## XII.

# *Amphimixis or the Essential Meaning of Conjugation and Sexual Reproduction.*

With twelve Figures.

1891.

# AMPHIMIXIS OR THE ESSENTIAL MEANING OF CONJUGATION AND SEXUAL REPRODUCTION.

## PREFACE.

The present treatise brings to a conclusion a series of essays upon biological problems which have appeared in the course of the last ten years. They commenced with an enquiry into the duration of life, which led on to the question of the biological origin of death, and then turned to certain phenomena of inheritance and reproduction. They endeavoured to ascertain with certainty and to elucidate the real conditions of these phenomena, and to search out their essence and significance.

I shall attempt to explain, as clearly as possible, the close connexion existing between certain apparently isolated problems and the subject of this essay, which, although mainly concerned with so-called 'sexual reproduction,' is in reality the keystone of the whole structure. My object is to express more fully than before, the thought that the process which we are accustomed to regard as reproduction, is not reproduction only, but contains something *sui generis*, something which *may* be connected with reproduction proper, and in the higher plants and animals *is* so connected, but which is entirely separate in the lower organisms. I shall show that its significance does not lie in the maintenance of life but in the mingling of individualities.

To attain this object it will be necessary first to consider the remarkable morphological processes which accompany the maturation of reproductive cells, and, as far as possible, to seek for a true interpretation in the results of the most recent researches. Furthermore, it will be necessary to apply the ideas thus gained to the problem of conjugation, and to bring within the scope of the enquiry many other phenomena, such as the various kinds of reproduction, certain phases of the question of heredity, and the immortality of unicellular organisms, because these are most intimately connected and indeed mutually dependent.

Thus the thoughts which run through the previous essays resemble tangled threads which are gradually unravelled and are ultimately all woven together. I will only add the wish that the new conceptions to which these researches have led may prove a fruitful field for further investigations.

AUGUST WEISMANN.

LINDAU, LAKE OF CONSTANCE,
*September* 12, 1891.

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# XII.

# AMPHIMIXIS OR THE ESSENTIAL MEANING OF CONJUGATION AND SEXUAL REPRODUCTION.

## INTRODUCTION.

FOR more than a decade biological enquiry has been engaged, with renewed energy, upon the problem of fertilization. When the brothers Hertwig, and Fol had taught and demonstrated the fusion of the nuclei of ovum and spermatozoon, and had further shown that, before fertilization, the egg undergoes certain preparatory changes resulting in the extrusion of the previously well-known polar bodies,—an attempt was made to understand the significance of these processes. What can this substance be that it requires to be thrown out from the ovum before fertilization? The first answer to this question depended on the then commonly received, although never clearly formulated opinion, that fertilization consisted in the union of two opposed forces,—of what may be described as a male and a female principle which, by their fusion, kindled anew that life which, without such rejuvenescence, must gradually come to an end. Considering the dominant theory as to the significance of fertilization, it was certainly justifiable to endeavour to look upon these bodies, expelled from the egg, as the bearers of one of the two antithetical forces, which were previously united in a single ovum, but which required to be separated in order to render the egg capable of fertilization. The polar bodies were thus looked upon as bearers of the male principle, by the removal of which the ovum became for the first time sexually differentiated, i.e. became female. This idea was not merely ingenious, it was the legitimate result of those indefinite ideas as to the essential nature of fertilization, which up to the present day have held the field. Such a view must inevitably have been brought forward, if we were ever to arrive at a solution of the phenomena. I should certainly be the last to reproach the three savants who developed this hypothesis, although I have perhaps contributed something towards the proof of its unsoundness. The path to truth often lies through inevitable error.

I was, from the first, predisposed against the view of Minot, Balfour, and Edouard van Beneden, being influenced not only by certain isolated phenomena of inheritance, phenomena which were at a later time and with perfect justice, urged against it, but by the facts of inheritance taken as a whole, and by that conception as to the nature of fertilization to which I had even then been driven by these very facts, although unable to prove to myself, or to others, the soundness of my views.

We recognize two phenomena in amphigonic reproduction :—first, fertilization in its strictest sense, i. e. the fact that the ovum can only develope into a new being when it has united with the spermatozoon, after which union a 'vitalization of the egg' takes place (Hensen); secondly, the mingling of two hereditary tendencies. From the very oldest times it must have been observed that the peculiarities of the father as well as of the mother, may appear, and to an equal extent, in the children. Such transmission was conceived by some writers in a material sense; for they imagined a part of the substance of the mother or of the father as the basis of the body of the offspring; but it was also looked upon by others as simply the transmission of an impulse. Thus according to Aristotle the father confers the impulse to movement, while the mother contributes the material. Löwenhoek and the other 'spermatists' held that the semen alone forms the substance of the embryo, while his opponents, Swammerdam and Malpighi, the so-called 'ovists,' returned to Aristotle's view in so far that they believed that the mother gives rise to the substance, that is the ovum, while the male influence is limited to an 'aura seminalis,' which at the same time acts as the transmitter of movement.

Some writers regard inheritance by means of fertilization as a purely immaterial occurrence: thus Harvey, in his remarkable and minutely thought-out theory of heredity, imagined conception as a mental process, the folds of the mucous membrane lining the uterus corresponding to the convolutions of the brain, and giving rise to the foetus under the influence of the semen; just as the brain, under the influence of external impressions, gives rise to thoughts. The term 'conception,' when figuratively applied to mental processes,—a term which has been obviously derived from conception on the part of a woman,—is here reversed, and used to explain the very process from which it is itself derived.

The same fundamental idea runs through all theories of fertilization up to the present time—the idea that the fertilization, i.e. the 'vitalization of the egg' is the important part, or, as we may say, the true purpose of sexual reproduction. The other side of this mode of reproduction has been comparatively neglected; the fact that two different predispositions, on the one hand that of the father, and on the other that of the mother, are by fertilization united in a single organism, has appeared as a secondary, but it is clear to some extent as an inevitable result of fertilization. Although this view is nowhere directly expressed, it is implied in all the utterances of both older and more recent writers. It must be admitted that so long as biologists were acquainted with no method of reproduction except the sexual, it was impossible to regard fertilization in any other light; it seemed that the co-operation of two individuals was indispensable in order to call a third to life, and it can scarcely have been surprising for this new organism to resemble its progenitors more closely than any other living being. But, even in recent times, when other methods of reproduction among plants and animals gained recognition, they did not at first cause any alteration in that view which regards fertilization as a process of vitalization, a calling forth of new life. In the case of all those higher beings which do not possess the power of asexual reproduction, it became evident that a certain complexity of organization excluded this method of increase. But then the asexual reproduction of the lower organisms is by no means always sufficient to fulfil every condition necessary for the maintenance of the species, and hence the origin of new individuals from unicellular germs capable of fertilization must have appeared as an essential advantage.

The first fact which tended to throw doubt on the view that fertilization is a renewal of life was the discovery of parthenogenesis by C. Th. von Siebold[1] and Rudolph Leuckart[2]. When it was understood that, under certain circumstances, an egg could develope into a new individual without fertilization, this fact by itself was sufficient to show that a 'vitalization of the germ' could not be the object of fertilization, and could not be the cause of its appearance among living beings.

But it was long before the facts of parthenogenesis were generally accepted: indeed, in some circles they are not received at the present day. Only ten years ago, a prominent physiologist, Pflüger, held them to be unproved, and most botanists were inclined to doubt their existence among plants as well as animals; for at that time parthenogenesis appeared to be wanting in plants and to have been erroneously believed in at an earlier date. Even when de Bary and Farlow had proved its undoubted existence in certain ferns, and others had found it in certain fungi, the Basidiomycetes, and the existence of parthenogenesis among some plants and many animals could no longer be denied, the attempt was made to crush the phenomena in the Procrustean bed of the received conception of fertilization. The ingenious French savant Balbiani had previously propounded the view that a certain occult and hitherto undiscovered fertilization took place at the seat of origin of the germs, in the ovaries and testes; this fertilization was supposed to be in addition to the regular, recognized process, and, in cases of parthenogenesis, to compensate for it. So deeply rooted was the idea that new life could only arise by means of fertilization.

Even those investigators who no longer doubted the reality of parthenogenesis could not immediately and completely rid themselves of the received view, but endeavoured to make the new facts harmonize with the old ideas. Probably the most interesting attempt of this kind proceeded from Hensen, who indeed recognized that the 'views on sexual reproduction held up to that time had been overthrown' by means of parthenogenesis, inasmuch as the fundamental proposition as to sexual propagation had failed, viz., that one of the two sexual cells is by itself incapable of development. He nevertheless believed

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[1] C. Th. von Siebold, 'Wahre Parthenogenesis'; Leipzig, 1856.

[2] Rudolph Leuckart, 'Zur Kenntniss des Generationswechsels und der Parthenogenesis bei den Insekten'; Frankfurt, 1858.

that we must 'not, on account of these isolated cases, underestimate the fact that the necessity for fertilization is predominant, and controls, to their most secret depths, the sources of life in animals and plants.' (Phys. d. Zeug. p. 160.) Hensen takes as his starting-point the fact that, among many animals, e.g. bees and wasps, parthenogenetic ova give rise to male individuals only, while in others, namely *Psyche* and *Solenobia* among Lepidoptera, and *Apus*, *Artemia*, and *Limnadia* among Crustacea, only females are thus produced; further, that in many Lepidoptera, as *Liparis*, single eggs possess a power of developing without fertilization, but only into male insects, or into caterpillars which afterwards die, or in other cases only as far as some earlier or later phase of embryonic life. From this he concludes that we are here 'dealing with a graduated series of phenomena,' 'with a gradation in the powers of development and of reproduction, that is of qualities which can be conveniently included in the term '*sexual force*.' Hence at that time V. Hensen considered, if I have rightly understood him, that the 'sexual force,' it is true, ordinarily reaches the egg by fertilization, but that it may, under certain conditions and in varying degrees, be included in the female germ-cells alone. Such ova can then undergo embryonic development without fertilization, and, according to the amount of contained 'sexual force,' can pass through a longer or shorter period of development; many reaching only a certain stage of segmentation, others the entire larval stage, while finally some may attain the condition of imago, with mature sexual organs. There are moreover various degrees of 'sexual force'; for Hensen considers that male offspring are produced by a smaller force than females. Eggs from which, without fertilization, males only can arise (bees), possess, in his opinion, a smaller 'sexual force' than those which without fertilization produce females. This view ultimately depends on the conception of the life-preserving effect of fertilization, since males alone cannot perpetuate the species; and hence eggs which, without fertilization, give rise to males, are unable to maintain the continuity of life, and would finally result in the disappearance of the species, just as eggs of still smaller 'sexual force' lead to the disappearance of the individual in the larval or even earlier embryonic stages.

A question arising out of this view, and one which Hensen doubtfully propounds, is 'whether the "sexual force" could increase to such an extent that males should become superfluous,' and whether parthenogenesis, like sexual reproduction, could continue, not only for a limited number of generations, but for an unending series.

