of the idants by longitudinal division.* There is at present no proof of this assumption; for no one has

[1] Schewiakoff's beautiful observations ('Ueber die karyokinetische Kerntheilung der *Euglypha alveolata*;' Morpholog. Jahrbuch, Bd. XIII. p. 193; 1888), show that the Infusoria are not the only Protozoa possessing idioplasm in the form of idants. Not only are idants (chromatosomes) shown to exist in the form of loops, but their behaviour during karyokinesis is so accurately described as to leave no doubt that an 'equal division' is its outcome. The longitudinal splitting of the loops was observed not only in microscopic preparations, but in the living animal in the act of dividing. It is clear that *Euglypha* is well adapted for observation, and it would be of great value to investigate the relations of its nucleus during conjugation from the standpoint of this essay.

[2] Maupas, 'Le rajeunissement karyogamique chez les Ciliés.' Archives de Zool. expér. et gén. 2 sér. Vol. VII. Pl. IX. Figs. 1–14. Paris, 1890.

[3] R. Hertwig, 'Ueber die Conjugation d. Infusorien.' Munich, 1889.

[4] A micron or μ is the $\frac{1}{1000}$ of a millimetre.

yet compared the number of the idants in a micronucleus preparing for conjugation with the number in a micronucleus of an Infusorian in the act of fission; and the few figures which we possess, of either of these stages, afford us no reliable information on the point. The figures which Maupas gives of the micronucleus preparatory to conjugation in *Paramaecium caudatum* and *Onychodromus grandis*, lend support to my view, in so far as the number of idants is very large. In the first species I counted twenty-one in the half spindle which is figured, giving a total of about forty-two. But I will not lay too much stress on this point; the simplicity of my attempted explanation of the changes in the micronucleus appears to me to be strongly in favour of the view upon which the explanation is based.

If this assumption be well founded it provides a very simple solution of the problem of the complex divisions and repeated disintegrations of the micronucleus. *The first and second divisions are reducing divisions* which diminish the previously doubled idants to half the normal number, corresponding exactly to the 'reducing divisions' of sperm- and egg-mother-cell. *The third division, however*, which produces the two reproductive nuclei (male and female), from one of the four grand-daughter-nuclei of the micronucleus, *is an 'equal division,'* which causes each daughter-nucleus to contain as many idants as were possessed by the parent nucleus. This last division has no analogue in Metazoa, simply because their germ-cells are invariably either male or female, while the Infusorian micronucleus must give rise to both kinds of reproductive nuclei.

Three out of the four grand-daughter-nuclei of the micronucleus disappear, only one dividing to form the reproductive nuclei (*D* in the diagram, Fig. XII.). The fact that the others disintegrate can be understood in so far that they are superfluous and functionless, just like the polar cells of the animal egg. It is more difficult to explain why these three are always present, and still harder to find the true reason, the *causa efficiens*, of their disintegration.

With regard to this last question, an observation of Maupas may put us on the right road. He believes that he has observed that, of the four grand-daughter-nuclei derived from the micronucleus, the one which lies nearest to the bridge connecting the two conjugating animals invariably gives rise to the reproductive nuclei. This is alone capable of further development, while the three which occupy more remote positions are destined to disintegrate and disappear. It is only the accident of position which fixes upon that one of the four which shall undergo development.

If this be true, the *causa efficiens* which decides upon that one of the grand-daughter-nuclei which shall give rise to the reproductive nuclei must be sought for in some influence which is exercised by the corresponding nucleus of the other animal, and which naturally affects most strongly that nucleus which lies nearest to it.