As regards an answer to these questions Hensen was quite unbiassed and awaited the decision of facts; moreover, from his point of view, no theoretical impossibility attended any such increase in the female 'sexual force.' He was, at that time, far nearer to the most recent views on fertilization than those numerous investigators who held parthenogenesis to be the consequence of fertilization which had taken place in earlier generations, and who considered that its effect could never last through an unlimited series of generations, but that the vitalizing or rejuvenating effect of fertilization must be renewed from time to time, or the power of reproduction would be lost. On these fundamental views as to the 'vitalizing of the germ by fertilization' depends the reluctance of nearly all writers to recognise the submitted facts of a continuous and purely parthenogenetic reproduction, as for example in the case of the Ostracoda. It is certainly true that absolute proofs of the indefinite duration of this mode of reproduction cannot be obtained; for unlimited time and innumerable generations are not within the limits of observation; but who doubts whether the sexual method, with which we are so completely familiar, and which is for this reason spoken of as the usual mode of reproduction,—who doubts whether this can endure without limit? And yet this assumption is as incapable of proof by appeal to experience as the other. It appears to be very difficult to get rid of the deeply rooted idea that fertilization is a vitalizing process, a 'rejuvenescence of life,' although we are quite unable to explain the nature of the renewal which is supposed to take place. The old idea of 'vital force' unconsciously bears a part in this view, an idea which certainly does not gain any scientific justification because, as Bunge has rightly said, we are to-day very far from laying bare the deepest roots of any one of the processes of life and explaining it by the operation of known forces. I hardly think that we shall ever reach this point, but until the explanation of vital processes by means of the well-known chemical and physical properties of matter is proved to be impossible, it will, in my opinion, be unjustifiable for science to relinquish the attempt. The conception of vital force and the conception of fertilization as a renewal of life hang more closely together than we are in the habit of thinking.

The facts of the transmission of hereditary tendencies from both parents to the child, together with the facts of parthenogenesis, induced me, at an early date, to look for the essence of fertilization, neither in the vitalization of the egg, nor in the union of two opposed polar forces, but rather in the fusion of two hereditary tendencies,—in the mingling of the peculiarities of two individuals. The substances which come together in fertilization, from the male and from the female, are not fundamentally different but essentially similar, differing only in points of secondary importance. This is what I meant by the statement, made shortly after the discovery of the fundamental phenomena of fertilization, that the two germ-cells which unite together, are in the proportion of one to one; that is that they are essentially alike.

If this conception be valid, the above-mentioned view as to the extrusion of polar bodies, propounded by Minot, Balfour, and E. van Beneden, must be erroneous; for a male principle such as their theory demands has no existence, and cannot therefore be expelled from the ovum. There is no male or female principle, but only a paternal and maternal substance. If, on the other hand, Minot's Gonoblastid Theory be sound, it follows that my view, which finds the essence of fertilization in the union of the different hereditary tendencies of two individuals, must be abandoned.

It seemed to me possible to settle the question by means of parthenogenesis. If parthenogenetic eggs develope without first expelling polar bodies, then Minot's theory, the 'compensation theory' as O. Hertwig has recently called it, receives material support: if however polar bodies are formed by them, it is impossible that such bodies can represent the male principle of the egg. I succeeded in proving the existence of a polar body, first in the ovum of a parthenogenetic Daphnid, *Polyphemus oculus*, and later, in conjunction with Ischikawa, in the parthenogenetic eggs of various other species of Daphnids, and also in some of the Ostracoda and Rotifera. Blochmann showed the existence of a polar body in the parthenogenetic ova of the *Aphidae*, and there is now no doubt that polar bodies are formed in most if not in all parthenogenetic eggs. The 'compensation theory' must therefore be given up, and the question arises as to the theory which can take its place.

Before the existence of polar bodies in parthenogenetic ova had been completely established, I had endeavoured to find, in opposition to the 'compensation theory,' another meaning in the polar bodies. The history of our earliest knowledge of the processes of nuclear division, by the work of Auerbach, Bütschli, Flemming, and others, is well known: the existence of most remarkable and excessively minute arrangements for cell-division were shown to exist in the mysterious 'chromatin substance' of the nucleus, the so-called nuclear loops, which are accurately divided in a longitudinal plane, the halves then entering the two daughter nuclei which are being formed. These chromatin rods acquired a new significance when E. van Beneden first showed that they were contained in equal numbers in both the male and female reproductive cells, and that they arrange themselves side by side, to build up the chromatin substance of the embryonic nucleus. Considering this and certain other facts, it became more and more probable that the chromatin rods were the essential factors in fertilization, the substance which was contributed by the parents and fused together in the offspring, and which was therefore, in all probability, the bearer of hereditary tendencies. Strasburger, O. Hertwig, and v. Kölliker also gave expression to this view for which I had contended. We regarded the nuclear loops as that idioplasm which Nägeli had been led, by his acute reasoning, to suggest; a substance which is not fluid, but organized, which possesses an extremely complex structure, and is transmitted from one generation to another.

But this view did not decide the question whether the ovum was not, after all, vitalized by fertilization. O. Hertwig was obviously still under the influence of this idea when in 1885 he maintained in the above-mentioned work, that 'the *fertilizing substance* transmits, at one and the same time, those peculiarities, which children inherit from their parents.' Such an explanation is, in a certain sense, defensible, and we may speak of a 'fertilizing substance,' in so far as the amounts of nuclear material which unite during fertilization seem to be necessary to determine the commencement of development. But this refers only to the restoration of a certain amount of nuclear substance, rendering its *quantity* sufficient for development, and parthenogenesis shows us that when the second polar body is absent this quantity can be supplied by a single sexual cell. In the precise meaning of the word, as it is ordinarily used, there is no such thing as a fertilizing substance, and the progress in thought from the old to the new doctrine of fertilization can only take place when the idea of such a substance in the old sense is completely abandoned, and when it is recognized that *fertilization has no significance except the union in the single offspring of the hereditary substance from two individuals.*

The advance which has occurred is due to Strasburger's writings as well as my own: the former agreed with O. Hertwig and me as to the essential similarity, as regards their chief constituents, of the two sexual cells, and as to the secondary nature of their differences: Strasburger in fact went so far as to say that all differentiations of sex were simply the means adapted to bring together the two cell-nuclei which were necessary for the sexual act. With this view I not only entirely agreed, but totally rejected the pre-existing dynamic theory of fertilization, in as much as I could not recognize the object of fertilization as the 'vitalization of the germ' or the 'rejuvenescence of vital processes,' but regarded it as simply *the union of the different hereditary tendencies of two individuals.* This union, which has hitherto been regarded, to some extent, as merely a necessary consequence, has become the important feature, while the 'vitalization of the germ' by the interaction of two opposed sexual cells,—formerly looked upon as the essential part of the process,—has declined from this high position and is regarded as only the means by which the process is effected.

I was, at that time, so completely convinced that the facts warranted no other explanation, that I maintained that the nucleus of an ovum might be fertilized as fully by the nucleus of another ovum,—i. e. might be rendered equally capable of development,—as by the nucleus of a spermatozoon. The passage in which I advocated this view runs as follows:—'If it were possible to introduce the female pronucleus of an egg into another egg of the same species, immediately after the transformation of the nucleus of the latter into the female pronucleus, it is very probable that the two nuclei would conjugate just as if a fertilizing sperm-nucleus had penetrated. If this were so, the direct proof that egg-nucleus and sperm-nucleus are identical would be furnished.'[1] Boveri succeeded in accomplishing this a few years later, although he made use of the nuclei of two spermatozoa instead of those of the ova.

I also hold, in opposition to the rejuvenescence theory, that there is no polar antithesis, and that, in the union which is the essence of fertilization, the nuclear loops contribute neither male nor female principle, but a paternal and maternal substance, and that the significance of fertilization is nothing more nor less than a mingling of the hereditary tendencies of father and mother.

## I. The Significance of the Process of Maturation of the Germ-cells.

### *The Maturation of the Ovum.*

Relying on the views set forth above, I have made the attempt to substitute a new explanation of the formation of polar bodies in the animal ovum for that which has hitherto found acceptance. If that substance which is expelled from the ripe ovum in the polar bodies be not the male principle, what can it be?

The cellular nature of the polar bodies has been demonstrated by Giard, Bütschli, and O. Hertwig; van Beneden has shown that they contain chromatin, and that at each of the two divisions which give rise to the two polar bodies, half of the chromatosomes leave the egg in the nucleus of a polar body. If then the chromatin be the idioplasm, the material basis of heredity, or, in other words, that substance which determines the nature and essence of the cell and its descendants, then cells of different kinds must contain correspondingly different varieties of idioplasm. Hence my theory of germ-plasm may be expressed as follows:—The fertilized ovum contains germ-plasm in its nucleus, i. e. idioplasm endowed with the collective hereditary tendencies of the species: at each of the cell-divisions by means of which the ovum developes into the organism, this idioplasm splits into two quantitatively similar

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[1] Vol. I, pp. 252, 253.

halves in order to form the nuclei of the daughter-cells. But these halves are not always qualitatively alike; they are only so when they are to give rise to similar cells: when the cells which arise by division have a different significance in development, their idioplasm also differs in quality. *The germ-plasm of the ovum is thus continually undergoing change during ontogeny, inasmuch as the developmental tendencies are being split up, and become more and more distributed among the members of successive cell generations,* until finally each kind of cell in the body contains only that developmental tendency which corresponds with its specific histological character. Each specific cell is thus dominated by a specific idioplasm.

As soon as I had arrived at this conclusion, it was easy and indeed inevitable to refer the differences between spermatozoon and egg-cell to a specific idioplasm which had stamped its peculiarities upon each cell. But since both male and female germ-cells contain the substance which fuses during fertilization to form the segmentation nucleus, and therefore germ-plasm, I concluded that a part of this true germ-plasm which forms the nuclear substance, splits off at the first ontogenetic stage, as specific sperm or egg idioplasm, which controls the germ-cell during its growth, and confers upon it a specific histological character. I sought for the meaning of the cell-division which results in the separation of the polar bodies, in the suggestion that by this means the spermogenetic or ovogenetic idioplasm, rendered superfluous after the attainment of the specific form, was removed from the germ-cell, while the germ-plasm, grown in the mean time to a larger mass, remained behind in the cell. I therefore recognised in the cutting-off of the polar bodies the removal of histogenetic idioplasm from the germ-cells.

While I was busy working out these interpretations, I discovered new facts which caused a modification of this view and led to the conclusion, which up to the present time appears to be sound, that the formation of polar bodies is a *process for the reduction of the hereditary substance.*

The fact which led to this conclusion was the *law of the number of polar bodies,*—the discovery that all animal eggs which require fertilization expel two polar bodies, one after the other, while all true parthenogenetic eggs give rise to one only. Now the ovogenetic idioplasm cannot, at the most, occupy more than the first polar body; the second must have some other meaning, for if I had been correct in assuming the necessity of the separation of the specific nucleoplasm from the egg, it follows that this substance must be separated as fully and completely from the parthenogenetic as from the sexual egg. The second polar body must therefore possess a different meaning. In the fifth of the essays here collected[1], I first indicated that this meaning is a reduction in the substance which forms the material basis of heredity, in that *the number of the contained ancestral plasms are diminished by one-half* during the halving of the nuclear substance to form the two daughter nuclei. By the term ancestral plasms, I referred to the separate kinds of germ-plasms from different ancestors which, according to my view, must be contained in the germ-plasm of each individual at the present day. If, before the introduction of sexual reproduction, the germ-plasm of each living being contained the developmental tendencies of *one* individual only, its structure would be altered by sexual reproduction; for after fertilization the different germ-plasms from two individuals would meet in the nucleus of the egg; furthermore, the number of these different kinds or units of germ-plasm must necessarily have been doubled with each succeeding generation, so long, at least, as they could have divided, preparatory to fertilization, without relinquishing the power of giving rise, collectively, to the whole organism,—that is, until the units had reached the minimal limits of their mass. From this point onwards sexual reproduction could only have been rendered possible either by a doubling of the nuclear substance, or since this was impossible, by a halving of the germ-plasm of both germ-cells before each act of fertilization, a halving which was not only quantitative, but was above all a separation of the contained individual units, a separation of ancestral germ-plasms, or briefly of ancestral plasms.

Hence, after the discovery of the law of the number of polar bodies, I interpreted the first division of the nucleus as the removal of ovogenetic idioplasm from the egg, and the second as a halving of the number of ancestral units contained in the germ-plasm. Such halving must have occurred, or the number of ancestral units would have been doubled. It necessarily

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[1] Vol. I. pp. 257-342.

followed from this view that the ancestral units contained in the spermatozoa must also have undergone a diminution by half. I postulated therefore a reduction of the spermatozoa by division, and, to my mind, there was 'no doubt' that this process occurred in them 'at some time and by some means[1],' although not perhaps in the same manner as in the ova. I even said from the very first[2] that 'it is quite conceivable' that this division might occur in a manner entirely different from that of the egg, since in the former case both daughter-cells might be of similar size and might become spermatozoa, in which case neither of them would shrink and become polar bodies.

### *The Maturation of the Spermatozoon.*

I have not been able to make out, by my own investigations, the facts which confirm the soundness of these views as to the spermatozoa; my impaired eyesight, which has so often put a stop to microscopic investigations, has again rendered the continuation of this research impossible. But Oscar Hertwig[3] has recently given us an account of the development of the spermatozoa of *Ascaris megalocephala,* which not only proves the reduction of the male germ-cells by division, but also shows that it takes place in precisely that way, which from the first I had regarded as most likely.

Since these new facts affect our conclusions with regard to many aspects of the process of fertilization, they are here shortly abstracted. They may possibly enable us to penetrate still more deeply into the meaning and significance of the processes by which the nuclei of germ-cells are reduced in size.

Ever since Edouard van Beneden's classical researches on the process of fertilization, it has been well known that *Ascaris megalocephala* is one of the most favourable objects for the observation of the minute arrangements and changes occurring *in the nuclei of germ-cells.* The nuclear loops are not only relatively very large, but are also very few in number. Boveri was the first to show that, as regards this number, two varieties of the species exist, one containing two nuclear loops in the young germ-cells, the other containing four. O. Hertwig then

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[1] Vol. I, p. 381. [2] Vol. I. p. 385.

[3] O. Hertwig, 'Ueber Ei- und Samenbildung bei Nematoden,' Archiv f. mikr. Anat. 1890.

proved, as might have been expected, that this difference in the number of loops in the youngest germ-cells exists also in the male sex. He called the variety which produces two loops *Var. univalens*, and that which produces four *Var. bivalens.* Since the development of the spermatozoa in both varieties differs only in the number of nuclear loops which are formed, I will, in the following account, deal with only one of them, the *Var. bivalens.*

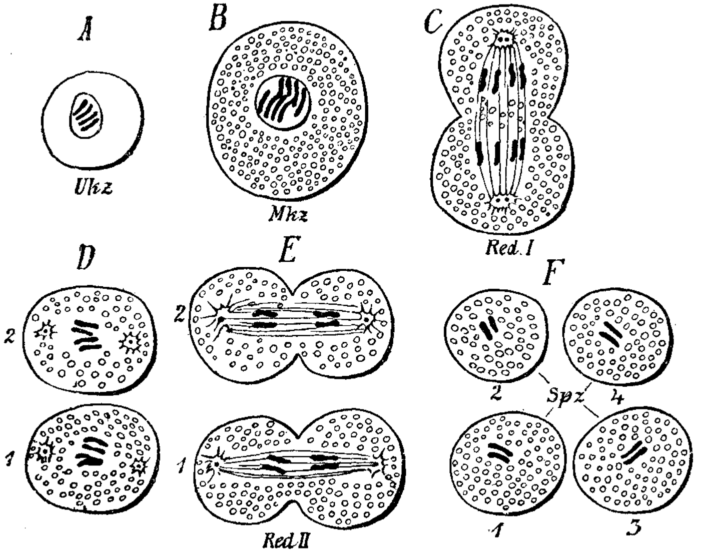

Fig. I.

Formation of spermatozoa in *Ascaris megalocephala*, var. *bivalens* (modified from O. Hertwig). *A.* Primitive sperm-cells. *B.* Sperm-mother-cells. *C.* First 'reducing division.' *D.* The two daughter-cells. *E.* Second 'reducing division.' *F.* The four grand-daughter cells,—the sperm-cells.

The formation of the spermatozoa falls into three stages; the first is that of the 'primitive sperm-cells': these youngest male germ-cells then proceed to increase by means of successive divisions. The division of the nucleus is effected by karyokinesis after the usual manner; the four nuclear loops split longitudinally and the halves form the two daughter-nuclei. After this process of multiplication has lasted for a considerable time, the cells pass into the second stage,—that of the 'mother-cells of spermatozoa.' They cease to multiply, grow considerably, and their nuclei pass into the resting condition, viz. the condition of a nuclear network into which the loops break up. When these cells have reached their full size they enter upon the preparation for fresh divisions, which are only two in number and rapidly follow each other. As soon as these are over, the whole development is complete. It is this last stage which brings about the 'reducing division' which I had predicted. The finely divided chromatin bodies contained in the nuclear network build up eight long, thin rods or threads, which afterwards shorten and form thicker rods, arranged by means of the pole-corpuscles or centrosomata, which act in such a manner that four rods are turned toward one pole and four toward the other. A division of the nucleus and of the cell now follows resulting in the formation of two daughter-cells, each of which contains as many nuclear loops as the original sperm-cells, i. e. four. This division is followed immediately by another on the same plan, but without any intervening resting stage: *the number of* nuclear rods is therefore again halved, so that each daughter-cell of the second order contains but two.

Hence the number of nuclear rods is at first increased from four to eight, and then by two consecutive divisions, this latter number is first halved and then quartered, the final result being *a halving of the number of rods in the original sperm-cells.*

It is well known that precisely the same results are brought about by those divisions of the ovum which give rise to the polar bodies. In the egg the nuclear rods are first doubled and then, by two consecutive divisions, reduced to half their original number. In all essentials, the development of the ovum passes through precisely the same process as that of the spermatozoa. The first two stages, described by O. Hertwig, in the development of the spermatozoa I also find in the formation of the egg. The primitive ova correspond to the primitive sperm-cells, the mother-cell of the ova, or the mature full-sized egg, immediately before reduction by division, corresponds to the mother-cell of the spermatozoa, the only difference being that the egg in this, the second stage, has, as a rule, attained its definite shape and size and is surrounded by its membranes, and that the two last divisions, which are together spoken of as the 'reducing divisions,' generally take place after the egg has been laid or has, at any rate, left the ovary. This probably explains, as I have already maintained, why the division is so unequal, and why all the daughter-cells cannot become ova, but only the largest of them, viz. that one which alone contains the food-material necessary for the building up of the embryo.

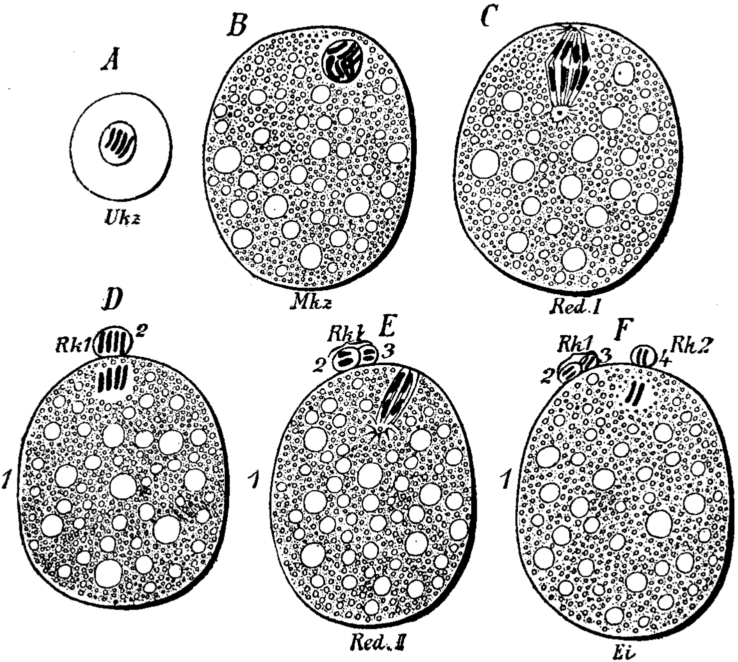

Fig. II.

Formation of ova in *Ascaris megalocephala*, var. *bivalens*.

In other respects the formation of the polar bodies corresponds with the two divisions of the mother-cells of spermatozoa: in both cases there are two successive cell-divisions, and furthermore in the egg both daughter-cells of the first generation divide again—not only the larger one, the ovum, but also the smaller or first polar body—for it is well known that the latter body generally splits into two secondary polar bodies, and the significance of this apparently aimless division has hitherto been sought in vain. But now we see that it depends on the persistence of a phyletic stage of development, on the survival of an earlier condition, in which the original egg-cells underwent a 'reducing division,' like that of the spermatozoa, *producing four cells, each of which was potentially an ovum.*

Moreover in another, and obviously a decisive point, the 'reducing divisions' of ova and spermatozoa are in correspondence;—in the manner and method of the division of the nuclear rods in the daughter-nuclei. The process of karyokinesis here differs from any other mode of nuclear division, in that there is no longitudinal splitting or doubling of the nuclear rods, bringing about a contribution from each rod in the equatorial plate to both daughter-nuclei; instead of this, half the whole number of rods passes to one pole of the nuclear spindle, and half to the other. Furthermore, there is no resting-stage between the two divisions, during which the rods break up into the nuclear network, but the two divisions follow each other without any interval. If *the 'reducing division,' for which* I *have argued,* has any existence, we must look for it here; for, so far as proofs can be afforded by observation, they are forthcoming. The number of nuclear rods is reduced to half, and hence the mass of the nuclear substance is certainly halved. And if we must concede that the rods in a nucleus are not absolutely alike, but are derived from the differing germ-plasms of various ancestors (viz. that the rods consist of such different kinds of germ-plasm), it follows that a reduction of the ancestral germ-plasms is admitted.