At any rate we are justified in assuming that the idioplasm of the four grand-daughter-nuclei of the micronucleus is, apart from individual differences, essentially similar, i. e. that each contains the same number of idants in the same stage of development, and this number will be half that which is normal for the species in question. Thus nine would be the number in *Urostyla grandis*, which would be reached in the following manner. According to my supposition, during the growth of the micronucleus from A^1 to A^2 (see Fig. XII), the 18 idants are doubled by longitudinal fission, becoming 36; the two following 'reducing divisions' not only diminish the idants from 36 to 18 in stage B, and from 18 to 9 in stage C, but lead to *a fresh grouping of the idants, just as in the analogous 'reducing divisions' of the egg- and sperm-cell.* Since the 18 idants are doubled, it is clear that each one of them will be represented by two idants in the enlarged micronucleus of stage A^2, and hence the two 'reducing divisions' can originate a number of different combinations of 9 idants, just as in the egg- and sperm-cell, described in the first part of this essay.

Although in any single individual, only four out of the numerous possible combinations would become actual, we may perhaps perceive,—in this very fact that there are always at least four different possibilities to select from,—the reason why all four grand-daughter-nuclei of the micronucleus are formed, and why both the daughter-nuclei undergo the second 'reducing division,' while the division of one of them alone would suffice to ensure the origin of two reproductive nuclei.

Objections.

It will be urged against my views that they are based upon a method of formation of the reproductive nuclei, which, although common among Infusoria, is by no means the only one. As a matter of fact, Maupas, whose researches form the only foundation for this part of my argument, describes another method in the *Oxytrichidae*. If I neglect the fact that in this case two micronuclei are found in the animal preparatory to conjugation, it is because this difference is merely due to the fact that two of the grand-daughter-nuclei (instead of only one) undergo a second division. Thus two pairs of reproductive nuclei arise, of which only one is functional, while the other disintegrates. But the theoretical explanation is in no way affected by these observations.

The only facts which do not at once harmonize with my view is the behaviour of the micronucleus in male *Vorticellidae*. In this case the period of growth of the micronucleus (stages A^1—A^2) is preceded by its division. I cannot at present explain this, unless it simply means that instead of four different combinations of idants out of which one functional reproductive nucleus is to be chosen, eight are in this case afforded. A glance at the figure given by Maupas (op. cit. p. 364) at once renders this suggestion clear. In any case, the extra division must be an 'equal division.'

Thus the departures from the ordinary modes of division of the micronucleus raise no definite objection to my explanation.

Evidence that the processes which I have explained as 'reducing divisions' are really such, is afforded by some of the figures given by Maupas, as in figs. 9–13 on Plate XVIII, in which the development of the spindle for the nuclear division of *Onychodromus grandis* is represented. The rod-like chromatosomes lie longitudinally in the spindle, and appear to be dividing transversely. Since we must imagine that the ids are arranged lengthwise, the transverse division of the idants must lead to a diminution in the number of ids in each rod to half their original number. Complete certainty cannot, however, be attained by an examination of these figures; the matter must be settled by fresh observations, especially directed to the point. The whole mechanism of nuclear division differs in essential points from that of the Metazoa, so that without first making renewed investigations it is impossible to form a correct idea as to what should be regarded as a 'reducing division.'

According to my view, the explanation of the thrice-repeated division of the micronucleus consists, on the one hand, in the reduction of the number of idants and their arrangement in new combinations, and, on the other hand, in the differentiation of the two reproductive nuclei.

Those who agree with me in looking upon amphimixis as the union of idioplasms built up of ids from two individuals, will not hesitate to believe that the ids are reduced to half the normal number. It is impossible that there can, in this respect, be any difference between the amphimixis of unicellular organisms and that of Metazoa. It is not equally certain that my view of the production of fresh combinations of idioplasm by means of amphimixis can be proved in the Protozoa. It might be objected that it is useless for one Protozoon to possess the theoretical possibility of producing a great number of individual varieties of idioplasm, because each single animal is only able to utilize one out of many possible combinations. The two animals which commenced conjugation remain at the end of it, and there is no increase in number: hence the different nuclei which originated from the 'reducing divisions' cannot be divided among different animals, as is possible in the case of the four sperm-cells which are formed by one sperm-mother-cell, and which contain four different combinations of idants.