The new facts discovered by O. Hertwig leave only one point obscure. We see indeed that, in the case of the spermatozoon as in that of the ovum, the nuclear rods are reduced to half, but we ask in vain why two successive divisions are necessary to bring about this reduction, when it seems that a single one would suffice. I had formerly concluded that since parthenogenetic eggs expel only one polar body, instead of the two which separate from all ova requiring fertilization, the first division must have a different significance from the second. I regarded the second division alone as the 'reducing division,' and this was a perfectly sound and logical conclusion, so long as it remained unknown that the mother-cells of ova contain twice as many nuclear rods as existed in the primitive egg-cells. Until this was known, the 'reducing division' was only required to effect a halving of the nuclear substance, and for this purpose one division would be sufficient. We now know that a second division is rendered necessary because the number of the rods is doubled before the process of reduction has begun. The object served by this doubling remains an obscure point upon which even the spermatogenesis of *Ascaris* does not at present enlighten us. My previous interpretation of the first polar body as the removal of ovogenetic nucleoplasm from the egg must fall to the ground: about this there is no possible doubt, but how can we better explain the necessity for two divisions? Why should the nuclear substance be doubled, only to be halved again? O. Hertwig has also propounded this question, but so far without being able to supply an answer. He hopes that a more accurate study of the manner and method of the arrangement of the chromatin elements in the two successive divisions will ultimately lead to a deeper knowledge of the essence of the whole process of maturation. I also hope the same. The processes which bring about the doubling of the chromatin rods in the resting nuclei of ova and sperm-mother-cells, contain, without doubt, the key to an understanding of the necessity for this increase in number, which at present appears to be so mysterious and superfluous.

Whether unaided observation will ever succeed in making clear the accessory processes, in other words, whether morphological events can be followed in minute detail so far that we can wrest from them the secret of their meaning, we cannot say. Without some guiding idea, it is scarcely possible that the observations of investigators could be directed to the most essential part of the process, especially in this case, where differences of substance are probably present — differences which might be invisible, but are perhaps capable of being inferred by processes of reasoning.

Thus it may be possible, on the basis of Hertwig's observations, to penetrate somewhat deeper into the meaning of the remarkable processes which attend the 'reducing divisions,' if only the subject be attacked from the point of view of the theory of ancestral germ-plasms.

### *The Double Division of the Nuclear Substance in the Formation of Germ-cells.*

With regard to the egg, the following question can be formulated—What is the meaning of the first division in the formation of polar bodies, since the second alone would suffice to *halve the nuclear substance? With regard to the* sperm-mother-cell however the question must run,—why should division take place twice, when its single occurrence would have sufficed to reduce the nuclear loops by one half? The simplest answer to these two questions is to be found in the fact that the number of nuclear rods is doubled at the beginning of the reducing process, and must therefore be quartered if a diminution to one half the normal number be the ultimate necessity. This leads us to enquire why the preliminary doubling of the nuclear rods is necessary.

Regarding spermatogenesis only, it might be maintained that here we are simply dealing with a process for increasing the number of spermatozoa as far as possible, but if we attempt thus to explain a fourfold instead of a twofold increase, comparison with the egg-mother-cell, producing four descendants of which one only undergoes development, renders any further discussion of this idea superfluous.

In attempting to explain the phenomenon I start from the conception which led me to the idea of a 'reducing division,' i. e. the building up of the germ-plasm, that is the active substance of the nuclear rods, from innumerable ancestral units As I explained on the first statement of this idea, it is a view which is necessarily suggested if we accept certain premisses, the chief of which is, that the hereditary substance from the two parents does not altogether become one during the fusion which occurs at fertilization, but that each retains a certain independence. This agrees with observed facts in so far that, as a result of fertilization, the paternal and maternal rods come to lie close to one another in the same nucleus, but undergo no true fusion into a single mass. If we assume that this remains true during the whole ontogeny, we can only suppose that half the nuclear rods of every cell are paternal and half maternal and that both these simultaneously influence the cell. We do not yet understand how this takes place, and must for the present dismiss the question; we do know however that it is an actual fact. We know that the paternal no less than the maternal nuclear rods of the fertilized ovum possess the developmental tendencies of the species, and that either of them alone, that is in the absence of the other, are present in sufficient numbers to regulate the development of the egg, each set containing all that is necessary to originate a mature individual of the species. And the same fact holds good for each successive stage of embryogeny, with just this difference, that the potentiality of stages to come, and not of those passed through, is contained in the embryonic cells. Furthermore every cell contains the separate paternal and maternal nuclear rods, and either set is capable of producing all the subsequent stages. This remains true throughout the whole course of development, from the fertilized ovum which produces the parent, to the male and female germ-cells of the offspring. No real fusion of the two nuclear substances into a single mass ever takes place, so that the corresponding predispositions of the two parents are arranged together, but the hereditary substance contributed by the father remains separate from that contributed by the mother. These substances are made up of units of which each contains those collective predispositions which are indispensable for the building up of an individual, but each possesses an individual character, i.e. they are not entirely alike. I have called such units ancestral plasms, and I conceive that they are contained, in larger or smaller number, in the chromatin of the mature germ-cells of living organisms, viz. that the parental nuclear rods are made up of a certain number of these.

I have thus briefly called to mind the manner in which I conceive that many such ancestral plasms are collected together in a single nuclear mass, and the consequent necessity for a 'reducing division.' It is not perhaps superfluous to return to this subject once more. Each of the parental germ-plasms which, at the phyletic origin of sexual reproduction, for the first time fused together in the segmentation nucleus of the offspring must have contained the potentiality of one individual only, and must have been, in a certain sense, completely homogeneous. Naturally, such a statement by no means excludes the existence of a very complicated structure, in which a number of different predispositions, or of different parts, are collected together, but it limits each such predisposition to being present only *once*, and *in only one variety*. I conceive of this primitive germ-plasm, as of one single ancestral unit of an existing species, only perhaps relatively larger, its separate predispositions not having been yet reduced to the present minimum.

All this however was altered in the germ-cells of the first sexually produced individual, in which the nuclear rods of the two parents came together, and together composed the hereditary substance of the child. If now, as has been argued above, the paternal and maternal hereditary substances did not fuse but only arranged themselves side by side, there will be found, in the germ-cells of the child, two substances similar as regards the species but dissimilar as regards the individual. If the mass of nuclear substance cannot be increased, both kinds of nuclear substance must be reduced by one half. If we imagine the nuclear material of one such germ-cell to consist of a single thread, one half of it would be made up of paternal and the other half of maternal germ-plasm.

I call to mind the diagram by which, in an earlier essay[1], I endeavoured to make intelligible how the number of ancestral plasms of various kinds which meet together in the germ-plasm are doubled in each successive generation, and how, in the formation of the germ-cells of each generation, the germ-plasms must be reduced to half their size, or their united mass would be doubled in every generation. But in time a limit to this continuous diminution of the ancestral plasms must have been set, and this would occur when the amount of substance necessary to contain all the predispositions of the individual had reached its minimum. Obviously these units cannot become infinitely minute; however small they may be they must always retain a certain size. This follows from the extremely complicated structure which we must without any doubt ascribe to them. These units which make up the germ-plasm of living animals I have called ancestral plasms, but my views about them have been misunderstood, and I have been treated as though I had applied the term to the ultimate biological units of idioplasm. Nothing was further from my mind: I look upon the single ancestral plasms as extremely complex, and built up of countless biological units. I have

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[1] Vol. I. p. 369.

retained the conception in its original form, as it is indispensable for the understanding of the 'reducing division.' When I maintained that the units of the germ-plasm are indivisible, I did not refer to mechanical divisibility, but to that division which a unit cannot undergo without losing its original character. If we divide a dog into two parts, neither part is a dog; and so, according to my views, half an ancestral plasm is not an ancestral plasm, is not an hereditary unit capable of calling forth a complete individual; or, to express this with reference to its minute structure, a half would no longer contain all the predispositions necessary for the whole individual. The number of these units would be doubled as the result of each fresh fertilization if the preliminary halving did not occur. Hence the necessity for such halving, which I have attempted to render clear by the foregoing train of thought.

Taking my stand upon this, I argued that a 'reducing division' of the nuclear material takes place before fertilization in both germ-cells,—that is a division contrary to the ordinary method, in that it does not divide the collective ancestral plasms in two equal and similar groups between the daughter-nuclei, as in 'equal divisions[1],' but halves their number so that one daughter nucleus receives one set and the other another set of ancestral plasms. In the ovum I recognised the necessary 'reducing division' in the formation of the second polar body, for it had then been shown by the careful observations of van Beneden and Carnoy upon *Ascaris megalocephala* that two out of the four nuclear rods pass into the second polar body while the other two compose the nucleus of the ovum.

The idea of a 'reducing division,' as I then conceived it, seems to have met with but little acceptance among the German biologists. Except Platner and recently O. Hertwig and Henking, I know of no one who has accepted it. The first-named employed the expression, but without indicating whether he used it in my sense. This cannot be taken for granted, as the simple halving of the chromatin mass may be so designated. All that we can see is a reduction in mass, and the discoveries of Platner and Hertwig do not *directly* teach us more than that in the division of the mother-

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[1] For a further account of these methods of division see Vol. I. pp. 369-377.

cell the number of nuclear rods, and therefore the mass of hereditary substance, is reduced to one-half. O. Hertwig appears to accept my views as set forth above: at any rate he thinks that I am 'on the right road in regarding the process by which the second polar body is formed as a reducing process, by means of which an amount of germ-plasm is removed, equal to that which is afterwards conferred by the nucleus of the spermatozoon.' Furthermore, his own account of the significance of the process seems to agree with mine when he says—'In this very simple way it is brought about that the fusion of the two nuclei resulting from the sexual act,—a union of the chromatin substance and the chromatin elements,—does not form double the mass which is normal for the species concerned.'

When, however, we remember that O. Hertwig rejects the theory of ancestral plasms, and takes the antagonistic view of a complete mingling of maternal and paternal germ-plasm, we must be convinced that the reducing process, in the sense in which I have spoken of it, has no existence for Hertwig, and that, from his standpoint, the only conceivable theory is that of a simple reduction of mass. And yet obviously such is not his view, for he speaks of chromatin elements; and hence the question arises as to the kind of elements which these can be if they are not ancestral plasms. It seems to me that the reducing process only acquires a meaning when taken in connection with the supposition of ancestral plasms, unless indeed it is merely a matter of reduction of mass. But it is most improbable that a mere reduction in mass is the object of this very remarkable double division of the nuclear substance, which is never again repeated in the whole developmental history of the animal. First, the mass of nuclear substance is doubled, and then reduced by two divisions to one-half its original bulk. Obviously it would have been simpler if this process had been omitted, and if the nuclear substance of the egg and sperm-mother-cell had, during its growth, merely stopped short at the requisite size. It may perhaps be objected that the growth of the ovum and sperm-mother-cell and their histological structure necessitate such a mass of nuclear substance. We know little or nothing about the relationship of the mass of nuclear matter to the mass of the cell-body, but it must be doubted whether in this case the relation is fixed, because as a rule ova and spermatozoa differ so enormously in size, and above all because the ova of different species vary so greatly in this respect. Moreover, Boveri has shown us that in one and the same species two otherwise indistinguishable germ-cells exist, one of which contains twice as many nuclear rods as the other, and therefore as far as we can tell twice the amount of nuclear substance. Hence the 'reducing division' cannot be a mere division of mass.

There remain for consideration the 'chromatin elements' of O. Hertwig. What are these elements? Are they the smallest possible portions of living matter, something like the *pangenes* of de Vries? This distinguished botanist in his highly suggestive and thoughtful writings has developed the idea that the nuclear substance of the fertilized ovum is composed of countless very minute particles, called by him pangenes. He thus recalls Darwin's pangenesis, with which his theory has something in common. These pangenes however do not, like the gemmules of Darwin, give rise to cells, but they are the bearers of the various qualities of cells. If we now assume with de Vries that the nuclear substance of germ-cells consists of innumerable kinds of such pangenes, we may regard these either as uniformly mixed together without any kind of arrangement, or as arranged in a definite order. In the first case, each division (reduction) of the mass would only result in a diminution, and the components of both halves would remain the same: the various kinds of 'chromatin elements' would not by this means be reduced to half, but all the elements would be contained in each portion. But if these pangenes were arranged in a regular order in the germ-plasm, and if with Hertwig we designate the groups of these as predispositions, without expressing in any way how such predispositions can be conceived, it follows that a halving of the mass of germ-plasm or nuclear substance would give rise to two halves, neither of which would contain all the predispositions necessary for the construction of an individual, although both might contain many double predispositions. Hertwig imagines that the predispositions which according to his view (loc. cit. p. 110) are present in the germ-plasm of the paternal and maternal germ-cells, mingle together, and de Vries has also assumed this. Hertwig states that 'it is not improbable,' that in the complete union and mingling of the parent nuclear substances presupposed by him, 'similar predispositions would arrange themselves closer to one another than dissimilar ones, and from the similar but varying paternal and maternal predispositions an *intermediate form* might arise by mutual influence.' I have printed the words 'intermediate form' in italics because it appears that so much depends upon it; for obviously the intermediate form of predisposition must be looked upon as *one* and no longer as two separate predispositions. Hence, according to Hertwig, the fusion of two parental germ-plasms produces an intermediate form of germ-plasm *in which each predisposition is not doubled, but remains single.* Furthermore, this germ-plasm could grow, and could be represented by a larger or smaller mass, but it is impossible that it could be halved without losing its character as germ-plasm, except it were first doubled in size, and all its predispositions were doubled and symmetrically arranged on each side of the plane of division like the antimeres in a bilaterally symmetrical animal. But even in this last case a 'reducing division,' that is a putting on one side of half the number of the corresponding but individually distinct chromatin elements, is impossible because both halves would contain precisely similar predispositions. O. Hertwig deceives himself in believing that he can assume a halving of the number of chromatin elements while his conception of the composition of the germ-plasm only admits of a halving of mass. In his germ-plasm, made by the fusion of paternal and maternal predispositions, there are no differing predispositions of one and the same part or organ: the parental differences have, according to his view, neutralized each other, and each predisposition is present as a single intermediate variety. Whence comes the necessity or the possibility of any reduction? What are the units which are to be reduced in number?

It is clear that we cannot avoid the assumption of higher units of germ-plasm, each one of which *contains, collected together, the varied predispositions of the species*, whether called by my term ancestral plasm, or by any other name. I shall attempt to explain elsewhere that this conception is not only indispensable for our understanding of the 'reducing division,' but that it is even rendered necessary by the phenomena of heredity. At present I do not propose to do more than show that the idea of a 'reducing division' presupposes the *multiplication of* the equivalent but individually characterized units in the germ-plasm of the fertilized egg, and that, without this presupposition, the 'reducing division' is entirely devoid of meaning.

If we may now feel greater certainty than ever before in regarding the double division of the egg and sperm-mother-cell as a 'reducing division,' we gain at the same time further proofs that the germ-plasm is composed of ancestral plasms, that is of hereditary units of a higher order, each one of which, if it alone dominated the ovum, would be capable of guiding the whole ontogeny and of producing a complete individual of the species.

Before I attempt to show how these fundamental views throw new light on the discoveries of recent years, I *will say a few* words on the independence of the maternal and paternal chromatosomes.

According to the views which I have expressed, the nuclear rods are built up of a series of ancestral plasms, which are not intimately connected together, but so far as mere position is concerned, are arranged next to one another. A rod does not represent a kind of 'individuality' (Boveri), by which term there is certainly implied the existence of an internal relationship of parts to one another, according to certain laws, a relationship which prevents any mechanical division of the whole into equivalent parts capable of living and performing their functions. 'Individualities' as defined above are to be found in my ancestral plasms, or as I propose to call them shortly, the '*Ids*'[1]. These cannot be divided without losing the power of building up an individual, while, according to my view, the series of ancestral plasms which compose the rods or '*Idants*'[2] might quite conceivably be removed bodily, by division occurring at any spot, and replaced by others, without any loss of the essential force which controls the ontogeny of the species in question. The only result of such replacement would be to cause a more or less marked alteration in

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[1] The expressions *Id* and *Idant* serve to recall Nägeli's 'idioplasm,' from which they are derived. I think it is very necessary to substitute some short expressions for the clumsy 'ancestral plasms' and 'chromatosomes,' or the frequently inappropriate 'nuclear rods' and 'nuclear loops.'

[2] See the preceding note.

the individuality of the being which is produced by this ontogeny.

There is therefore, in my opinion, nothing inadmissible in the idea of the breaking up of the chromatin rods or idants, during each nuclear resting stage, if only the single ids remain unchanged; but certain facts in heredity, to be mentioned immediately, support the view that the specific hereditary substance from one or both parents can be contained in the germ-cells of the child, and this presupposes that it is at least possible and perhaps the rule, for the order and arrangement of the ids in the idants to remain unchanged from the germ-cells of the parent to those of the offspring. I would, then, assume that, at least on the way from germ-cell to germ-cell, the views of van Beneden and Boveri are upon the whole correct, viz. that the chromatosomes (idants) only apparently break up during the nuclear resting stage, but in reality persist. I imagine that, after the period of the resting stage, they are generally composed of the same ids, for the most part arranged in series similar to those which existed before the preceding nuclear division. We are already acquainted with such astonishingly delicate mechanical arrangements in cells, that the existence of special provision for maintaining the original arrangement of the rod elements (ids) might be looked upon as very far from an impossibility. Even if direct observation should fail to answer this question in the future, some certainty might be reached by those indirect means which often lead us to a final decision in such excessively minute biological questions—viz. the means provided by an examination of the facts of heredity. Even now there is, I think, one such fact, supporting the idea of a continuity of the idants; I mean the frequently observed fact that a child may predominantly or even exclusively resemble one of its parents alone. If the elements of the chromatin rods, i. e. the ancestral plasms, were irregularly mingled together in each nuclear resting stage, to be rearranged at random in the idants, it would scarcely ever happen that the scattered ids would come together in a series like that which existed in the original paternal or maternal idants. The individual stamp of a nuclear rod (idant) must entirely depend upon its construction out of particular ids. Nevertheless, we must not regard this constitution as for ever unchangeable. The universally observed change of individuality which takes place in the course of generations, and the fact that one and the same individuality is never twice repeated, suggest to my mind an occasional change in the arrangement of ids within the idants—a change which, if it does not occur at every opportunity afforded by reconstruction, will at any rate take place in the course of generations.

I will not now enter more fully into the foundation of such protracted, and, to a certain extent, secular changes of the idants, but will turn at once to the problem propounded above as to the meaning and significance of the fact, which has been firmly established by the researches of O. Hertwig upon *Ascaris*, that a double division of nucleus and cell is rendered necessary by that reduction of idioplasmic elements which is required by my theory in both ovum and sperm-cell; in other words, *to explain the fact that the number of idants is doubled before being halved.*

Inasmuch as two primary polar bodies are formed, so far as we know, by all eggs which require fertilization, we may conclude that the significance of the double division of the sperm-mother-cell of *Ascaris megalocephala* is typical and far-reaching, rather than merely accessory or secondary.

If, as I have shown above, the significance of the original increase of the chromatin rods to double their number does not lie in the needs of the growing ovum or spermatozoon, it must be sought for in some other direction. *It lies, as I believe, in the attempt to bring about as intimate a mixture as possible of the hereditary units of both father and mother*[1].

If the first object of sexual reproduction is to combine the hereditary tendencies of two individuals, and not in a mere transitory manner (viz. in the single individual proceeding from one act of fertilization), but permanently, because such a combination affects also the germ-cells of each single individual, and therefore of all succeeding generations,—if this be its object, then we must admit that it is mechanically possible for a combination of paternal and maternal idants to exist side by side in the mature germ-cells of the individual. This is obviously conceded if the 'reducing division' makes

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[1] Histologists may perhaps object that the doubling of the idants simply depends upon a postponement of the normal longitudinal fission until the time at which the spindle is formed. This is probably correct, but it only explains the existence of the doubling and not its significance.

no difference between the maternal and paternal nuclear rods, but leads to a halving of their number in such a manner that the most varied combinations can arise; so that if $a+b$, and $c+d$ represent four rods, there will be found in the mature germ-cell not only the paternal group $a+b$ and the maternal $c+d$, but also the combination $a+c$ and $b+d$ or $a+d$ and $b+c$, that is combinations of any paternal with any maternal element.

Now it is clear that only very few distinct combinations can be brought about in this way,—in the above-mentioned case of four rods, only six combinations. But if, as actually happens, each of the rods is doubled before their number is halved, there are a greater number of possible combinations, viz. in the above case, ten. Hence an individual of such a species could produce ten kinds of eggs or spermatozoa with differing hereditary tendencies. At the fertilization of one of these eggs by a spermatozoon of another individual of the same species, two different idants would meet each other. Each parent produces ten different kinds of germ-cells, hence as many different children can proceed from such a union, as there are possible combinations between the ten kinds of spermatozoa of the father and the ten kinds of ova of the mother, namely ten times ten or a hundred. I therefore believe that *the significance of the longitudinal splitting of the idants, and the consequent doubling of their number, is an increase in the number of possible combinations.*

It may be doubted whether the increase which is thus rendered possible is sufficient to explain certain phenomena of heredity. So far as our knowledge extends, it has never happened that two children of the same family born successively have had that resemblance to each other which is familiar in the case of identical twins. Precisely similar germ-plasm never seems to be twice formed in the unions of the same parents; it only occurs in those exceptional cases in which a fertilized ovum produces two children, when the germ-plasm which gives to both of them proceeds from a single egg and a single spermatozoon. Now a hundred different combinations of germ-plasms can occur under the given conditions, while a human pair can scarcely produce more than thirty children: but if only ten were born, one of the hundred possible combinations *might repeat itself. From this point* of view, it might therefore be doubted whether the doubling of the idants in the germ-mother-cells, together with the succeeding two 'reducing divisions,' are sufficient to explain the fact that identical children only appear in the form of twins developed from a single ovum.

It may however be urged that the assumption of only four idants may not hold for the human species, and that in such animals as *Ascaris megalocephala bivalens*, which undoubtedly *possess only four idants, we cannot appreciate the phenomena* of heredity when applied to the minutest individual differences, as we can in the case of man. It is quite conceivable that many fertilized ova of this species of *Ascaris* contain precisely the same kind of germ-plasm, that is the same combination of ids; we do not however know that this is the case. We are unfortunately ignorant of the number of idants which is typical for man, and can only assert that it is probably higher than four. But the number of possible combinations increases very rapidly with an increase in the number of idants. Certain Mollusca, as *Carinaria* and *Phyllirhoë*, possess thirty-two idants, and in Crustacea the number is even higher. Eight idants, without doubling, would render possible seventy combinations, doubled, they would produce 266: similarly, without and with doubling twelve idants would yield 924 and 8074 combinations respectively; sixteen would yield 12,870 and 258,570; twenty would yield 184,756 and 8,533,606. With thirty-two idants doubling increases the number of combinations about 500 fold[1].