This objection is easily met, for exactly the same thing happens in the development of the ova in Metazoa. Just as only a single egg, with a single combination of idants, can proceed from each egg-mother-cell, while the other three combinations disappear in the polar cells,—so, in this case, three grand-daughter-nuclei of the micronucleus disappear, and one only persists. The process receives a meaning when we remember that countless numbers of egg-mother-cells, containing precisely similar combinations of idants, are destroyed by the process of arranging the idants in fresh groups. *The same explanation holds among Infusoria; for here also countless individuals contain precisely similar combinations*, this being true of all individuals which are derived from either of the animals proceeding from any one conjugation. Just as the collective egg-cells of a mother would contain identical germ-plasm, if they did not undergo the 'reducing divisions' before reaching maturity,—so all the descendants of an Infusorian after conjugation would contain similar combinations of idants, if the repeated 'reducing divisions' did not precede the formation of the reproductive nuclei.

Variety of individual character in the hereditary substance is thus brought about by means of these divisions.

The Deeper Significance of Conjugation.

No one will attempt to oppose the view that the deeper meaning of conjugation is closely connected with that of sexual reproduction. The process is, in both cases, that of nuclear fusion, and, in fact, the formation of a complete nucleus by the union of two 'half-nuclei,' as they may be called, that is, two nuclei which contain only half the normal amount of hereditary substance or idioplasm, and only half the normal number of individual hereditary units or ids. From this fusion a new nucleus is formed which contains that amount of hereditary substance and that number of ids which are normal to the species. This is my explanation of the process of fertilization in the Metazoa, an explanation which I can extend to the Protozoa, now that the long looked for and, indeed, partially observed nuclear fusions accompanying conjugation have been proved by Maupas to be actual facts. Those who do not accept my theory of ids can only maintain that the nuclear fusion of conjugation and fertilization leads to the formation of a new nucleus by the fusion of two equal masses of individually distinct hereditary substance or idioplasm.

The view which I expressed in 1873, and which has since then been established by Strasburger, O. Hertwig, and myself, of the essential similarity of the male and female sexual cells, can now be confidently extended to conjugation; for Maupas has already acknowledged the two reproductive nuclei to be essentially similar. They certainly are so, inasmuch as they exhibit no traces of the fundamental antagonism which has been spoken of as a 'male and female principle' in the egg- and sperm-cell.

If we may now assume that the nuclear substance which arises in the same way in Infusoria and Metazoa bears a similar significance in both, we may then proceed to the conclusion set forth above that conjugation and fertilization are both essentially concerned with the mingling of the *hereditary tendencies of two individuals.*

At the time when I developed this view, which sought the ultimate meaning and true cause of the existence of sexual reproduction in the continual supply of fresh combinations of hereditary tendencies, I contrasted the Metazoa and Metaphyta on the one hand with the Protozoa and Protophyta on the other, and maintained that the chief sources of variability in the former, the multicellular beings, viz. the external influences (including the effects of use and disuse) which alter the body, can have no influence on the processes of selection which alter the species, because their effects are somatogenic and as such cannot be inherited. Only those predispositions can be inherited which are contained in the germ-plasm, but these are either entirely uninfluenced by external agencies, or, if altered at all, only very rarely in the same direction as that taken by the somatogenic changes which follow the same cause. Although I naturally did not assume that the germ-plasm itself was entirely unchanged by external influences, the extraordinary persistence of heredity taught me that the change was small and could only take place by imperceptibly small steps. Such causes might well have been the source of the gradual uniform changes in *all* individuals of a species, if the latter were subjected to the same modifying influences during long series of generations, but not the source of the countless individual differences, ever-varying in direction. This protean individual variability is the indispensable preliminary to all processes of selection, and the unceasing mingling of individual hereditary tendencies, which is brought about by sexual reproduction, was in my opinion the source of this variability. I am now, if possible, more firmly convinced than ever of the soundness of this view, and I wish to extend it in one direction.