If we now remember that an equal number of idants from each parent meet together during fertilization, and that each of the parental groups of idants represents only one of the numerous combinations which are possible for the species, it is evident that the number of possible variations of germ-plasm which a single pair is capable of producing must be extremely great, for it is a number obtained by multiplying together the maternal and paternal number of combinations. Thus twelve idants yield 8074 × 8074 variations. Although even this large number of combinations does not exclude the

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[1] For these figures I am indebted to the kindness of my mathematical friend, Professor Lüroth of Freiburg im Breisgau.

possibility of a repetition (two or more times) of the same combination, and the further possibility of the development of those very germ-cells which contain identical germ-plasm—the probability of such an occurrence is so excessively remote that it may be considered practically non-existent, and we have no reason for wondering that identical individuals have *never been observed among the children successively born* in any human family.

To my mind the doubling of the idants before the 'reducing division' possesses this very significance:—it renders possible an almost infinite number of different kinds of germ-plasm, so that every individual must be different from all the rest. And the meaning of this endless variety is to afford the material for the operation of natural selection.

It might perhaps be objected that sufficient variety could have been attained without the doubling of the rods, and that, although the difference between the numbers of combinations produced with and without doubling is certainly very considerable, the number of rods would have been large enough without increase, since, as a matter of fact, the number of descendants developed is always smaller than the number of possible combinations. Eight idants without doubling give seventy combinations; these multiplied by the seventy combinations of the other parent yield 4900 varieties of germ-plasm in the fertilized ova, and potentially an equal number of different offspring. We might suppose that this number would suffice in all cases; for when the germ-cells are far more numerous (many animals producing 100,000 or even upwards of 1,000,000 ova, not to mention spermatozoa) only a very small percentage can enter upon development, and of these but very few can arrive at maturity and reproduce themselves. It would be sufficient, we might think, if there were only a few more thousand combinations of germ-plasm than of individuals which attain maturity.

There is, however, much to be said on the other side. If we are not able to determine by calculation the number of differing individuals which are necessary in order that the development of the species may be guided by natural selection, we can scarcely fail to recognize that it is only by the widest possible choice that the best possible adaptation of all parts and organs can be ensured in every case. The extraordinary superfluity of individuals in each generation is indispensable for that intense selective process which must have operated without ceasing if it is to afford the explanation of universal adaptation. And if among the thousands of germs, which sooner or later succumb in the struggle for existence, there were always a hundred which contained the same combination of individual characters, *it is clear that this number would not count for more than one, as material for natural selection.* It is just because each fertilized germ, and the individual arising from it, are different from others as regards the combination of characters, that the completeness of adaptation is rendered possible. It follows from this arrangement that the highest possible number of combinations of germ-plasm are offered for the operation of natural selection.

It must furthermore be borne in mind that the full number of possible combinations, which is mathematically calculable, is, in practice, very far from being attained. We must assume in the calculation that the nuclear rods possess a limitless power of combination; but this is neither proved, nor is it probable. We are on the safe side in assuming that certain combinations are formed more readily than others, and are for this reason of more frequent occurrence. And it must not be forgotten that identical ancestral units (ids) and identical idants may be present in the germ-plasm. Widely different ids are not contained in every individual of a species, and perhaps never occur in the same individual. In many cases the two parents are in some degree blood relations, and would contain similar or similarly composed idants. Although direct observation can tell us nothing on this point, it can still be shown that identical idants may be found in one and the same nucleus. This is proved by the doubling of the rods which takes place before the 'reducing division,' and it can be inferred with equal certainty from other conditions.

The two idants which arise in the mother-cell of the ovum, by the longitudinal splitting of a single one, must contain similar combinations of ancestral units. If this were not so, it would follow that each of the two daughter nuclear rods would contain different ids, and hence the number of ids in each single idant would necessarily be diminished by half. But this cannot be the case, or the two successive 'reducing divisions' would lessen the total number of ids, in each germ-cell, to one quarter. Two idants are the normal number in *Ascaris m. univalens*, and they are increased to four, by longitudinal fission : a single idant is contained in each mature spermatozoon or ovum which is formed by the two successive 'reducing divisions.' Hence

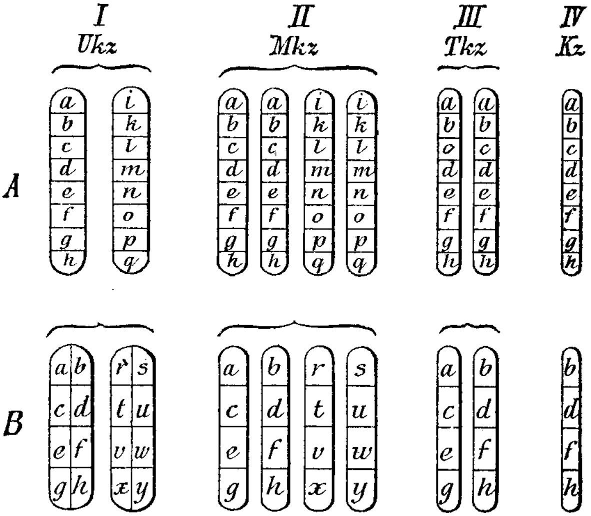

FIG. III.

Diagram showing the behaviour of the idants in the various stages of the development of the germ-cells in *Ascaris megalocephala*, var. *univalens*. *A* shows the actual behaviour of the idants, the final result (*IV*) of which is a halving of the number of ids present in the first stage (*I*). *B* shows that the arrangement of ids as a double row within the idants would cause the final number (*IV*) to be a quarter of that present in the first stage (*I*). Each of the four groups of figures in both *A* and *B* represents the idants of a single cell of the corresponding stage.

these mature germ-cells must contain half the total number of ids contained in the two idants of the original germ-cell. If this be so it is clear that the ids in the mother-idants are doubled in number by longitudinal fission. The small letters *a*, *b*, *c*, &c. in the diagrammatic figure III, represent the ids which compose the idants. The numbers *I-IV*. represent the idants of each of the four stages,—the primitive germ-cells, the mother-cells of the first and second order, and the germ-cells. The series *A* represents eight ids in each of the two idants of a primitive germ-cell, arranged as a single row; whereas in series *B* they form two rows. In *A* the idants of stage *I* give rise, by longitudinal fission, to the four idants of stage *II*, *that is to two pairs of identical idants*: in series *B* the two original idants similarly produce the four idants of stage *II*, each of which is different from the others and contains only four ids. In consequence of this, in series *B*, the two successive 'reducing divisions' diminish the total number of ids in the cell, first (stage *III*) from 16 to 8, and then (stage *IV*) from 8 to 4—i. e. to one quarter the normal number of ids; in series *A*, on the other hand, the corresponding divisions lead to that halving of the normal number of ids which is in accordance with theory—i. e. from the 16 of stage *I* to the 8 of stage *IV*.

It should be regarded as certain that many identical ancestral *units may be present in the germ-plasm of a germ-cell, and that* identical nuclear rods may exist side by side. Furthermore, during fertilization, as has been mentioned above, identical nuclear rods from the two parents must meet together, the frequency of this depending upon the amount of interbreeding (using the term in its widest sense) that has occurred, or in other words upon the limit set to the number of individuals in *any given area, and upon the restriction in the number* of ancestors of the species. Such considerations enable us to understand why nature has provided such superabundant variations in the germ-plasm of the reproductive cells of a single individual. It is the same with the more obvious prodigality that she lavishes in the millions of germ-cells brought forth by every individual *Ascaris* or sturgeon. We now know that this apparent waste is necessary in order to ensure that, on the average, at least one or two germs may reach maturity, and that thus the species may be maintained.

### *Other Types of Maturation of Germ-Cells.*

I would here repeat that, before O. Hertwig, Platner had shown that an entirely similar process occurs in the double 'reducing division' of the mother-cells of the spermatozoon in both the butterfly and the snail. He observed the original doubling of the idants (chromatosomes) and their subsequent reduction to half. Furthermore, the observations of Flemming on the formation of spermatozoa in the salamander prove that there is an initial increase of the nuclear loops to double the normal number. These facts enable us to recognize a relationship, which Hertwig has already propounded in his account of the type of 'reducing division' met with in *Ascaris.* Platner had previously recognized the homology between the formation of spermatozoa and of ova, between the two divisions of the sperm-mother-cell and the formation of the two polar bodies. Inasmuch as these homologies have been proved to exist in a worm, in insects, and in a vertebrate, and since also that double division which leads to the extrusion of the two primary polar bodies is certainly a character common to the Metazoa, we may well believe that we are dealing with a process of general significance, and one which is repeated during the formation of the sexual cells of, at any rate, all the higher Metazoa, in essentially the same way.

Hence, after writing the remarks which appear above, I was much astonished by Henking's pamphlet on the formation of ova and spermatozoa in an insect, *Pyrrhocoris apterus,* in which the process is described as following an entirely different plan. The observations are clearly exact and trustworthy, and if the author's explanation be valid, it is impossible to attach to the processes of maturation in this insect a meaning similar to that found in the other animals which have been studied. I believe, however, that Henking's interpretation is erroneous on one point, and that the apparently profound differences can be reconciled, in fact that they are beautifully adapted to make clear the essential parts of the process.

The difference between the formation of spermatozoa in *Pyrrhocoris* and *Ascaris* depends upon the fact that, in the former, there is no doubling of the idants before the first division of the sperm-mother-cell, yet the first division takes place as it does in *Ascaris,* so that the existing number (24) of idants is halved, twelve passing to each daughter-nucleus. The latter then enters upon the second division in the usual manner, each of the twelve idants splitting longitudinally, and their halves passing into the grand-daughter-nuclei. These last grand-daughter-cells constitute the sperm-cells, and the final result of the process is the same as in other cases; for the mature germ-cells contain only half the number of idants which are normally found in the species.

Henking interprets his corresponding observations upon the development of the ova, in the following manner:—The first division of the mother-cell is the 'reducing division' suggested by me, for this alone reduces the idants to half their normal number: the second division is that which I have called the 'equal division,' i. e. the means by which a number of ids, equal to that present before this division commences, passes into each daughter-nucleus; and this is rendered possible because the longitudinal splitting of the idants depends upon a doubling of the ids by division.

If this explanation be valid, the interpretation offered above of the doubling of the idants in the mother-cells of *Ascaris* must fail, and I doubt whether any other feasible explanation is to be found. Henking attempts to reconcile the discrepancy between the two observations by altogether doubting the doubling of the nuclear rods of *Ascaris*. I have, however, convinced myself, by an examination of the preparations of my pupil, Herr Arnold Spuler, that the doubling cannot be denied. Furthermore, it was this very process which first afforded an explanation of the double division of the mother-cells. Why then should there be this universal double division of which we are so completely assured by the general occurrence of the two polar bodies of the ovum? Regarding spermatogenesis only, we might perhaps be inclined to be satisfied with the answer that the number of sperm-cells must be four times that of the mother-cells. But, as I have indicated above, the mere increase of the spermatozoa might be brought about, and to any extent, by additional division of the original sperm-cells; and when we remember that the mother-cell of the ovum undergoes this double division, whereby three out of the four daughter-cells simply disappear as polar bodies, it becomes clear that the process is controlled by some deeper necessity. And if any-one doubts this, and is inclined to think, with Lameere and Boveri, that the polar bodies are merely a phyletic reminiscence, he should remember that rudimentary organs and processes always tend to vary, and that it is inconceivable that, in all sexually reproduced Metazoa, these two nuclear divisions

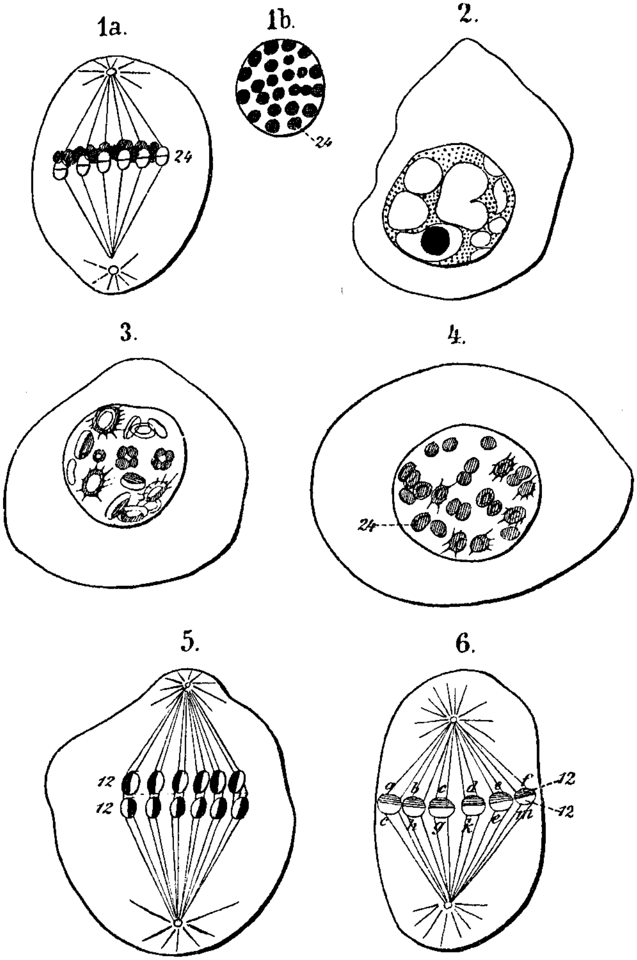

FIG. IV.

Formation of spermatozoa in *Pyrrhocoris* (modified from Henking).
1. Primitive sperm-cell containing nuclear spindle preparatory to division : a. The equatorial plate as seen from the side, b. as seen from above. 2. Sperm-mother-cell. 3. Sperm-mother-cell preparatory to the 'reducing division.' 4. The same, after division of the chromatin-wreaths into 24 double idants. 5. First 'reducing division.' 6. Second 'reducing division.'

should have been retained if obsolete, *and should have shrunk to only one, as soon as regular parthenogenesis commenced.*

The double division must have some meaning, and one which is the same in the formation of both spermatozoa and ova.

I accept the meaning which has been indicated above, and believe that Henking's observations can be easily brought into accord with the plan of formation of sexual cells observed in other species. Henking looks upon the first division of the mother-cell as a 'reducing division,' the second as an 'equal division,' and considers that he uses these terms in the sense in which I have employed them. But this is not quite the case. I understand by a 'reducing division,' one in which the number of ids present in the passive nucleus is reduced to half in each of the daughter-nuclei: I understand by an 'equal division' one in which each daughter-nucleus is provided with the full number of ids present in the passive nucleus of the mother-cell. In the latter case, the daughter-nuclei will contain similar ids, but, in the former, this can only occur when the ids of the mother-cell are precisely identical. I have never maintained that these two contrasted modes of division must be invariably recognizable and distinguishable by external characters, and I have never identified the chromatosomes of authors with my ancestral units. But only when such an identification is assumed does the reduction of the number of ids by one-half (i.e. a 'reducing division' in my sense of the term) necessarily imply a reduction in the number of chromatosomes as well. The types of 'reducing' and 'equal divisions,' as I propounded them in 1887[1], are so conceived that the first involves a halving of the number of idants, while the second does not. But I expressly added—'I do not mean to imply that it is impossible to imagine any other form in which they [viz. these modes of division] may occur[2].' It then seemed to me that the form of nuclear division which is accompanied by a longitudinal splitting of the idants arranged in the equatorial plate of the spindle, can scarcely be conceived of as other than an 'equal division,' but even then I added the words 'as far as I can see[3].' If we assume the linear arrangement of ids in a single row in

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[1] See Vol. I. pp. 366–379, and especially pp. 375–377.

[2] See Vol. I. p. 375.

[3] See Vol. I. p. 375.

the idant, the longitudinal splitting of the latter certainly involves an 'equal division.' It appears doubtful, however, whether this arrangement is universally present, and I should be inclined to question its existence in the second division of the mother-cells of *Pyrrhocoris*, and to believe, on the other hand, *that the ids are arranged in two rows, and that the idant is in reality double.* This arrangement would then lead to a new and different type of 'reducing division.' If the letters *a b c*, &c.—*m.* in Fig. V, represent the ids, and the vertical line drawn through *A*, the plane of splitting, it is clear that division of the idant would result in a reduction of the total number of ids to half in each of the daughter-nuclei, as is shown in *B*.

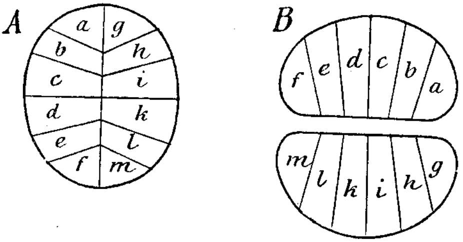

FIG. V.

*A*. One of the double idants from the equatorial plate of the nuclear spindle of the first 'reducing division.' *B*. The same, showing its position after the occurrence of the first 'reducing division' in the equatorial plate of the nuclear spindle of the second 'reducing division.' (Compare Fig. IV. 5 and 6.)

In support of this assumption there is not only the impossibility of conceiving the universal occurrence of a second division which is not also an *essential* change in the nuclear substance, but, as will be afterwards shown, there is in addition the evidence derived from the figures of the process which Henking has published.

The equatorial plate of the nuclear spindle of the first 'reducing division' is composed of two sets of twelve idants arranged in two wreaths opposite to each other (see Fig. IV. 5). Twelve then pass to one and twelve to the other pole, completing the first 'reducing division.' Now it can be clearly seen that each idant is *double* from the *very first*, consisting of two halves which are arranged side by side in the spindle *of the first 'reducing division' (see Fig. IV. 5). In the second* 'reducing division' they are twisted so that the two halves of each idant come to lie upon each other, and between them passes the plane of division which confers upon each daughter nucleus its predetermined half (Fig. IV. 6). If then, these two halves, which are prepared so early, contain similar ids, we have to do with an 'equal division'; but, in my opinion, there is little to be said in favour of this assumption and much for the contrary.

If we enquire as to the origin of the double idants in the equatorial plate of the first 'reducing division,' we find that deeply staining strands and granules of chromatin separate out from the passive nucleus of the mother-cell (Fig. IV. 2) and *arrange themselves in the very remarkable likeness of a series* of wreaths[1] (Fig. IV. 3), of which there appear to be twelve. The full number may not be visible at the same time, because one or more is as yet incomplete or is already broken up. Each wreath then divides into two similar halves, which by contracting become spheres and give rise to the twenty-four spherical idants in the equatorial plate of the first 'reducing division' (Fig. IV. 4 and 5). There is, indeed, good cause for regarding a process of so definite a character as by no means devoid of meaning, and we naturally ask for the significance of this wreath-formation. We cannot expect to find the answer by direct observation alone, but when we seek assistance from the suggestive conception of the idioplasm, as built up of ids, a certain meaning is seen to underlie the process.

During the resting-stage the ids are scattered through the nucleus; they then collect together again into idants, as I assume, in an order nearly the same as that previously taken; the idants then grow *and double themselves* without any separation of the halves from each other (Fig. VI. 1).

These double idants unite together in pairs, forming wreaths (Fig. VI. 2 and 3), and each of the latter divides into two similar halves (Fig. VI. 4), giving rise to two new double idants (Fig. VI. 5), which may be different from those of the original pair. For the adjoining Fig. VII shows that according to the position of

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[1] The term 'wreath' or 'rosette' is sometimes given to the equatorial plate of Flemming (see Klein 'Atlas of Histology,' p. 442). This is of course entirely different from the wreaths mentioned above.—E.B.P.

the plane of division ($x-x$) the halves of the wreaths may be built up of different combinations of ids.

Hence, according to this hypothesis, in the first 'reducing division,' we find in the equatorial plate of the nuclear spindle, twenty-four double idants, the halves of which lie over each other in two rows (Fig. IV. 5), and, which separating into single idants, bring about the second 'reducing division' (Fig. IV. 6).

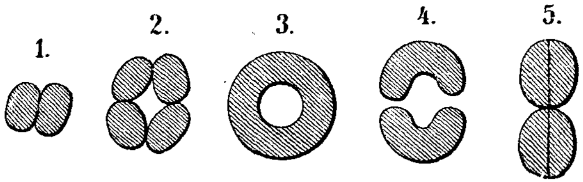

FIG. VI.

Formation of double idants in *Pyrrhocoris.*

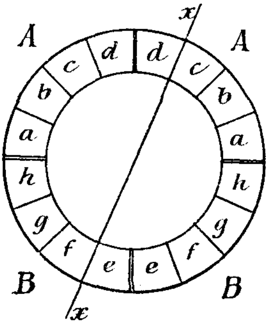

FIG. VII.

A wreath, formed of the four idants *A*, *A*, *B*, *B*, about to divide, through the moveable plane $x$—$x$, into two double idants. The small letters denote the ids, of which only four are shown in each idant.

For some years I have imagined to myself the grouping of the ids into idants, by the arrangement of the former in the figure of a wreath, a form which renders possible a moveable plane of division. It would seem that this arrangement actually obtains in the 'reducing division,' and that nature produces a form which I had only conceived as a diagram.

The formation of wreaths by the idioplasm, during the 'reducing division' of the germ-cells, is not confined to *Pyrrhocoris*; for Flemming long ago described an entirely similar ring-like structure in the salamander, and my assistant, Dr. Häcker, has recently observed the formation of wreaths of idioplasm in the egg-mother-cells of certain Copepoda. The development of these latter does not, however, altogether agree with that of the wreaths of *Pyrrhocoris*, although the same purpose is served—viz. the arrangement of the ids in fresh groups.

### *Objections.*

The objection may be raised to my interpretation of the processes of maturation in *Ascaris*, that, although it corresponds sufficiently well with the variety *bivalens* and with all other animals possessing four or more idants, it does not apply to those with only two, such as the variety *univalens*. When the mother-cells contain only two idants, the mature germ-cells contain only *one*, and hence it is a matter of indifference whether the 'reducing divisions' are preceded by the doubling of the idants or not. It might be maintained that this doubling and the consequent necessity for two divisions, are not explained by my interpretation.

For this variety of *Ascaris megalocephala*, the objection is certainly valid; but the question arises whether this is by itself sufficient to undermine the whole attempt at explanation.