At the time I have been speaking of, I looked upon unicellular beings as organisms in which external influences could directly call forth hereditary changes; for in them reproduction involved the fission of the cell so that changes undergone by the latter must be transmissible to either half. As an example, I selected a Moneron as defined by Häckel, viz. an organism without a nucleus. I purposely abstained from considering those unicellular beings which possess nuclei, because I was then only concerned with bringing forward the general conception that sexual reproduction exists in order to ensure individual variability. I was, however, well aware that in the nucleated Protozoa, and especially in those Infusoria, which although unicellular are extremely highly differentiated, such a simple transmission of acquired peculiarities was hardly conceivable. Now that we possess accurate knowledge of the most essential points in the process of conjugation, it is possible to approach this problem somewhat more closely.

The fact, as we now know it, that conjugation in Infusoria is a mingling of the nuclear substances of two individuals, permits the conclusion that, in these animals, the whole individuality of the cell, and thus of the cell-body, is contained in the nuclear material as predispositions or hereditary tendencies, just in the same manner as has been proved in the case of the germ-cells of the Metazoa. Nussbaum's experiments upon the artificial fission of Infusoria, and those which Gruber undertook at my suggestion in the Zoological Institute at Freiburg, prove that the nucleus determines the regeneration of the mutilated animal, and that it contains, in some way, the essence of the whole organism in all its details. Hence we must believe that all those variations which appear in Infusoria, in consequence of external influences, can only pass on to the products of fission *when they are accompanied by corresponding changes of the nuclear substance*; or, in other words, we come to the conclusion that the hereditary transmission of *somatogenic* changes does not, as a rule, take place, or only does so when they are accompanied by corresponding *blastogenic* changes. The use of both these expressions only implies a correspondence, and not a similarity of application, the 'soma' of Metazoa corresponding to the cell-body of Infusoria, the 'germ' to the nuclear substance. The broken bristles of an Infusorian are renewed in the products of fission because the predisposition to form them is contained in the nuclear substance. Mutilation is no more hereditary here than in the Metazoa. Furthermore, all changes in the cell-body of an Infusorian are not accompanied by corresponding changes in the nuclear substance, and all cannot therefore be inherited;

not only is this the case but it seems very questionable whether the changes originated by use and disuse are in any way more hereditary than they are in Metazoa. There are no direct observations to test whether any of the cilia in an Infusorian could be strengthened by increased use, either in connexion with some new kind of food, or with a struggle against stronger currents in water; but we need not doubt that in these organisms, small and relatively simple as they are, functional hypertrophy and atrophy play the same rôle as in larger and more complex beings. I would refer my readers to Wilhelm Roux's excellent treatise on this subject in the higher organisms. If certain cilia in an Infusorian were to increase in size as the result of more active function, how can we conceive the transmission of this change to the hereditary substance contained in the nucleus? The path is certainly shorter than that from the human brain and finger muscles to the reproductive cells; but distance, like all measurements, is only a relative idea, and the question arises whether there is any ground for the assumption that such increased growth in the cilia causes any *corresponding* change in the nuclear substance of the animal. But if this does not occur, any inheritance of acquired characters is as impossible as it is in man. How, for instance, can an increase of the adoral ciliated zone of a *Stentor* be transmitted to both the products of its fission, considering that the hindmost of these has to form an entirely new mouth? It might perhaps be pointed out that R. Hertwig believes he has seen the mouth of the hinder offspring arise by budding from that of the anterior; but the artificial division of *Stentor*, as effected by Gruber, proves that the mouth of the posterior part is not dependent on the existence of the original mouth, but can arise quite independently, provided only that a portion of the nucleus is present.

I therefore hold that *a belief in the inheritance of acquired characters by the highly differentiated Protozoa, as well as by Metazoa, must be opposed*, and I imagine that *the phyletic modifications of Protozoa arise from the germ-plasm, that is from the idioplasm of the nucleus.*

We can now understand why nature has laid so much stress on the periodical mingling of the nuclear substances of two individuals,—why she has introduced amphimixis among these animals. Clearly it has arisen from the necessity of providing the process of natural selection with a continually changing material, by the combinations of individual characters.

Amphimixis in all Unicellular Organisms.

We may extend this conception and enquire whether it may not, in reality, apply to all unicellular organisms, that is all which possess a nucleus and cell-body. The conclusion can scarcely be avoided if it be admitted that the nucleus invariably bears the same essential significance, and this can hardly be doubted. If, as a matter of fact, the lowest, apparently structureless unicellular organisms contain a nuclear substance which dominates and controls the entire animal, it follows that all lasting and therefore hereditary variations of both cell-body and nucleus must proceed from the latter, while those direct changes of the cell-body which are produced by external influences, are as incapable of hereditary transmission as the mutilation of the body of an Infusorian. Thus changes in the molecular constitution of the cell-body, such as we might imagine to be the result of the exercise of particular functions (for example, the more powerful movements of an amoeba) would probably be transmitted to the immediate offspring, but would disappear with the cessation of those causes which rendered necessary the increased exercise of the function concerned.

My earlier views on unicellular organisms as the source of individual differences, in the sense that each change called forth in them by external influences, or by use and disuse, was supposed to be hereditary, must therefore be dismissed to some stage less distant from the origin of life. I now believe that such reactions under external influences can only obtain in the lowest organisms which are without any distinction between nucleus and cell-body. All variations which have arisen in them, by the operation of any causes whatever, must be inherited, and their hereditary individual variability is due to the direct influence of the external world. Loss of substance must not however be included among such individual variations: repair would take place by regeneration in these simplest forms of life just as in higher Protozoa. At least, I think this is not contradicted by the fact that the molecular structure of such a Moneron, although without the guidance of a nucleus, retains a certain external form and limit of size, which it will regain after being mutilated. Growth and division are themselves the outcome of such tendencies implanted in the molecular structure: this, for example, is the case in Bacteria. The whole question comes to an end when we reach those lowest of all beings, which are entirely formless and have no fixed size,—beings which we must regard, little as we know about them, as crossing the very threshold of organic life[1].

It is interesting to observe that, from this point of view, the nucleus presents itself in a new light. By the agency of conjugation and fertilization it becomes *an organ for maintaining the constant renewal and transformation of hereditary individual variability.* Besides this, it plays the part of protecting the species from the too powerful effect of transforming external influences upon the body, inasmuch as it tends to prevent these from becoming hereditary, not indeed actively, but simply because every external influence does not cause a corresponding alteration in the nuclear substance, and thus the latter containing the older predispositions tends to restore, after each fission, the older condition of the cell-body. It simultaneously acts as a conserving and as a progressive principle, exactly as the sexual cells of higher beings are, according to my views, supposed to behave. The reproductive cells exert a conserving force, inasmuch as they retain, with incredible tenacity, the hereditary tendencies contained within them, and, above all, because they are unaffected by those changes in the soma which are brought about by external influences: but they also act progressively by means of amphimixis and the consequent periodical mingling of the hereditary predispositions of two germ-cells, one from each parent, which as we have seen, takes place by the removal of half of these predispositions and by the arrangement of those which remain in fresh combinations.

If I am correct in my view of the meaning of conjugation as a method of amphimixis, we must believe that all unicellular organisms possess it, and that it will be found in numerous low organisms, in which it has not yet been observed. But it is by no means safe to make the *a priori* assumption that conjugation

[1] Nägeli, 'Mechanisch-physiologische Theorie der Abstammungslehre.' Munich, 1884.

may not also take place in the form of a fusion of two individuals among the non-nucleated animals, the Monera: and it may be precisely here that a fusion of two whole animals with a view to the mingling of characters was first effected. We are acquainted with a form of conjugation in certain of the *Bacillariaceae*, and even if it is not absolutely certain that the species in question, *Cocconeis pediculus*, is without a nucleus, many details of the process indicate that the whole mass of the organism contains the conjugating idioplasm: this is chiefly suggested by the minute size of the conjugating individuals, which invites comparison with the nucleus, diminished by 'reducing divisions,' in order to facilitate amphimixis. For this reason I believe that we ought not to follow Maupas in constructing a general definition of conjugation as the fusion of nuclei.