In the first place, in no other living being have so small a number of idants been found as in this variety of *Ascaris megalocephala*. Even so few as four idants occur but rarely; and in the nearest relatives of the species, for instance in *Ascaris lumbricoides*, twelve idants are found; in other Nematodes, according to Carnoy, there are eight to sixteen; in *Sagitta*, according to Boveri, eighteen; and the same number in *Echinus*; in a Medusa, *Tiara*, twenty-eight; and in three different genera of molluscs thirty-two. *Ascaris m. univalens* is in this respect an exception, and should perhaps be dealt with from this point of view, especially as the variety *bivalens*, with four idants, appears to be the more common. We know nothing about the phenomena of heredity in this parasite of the horse, and cannot decide whether the descendants of the variety *bivalens* are not perhaps a really different species from those of the variety *univalens.* In any case *bivalens* would be the ancestral form.

While studying the last of O. Hertwig's works, the thought occurred to me whether the fresh combination of ids in *Ascaris univalens* might not be brought about in a manner different from that of the simple rearrangement of idants, and I will take this opportunity of expressing the idea, in order that its accuracy may be tested by the facts. The material for such proof or disproof is not at present accessible to me; for the variety *univalens* does not seem to occur in south-west Germany.

In the sperm-mother-cells of *Ascaris m. univalens* four long thin threads are formed from the chromatin distributed in the nuclear network of the resting-stage; these threads are arranged so that they cross each other at one point and are there joined together by means of a connecting cement-substance ('Linin'). Thus they form an Ophiurid-like figure in which the body of the Echinoderm represents the place where crossing occurs, while the paired arms represent the halves of threads. According to O. Hertwig, each of the threads then gradually shortens itself until at length it resembles a short thick rod. The four rods arrange themselves in two pairs, all four bases being closely apposed, the spindle of the first 'reducing division' is formed, and finally each daughter-nucleus receives one of the pairs.

Naturally, O. Hertwig was unable to follow these processes directly, but he inferred them by combining the very numerous stages observed. I should be inclined to look for a somewhat different interpretation of the figures given by him, and would ask whether the four threads which take the form of an Ophiurid, are converted into the rods, not merely by shortening, but by the simultaneous *fusion of two half threads* just as if the paired arms of the Ophiurid, which lie side by side, were to grow together. Many details support this view. First, the connecting cement-substance at the point where the threads cross certainly possesses some significance. If, however, the nuclear rods arise by the shortening of the long threads only, it would appear to have no meaning. Only if we consider that it arises from the coupling together of different halves of threads, would it possess a meaning, as will be immediately seen. If the halves of threads, representing the arms of the Ophiurid, are directed to each other by the activity of the achromatin nuclear network as they are moved hither and thither, it is essential for them to have a central point of support, i. e. the part representing the body of the Ophiurid. No conclusive objection can be raised against the view that the shortening process is by itself sufficient to convert a long thread into a short thick rod; for we know that nuclear threads are subject to great shortening. But Hertwig himself seems to have had some doubts as to the validity of this explanation which he offers. In support of it he reminds us of 'the considerable shortening undergone by the threads in the spermatozoa of the salamander,' but he adds that this amount is very far below that required in the case of *Ascaris* if his interpretation is to be accepted.

The bifid form of the rods indicates the longitudinal fusion of two threads with their points left free, and finally the position of the rods with their bases apposed, and thus standing as it were, back to back, is more intelligible when we suppose that adjacent arms of the Ophiurid are fused together, rather than that each of the long chromatin threads has shortened to a rod. If the latter were true we should expect that the rods would lie in the middle of the mass of 'linin' representing the Ophiurid body[1], and this, according to Hertwig's figures, does not seem to be the case.

We may very properly be asked for the observations which support this view of a fusion between the halves of threads. So careful an observer as O. Hertwig can scarcely have overlooked these stages, if they have any existence. This I freely acknowledge; but in Plate I he shows a series of figures in which two arms of the Ophiurid are approaching each other, and are more or less fused together. Perhaps Figs. 27, 28, 29 should be understood in this way, and we might then conclude that the threads only begin to fuse after they have already undergone considerable shortening, and further that the fusion commences at the position of crossing and proceeds

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[1] Because the middle of each long thread passes through the centre of the 'linin,' while the gradual shortening of the two ends would finally reduce the thread to this greatly thickened middle part. If adjacent halves fused together there would be no such arrangement: they would tend to radiate away from the mass of 'linin' in which their bases alone would lie.

towards the ends, so that at last only the two points are left free. Of course all this can only be tested by the preparations themselves, and O. Hertwig is in the best position, from the great number of his sections, to decide whether his interpretation or that which I have offered, is the right one.

Should my surmise be confirmed, it follows that even in so small a number of idants as exist in the variety *univalens*, a number of combinations would be possible, inasmuch as halving the rods doubles the number of units capable of combination, and, of course, any two half rods might fuse in the manner described above.

It would be very easy to explain the fresh combinations of germ-plasm in all species, *Ascaris m. univalens* included, if we might assume that the idants were freshly built up of irregularly distributed ids after each resting-stage of the nucleus. But the above-mentioned facts concerning hereditary transmission from one parent alone, which have already been used as evidence, are opposed to this view.

It is self-evident that I am far from claiming to have found the correct interpretation of the details in every case. When other workers have tested anew the processes with which my attempted explanation deals, and when new facts have been discovered, we shall gradually arrive at greater certainty. I chiefly look for progress from the comparative investigation of corresponding processes in many different groups of animals. For the present we may well rest satisfied, if at any rate the meaning and significance of the two nuclear divisions are, *upon the whole*, recognized as true.

The future will teach us whether this is the case. In the meantime it promises well that, under the guidance of this thought, the apparently irreconcilable processes in *Ascaris* and *Pyrrhocoris* can be brought together under a common point of view. From this standpoint the two divisions of the germ-mother-cell signify *a period of reduction and of reconstruction of the idioplasm.* If reduction alone were needed—i. e. a diminution of the number of ids by half—a single division would have sufficed; but the second was rendered necessary in order to attain the greatest possible diversity in the germ-plasm. The accomplishment of these two ends is not always brought about by precisely the same course, but nature pursues somewhat different routes, which however always meet at the principal stations, viz. the two nuclear divisions. We have learnt two of these routes, on the one hand from O. Hertwig, on the other from Henking: the observations of Flemming on the formation of spermatozoa in the salamander may possibly point to a third, those of Häcker to a fourth, but all agree in leading to the same end.

## II. INHERITANCE IN PARTHENOGENETIC REPRODUCTION.

### *The Processes of Maturation in Parthenogenetic Eggs and their Meaning.*

It has for some years been recognized that the characteristic development of an egg into a fully formed individual is chiefly dependent on the nuclear substance, in so far as it is this which compels distinct differentiation in a cell-body which was previously, at any rate to some extent, indifferent, and which communicates to the total product of the egg-cell distinct modes of multiplication and development. When this became known it was obvious that the amount of nuclear substance possessed some significance, and that a certain mass of it was essential for the commencement of embryogeny in an egg-cell. I have therefore for some time agreed with Strasburger in seeking for the power of development without fertilization possessed by many ova, in the assumption that they contain an amount of germ-plasm which is twice as great as that present in eggs requiring fertilization, or that they can give rise to this amount by means of some process of growth. When the proof was afterwards afforded that parthenogenetic eggs produce only one polar body instead of two, I concluded, as is mentioned above, that the formation of the second polar body alone signified the halving of the number of ids which was required by the theory; for we could not assume that such a halving took place in parthenogenetic eggs. I looked upon the first halving of the nuclear substance, common to both kinds of eggs, as the removal of some nuclear substance which had no further use in either case, and the omission of the second nuclear division in parthenogenetic eggs I regarded as the means for retaining the amount of germ-plasm necessary for the egg to complete its course of embryogeny.

As I have already stated, that part of my former view of the significance of the polar divisions, which interprets the first as an extrusion of a specific ovogenetic nucleoplasm, must be abandoned. The facts of spermatogenesis, as we have recently learnt them from the researches of O. Hertwig, have overthrown these views, inasmuch as they prove that the nuclear idioplasm of all polar bodies, as well as that which is retained in the egg, must be germ-plasm. The polar divisions of the egg correspond exactly with the two divisions of the sperm-mother-cell, as will be seen at once by comparing Figs. I and II. By this means, four sperm-cells arise from the sperm-mother-cell, and of these four each contains half the number of idants characteristic of the species (see Fig. I, *F*). By means of the two polar divisions the egg-mother-cell similarly gives rise to the egg (Fig. II. *D E F*, 1), and the three polar cells (Fig. II. *D E F*, 2, 3, and 4), each of which contains the same number of idants, viz. two. As it cannot be doubted that the idioplasm of the four sperm-cells is germ-plasm, it must also follow that the same is true of the three polar bodies as well as of the ovum.

If then *one* polar body is always formed in regular parthenogenetic eggs, it might seem that an explanation is to be found by regarding it as a mere phyletic reminiscence. The question arises whether such a view is a just one, and in order to gain as clear a solution as is possible at the present time, I have added this chapter on parthenogenesis to the essay.

Spermatogenesis undoubtedly teaches us that the two 'reducing divisions' of the female germ-cell originally performed the primary duty of producing four distinct germ-cells from each mother-germ-cell. But spermatogenesis at the same time shows us that a very remarkable reduction of the idants accompanies these two divisions. The normal number of idants present in the mature spermatozoon is by this means reduced to half that in the primitive sperm-cell, and the result is reached by a most circuitous route, for the original number is first increased to double, and then, by two successive divisions, finally diminished to half.

When, however, we recognize that in normal parthenogenesis one of the two 'reducing divisions' is absent, while the other persists, we can hardly regard the latter as the meaningless reminiscence of a process which was full of significance in an earlier phyletic stage: we cannot offer such an interpretation because this single polar division is found in *all* regular parthenogenetic eggs in which it has hitherto been sought for. It has been found, it is true, in eighteen species only, but these belong to different groups of the animal kingdom, viz. in eight Daphnids, a Branchiopod, two Ostracodes, three Rotifers, and four Insecta. In each of these a single polar body corresponding to those of the other seventeen, is expelled, and in each we must conclude that an apparently useless doubling of the idants takes place, together with an ensuing diminution to half, as is shown in the accompanying diagram (Fig. VIII), in which the normal number of idants has been fixed at four, in order to facilitate the comparison with Figs. I. and II. In view of the regular occurrence of the phenomena in all the cases which have been examined, it is worth while enquiring whether a meaning and significance are not to be attributed to these most unexpected processes.

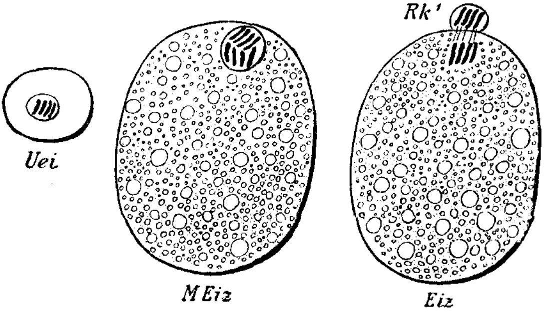

FIG. VIII.

Diagram of the maturation of the parthenogenetic egg.

In the first chapter the attempt was made to show that the significance of the two 'reducing divisions,' in male and female germ-cells, is a double one, first, the *diminution* of the ids to half, and, secondly, the *arrangement* of the idants in fresh combinations. The first object might be gained by a single nuclear division, but the second would be attained only very incompletely, because a fresh combination of the idants occurs most readily, when associated with a previous doubling in number.