The Theories of Rejuvenescence and of Mingling.

I hold that the deeper significance of every form of amphimixis,—whether occurring in conjugation, fertilization, or in any other way,—consists in the creation of that hereditary individual variability which is requisite for the operation of the process of selection, and which arises from the periodical mingling of two individually different hereditary substances.

That such a mingling is the immediate result of amphimixis is no longer open to dispute, and perhaps at no distant date it will be admitted that the variability I have spoken of must follow as a direct consequence. It is well known, however, that many and indeed the majority of scientific men, who have expressed themselves on the point, hold the opinion that this mingling of two hereditary substances is not the one object of amphimixis, —its ultimate and most important consequence, and does not explain the reason why it was introduced into the organic world. It is obvious that my view as to the effect of amphimixis in originating variability may be perfectly correct, without the essence of fertilization or of conjugation being thereby explained. What I regard as its chief object may after all only be secondary, and the true significance of the process may lie in some consequence unknown to me or which I have overlooked.

We know that, up to the present time, fertilization has been regarded as a vitalizing process, without which the development of the egg either cannot occur at all, or only exceptionally. I need not repeat what I have already said upon this idea in the first part of the essay, and it is not necessary to follow the gradual modifications which have been introduced; but I should like to submit to a trial the support which the upholders of these views have always sought in the process of conjugation, and which they are still seeking to-day.

Maupas, the able investigator of the vital processes of Infusoria, considers that the effect of conjugation is such as to ensure the continuation of the species; it imparts to the animal the power 'de renouveler et rajeunir les sources de la vie.' Hence, according to this view, the most profound significance of conjugation is to be found in rejuvenescence, an idea which was long ago accepted and applied, sometimes to fertilization, sometimes to conjugation, and sometimes to both together, by Bütschli, Engelmann, Hensen, E. van Beneden, and more recently by R. Hertwig. Maupas also looks upon these two processes as essentially similar, and regards both as a 'rejuvenescence,' without which life would, sooner or later, come to an end. He sharply distinguishes between this somewhat mystical rejuvenescence and that which consists in the renewal of many of the external parts of the animal, such as mouth, bristles, cilia, &c. Such regeneration is certainly connected with conjugation, but it also occurs at every fission of an Infusorian and cannot therefore be an essential part of the former process. The rejuvenescence which Maupas regards as the essence of conjugation is something entirely different, and can hardly be described except as a 'renewal of vital force,' using the expression in the sense of the old natural philosophers. All other attempted definitions of this rejuvenescence are vague and unsatisfactory. It may well be doubted whether the return to a certain form of 'vital force' is in harmony with the physiology of to-day. On the other hand, no period of time has been entirely without an advocate of this principle, and quite recently the accomplished physiologist Bunge has, although with much reserve, again supported the ancient belief in a vital force. In any case we could only accept this idea if it were shown that there is no chance of explaining the phenomena of life, even in principle, without such acceptance. Bunge[1] is certainly correct in maintaining that we are not at present in a position to completely explain any of the simple processes of life from known chemical and physical forces; but it by no means follows that they are inexplicable by such means. All we can say is, that everything that we do know about natural processes tells against the rejuvenescence of life by conjugation believed in by Maupas, as I have already pointed out in an earlier essay. To my mind it is difficult to understand how an almost exhausted vital force could be raised again to its original state of activity, as the consequence of a union with another equally exhausted force. Maupas can only reply that we do not understand the essence of any 'phénomène primordial'; but if we cannot follow all the details of the chemical processes which for example bring about the phenomena of assimilation, because they are so extremely complex, and do not admit of our tracing the changes which succeed each other through the rapidly shifting stages—because this is so, we do not therefore take refuge in the assumption that the whole process is unintelligible. But this, in my opinion, is the case with the 'rajeunissement karyogamique' of which we know neither the beginning—the exhausted condition of the vital force, nor the end—the rejuvenescence, nor any intermediate stage. The whole conception is simply a fancy, the outcome of earlier deeply rooted convictions as to the necessity of death and the 'vitalizing' influence of fertilization. I do not care, however, to base my opposition to Maupas' views on the rejection, as fundamentally untenable, of the theory of rejuvenescence ; the argument is superfluous.

In considering *how it is that amphimixis has come to be regarded as a renewal or rejuvenescence of vital force*, the question naturally arises—why are we not content to see in this union of two nuclei, that which observation shows to us, viz. the union of two nuclear substances, and hence the mingling of two individually different hereditary predispositions? Maupas himself admits that this occurs, and indeed allows that variability is favoured thereby, thus supplying the necessary material for processes of selection. Why are we not content with this explanation, why do we seek for something further?

[1] Gustav Bunge, 'Vitalismus und Mechanismus'; ein Vortrag. Leipzig, 1886.

Obviously for no other reason but that we are saturated with the old notion that the egg cannot develope without fertilization, that fertilization is the same as vitalization. But was not this view overthrown long ago by facts? Are we not aware that, under certain circumstances, the egg can develope without fertilization? And is not this often true, for example in the Bee and in *Apus*, of that very egg which is also capable of fertilization? No one would have regarded fertilization as the vitalizing of the egg if the great majority of ova had developed parthenogenetically, or if science had first become acquainted with parthenogenesis and, later on, with fertilization. We should then have said that there must be some advantage in the mingling of two hereditary tendencies which has led to the introduction of amphimixis. But the facts are otherwise,—for centuries mankind has recognized this mingling as the indispensable antecedent to the development of offspring, and now, when we find that, under certain circumstances, an egg can develope without fertilization, we are unable to get rid of the old prejudice in favour of the view that the mingling is something more than a mere preliminary to development,—that it is an accessory force which bears some special and entirely peculiar significance. We cling to some supposed after-effect of the vitalizing influence of fertilization, extending through many generations, and against such an illogical theory even facts fight in vain, for the number of generations through which this after-effect is supposed to extend, is entirely dependent on the will of the controversialist, and keeps pace with the increasing length of the observed series of parthenogenetic generations. Maupas himself finds the number of such generations, which may succeed each other in some 'rare' species of Crustacea and Insecta, entirely insufficient to justify the conclusion that these agamic generations can continue indefinitely. I certainly believe that in most cases they are not of unlimited duration, because nature has chiefly fitted them for a cyclical method of reproduction,—for a regular alternation of parthenogenetic with sexual increase. But there are species like *Cypris reptans* which I have investigated (see Part II of this essay), in which it is certain that no such cycle exists, and that parthenogenesis continues without interruption. I have observed about forty generations in the case of *Cypris* *reptans*: this is not an unending series, but we do not know of any reproductive cycle which, after forty agamic generations, returns to a sexual one. So far as the argument is concerned, it does not signify at all whether such cases are rare, as Maupas thinks, or common: even their entire failure would afford no proof of the theory of rejuvenescence. For the theory of mingling,—if I may so designate my hypothesis,—is founded on the species-preserving influence of amphimixis, and leads us to expect that, wherever it is possible, nature will always introduce amphimixis into the reproductive history of a species and will render its employment obligatory. We should have no ground for wonder if purely agamic reproduction had no real existence. The vitalizing influence of amphimixis would not be proved even if this were the case.

On the other hand, I think a single example of continuous agamic reproduction proves that amphimixis is not absolutely necessary for the unlimited duration of life.

But if amphimixis is not absolutely necessary, the rarity of purely parthenogenetic reproduction shows that it must have a wide-spread and deep significance. Its benefits are not to be sought in the single individual; for organisms can arise by agamic methods, without thereby suffering any loss of vital energy: amphimixis must rather be advantageous for the maintenance and modification of species. As soon as we admit that amphimixis confers some such benefits, it is clear that the latter must be augmented as the method appears more frequently in the course of generations; hence we are led to enquire, *how nature can best have undertaken to give this amphimixis the widest possible range in the organic world.*

The following is an attempt to supply an answer to the question. The increase by means of budding and fission would be retained in multicellular plants and animals, on account of its great advantages, but it would only endure for a shorter or longer series of generations. Moreover, the expected advent of amphimixis would only take place when the collective hereditary tendencies of the individual are concentrated in the nucleus of a single cell; hence the mechanism of reproduction must have been associated with unicellular germs, and amphimixis became bound up with reproduction. I cannot remember that it has ever been maintained that the ontogeny of Metazoa and, so far as I am aware, of Metaphyta also, primarily depends on the necessity for sexual reproduction, or, better still, on the existence of *unicellular germs*. An ontogeny must then follow; for the collective hereditary tendencies of an animal being concentrated in a single cell, they must therefore, during development, pass through a series of stages very similar to those of their phyletic history. But, besides the germs destined for sexual reproduction, there are other unicellular germs, spores, &c.; and hence it is clear that the unicellular condition brings other advantages than those which amphimixis confers; but these unicellular agamic germs never exhibit any approach to the extent of range witnessed in sexual cells, and the origin and universal existence of unicellular germs are therefore to be sought in the latter.

I have already shown that the sexual cells, upon their first appearance, in some simple cell-colony such as *Pandorina*, would be compelled to undergo a nuclear 'reducing division,' after a relatively small number of sexually reproduced generations; because otherwise a continued doubling of the nuclear units must have occurred in consequence of the periodically repeated union of the nuclear substance of different individuals. This 'reducing division,' which is now securely proved for both male and female sexual cells in Metazoa, has, however, another meaning.

I proceed from the assumption that nature aims at the widest possible range for amphimixis. *How could this be obtained more effectually than by rendering the unicellular germs incapable of developing alone?*

The male germ-cells, being specially adapted for seeking and entering the ovum, are, as a rule, so ill provided with nutriment that their unaided development into an individual would be impossible; but with the ovum it is otherwise, and accordingly the 'reducing division' removes half the germ-plasm, and the power of developing is withdrawn.

What happens in the unicellular organisms? Here also our theory demands that periodic amphimixis should be provided by nature. For the attainment of this object it was indispensable that, as in Metazoa and Metaphyta, the organisms should, at certain periods, arrange themselves in pairs, and that their nuclei should be in the state best adapted for fusion,—viz. that the mass should be diminished so far as to reduce the hereditary units, or ids, to half. And all this as a matter of fact takes place. But it is nevertheless insufficient to ensure the desired result; for Maupas' experiments show us that, in spite of it, conjugation may be absent. The impulses which induce Infusoria to seek one another, and to pair, appear at certain periods and under certain external conditions, but if the latter are not favourable the impulses are not manifested and after the lapse of some time the power of conjugation is completely lost in the colony in question. I assume that Maupas' observations are correct, and am not criticizing them; but his own results prove, in my opinion, that his interpretations are erroneous in so far as he endeavours to find support for the theory of rejuvenescence by means of the facts which he has observed. Those colonies which have passed the proper time for conjugation gradually die out. Maupas considers that they die *a 'natural' death* in consequence of *old age*. He claims to have proved the occurrence of 'physiological' death in unicellular organisms, and to have refuted my views as to their potential immortality.

But I believe that the facts brought forward by him are capable of a different and a more correct interpretation.

What happens when a colony has passed the appropriate period and has therefore lost the power of conjugation? The very same thing which happens to the ovum which has attained maturity and has extruded its polar bodies — *disintegration, preceded by the loss of all power of development.* I believe that this result proceeds from the same cause in both cases,—*the reduction of nuclear substance*, i. e. in the Infusorian, the substance of the micronucleus. The egg disintegrates because the nuclear substance is insufficient for the commencement of ontogeny, and is imperfectly adapted for its preservation; the Infusorian disintegrates because its macronucleus must be renewed periodically, and because this cannot occur after the micronucleus has perished. And Maupas informs us that the latter disintegrates sooner or later, if the proper time for conjugation has passed by.

If we ask, how is it that the micronucleus disappears when conjugation is excluded, Maupas answers that the necessary