For if the specific molecular structure of a cell-body is caused and determined by the structure of the nucleoplasm, every kind of cell which is histologically differentiated must have a specific nucleoplasm. But the egg-cell of most animals, at any rate during the period of growth, is by no means an indifferent cell of the most primitive type. At such a period its cell-body has to perform quite peculiar and specific functions; it has to secrete nutritive substances of a certain chemical nature and physical constitution, and to store up this food-material in such a manner that it may be at the disposal of the embryo during its development. In most cases the egg-cell also forms membranes which are often characteristic of particular species of animals. The growing egg-cell is therefore histologically differentiated: and in this respect resembles a somatic cell. It may perhaps be compared to a gland-cell, which does not expel its secretion, but deposits it within its own substance[1]. To perform such specific functions it requires a specific cell-body, and the latter depends upon a specific nucleus. It therefore follows that the growing egg-cell must possess nucleoplasm of specific molecular structure, which directs the above-mentioned secretory functions of the cell. The nucleoplasm of histologically differentiated cells may be called histogenetic nucleoplasm, and the growing egg-cell must contain such a substance, and even a certain specific modification of it. This nucleoplasm cannot possibly be the same as that which, at a later period, causes embryonic development. Such development can only be produced by true germ-plasm of immensely complex constitution, such as I have previously attempted to describe. It therefore follows that the nucleus of the egg-cell contains two kinds of nucleoplasm:—germ-plasm and a peculiar modification of histogenetic nucleoplasm, which may be called *ovogenetic nucleoplasm*. This substance must greatly preponderate in the young egg-cell, for, as we have already seen, it controls the growth of the latter. The germ-plasm, on the other hand, can only be present in minute quantity at first, but it must undergo considerable increase during the growth of the cell. But in order that the germ-plasm may control the cell-

[[1] Such gland-cells are known in both animals and plants. See W. Gardiner and Tokutaro Ito, On the structure of the mucilage-secreting cells of *Blechnum occidentale* L., and *Osmunda regalis* L., 'Annals of Botany,' vol. i. p. 49.—S. S.]

body, or, in other words, in order that embryonic development may begin, the still preponderating ovogenetic nucleoplasm must be removed from the cell. This removal takes place in the same manner as that in which differing nuclear substances are separated during the ontogeny of the embryo: viz. by nuclear division, leading to cell-division. The expulsion of the polar bodies is nothing more than the removal of ovogenetic nucleoplasm from the egg-cell. That the ovogenetic nucleoplasm continues to greatly preponderate in the nucleus up to the very last, may be concluded from the fact that two successive divisions of the latter and the expulsion of two polar bodies appear to be the rule. If in this way a small part of the cell-body is expelled from the egg, the extrusion must in all probability be considered as an inevitable loss, without which the removal of the ovogenetic nucleoplasm cannot be effected.

This is my theory of the significance of polar bodies, and I do not intend to contrast it, *in extenso*, with the theories propounded by others; for such theories are well known and differ essentially from my own. All writers agree in supposing that something which would be an obstacle to embryonic development is removed from the egg; but opinions differ as to the nature of this substance and the precise reasons for its removal[1]. Some observers (e.g. Minot[2], van Beneden, and Balfour) regard the nucleus as hermaphrodite, and assume that in the polar bodies the male element is expelled in order to render the egg capable of fertilization. Others speak of a rejuvenescence of the nucleus, others again believe that the quantity of nuclear substance must be reduced in order to become equal to that of the generally minute sperm-nucleus, and that the proportions for nuclear conjugation are in this way adjusted.

The first view seems to me to be disproved by the fact that male as well as female qualities are transmitted by the egg-cell, while the sperm-cell also transmits female qualities. The germ-plasm of the nucleus of the egg cannot therefore be considered as female,

[1] Thus in 1877 Bütschli thought that 'the chief significance of the formation of polar bodies lies in the removal of part of the nucleus of the egg, whether this removal is effected by simple expulsion or by the budding of the egg-cell.' 'Entwicklungsgeschichtliche Beiträge;' Zeitschrift für wissenschaftliche Zoologie, Bd. XXIX. p. 237, footnote.

[2] C. S. Minot, 'Account, etc.;' Proc. Boston Soc. Nat. Hist. vol. xix. p. 165, 1877.

and that of the sperm-nucleus cannot be considered as male: both are sexually indifferent. The last view has been recently formulated by Strasburger, who holds that the quantity of the idioplasm contained in the germ-nucleus must be reduced by one half, and that a whole nucleus is again produced by conjugation with the sperm-nucleus. Although I believe that the fundamental idea underlying this hypothesis is perfectly correct, viz. that the influence of each nucleus is as largely dependent upon its quantity as upon its quality, I must raise the objection that the decrease in quantity is not the explanation of the expulsion of polar bodies. The quantity of idioplasm contained in the germ-nucleus is, as a matter of fact, not reduced by one-half but by three-fourths, for two divisions take place one after the other. Thus by conjugation with the sperm-nucleus, which we may assume to be of the same size as the germ-nucleus, a nucleus is produced which can only contain half as much idioplasm as was present in the original germ-nucleus, before division. Strasburger's view leaves unexplained the question why the size of the germ-nucleus, before the expulsion of polar bodies, was thus twice as large; and even if we neglect the theory of ovogenetic nucleoplasm and assume that this larger nucleus was entirely made up of germ-plasm, it must be asked why the egg did not commence segmentation earlier. The theory which explains the sperm-cell as the vitalizing principle which starts embryonic development, like the spark which kindles the gunpowder, would indeed answer this question in a very simple manner. But Strasburger does not accept this theory, and holds, as I do, a very different view, which will be explained later on.

If, on the other hand, we assume that the germ-nucleus contains two different kinds of nucleoplasm, the question is answered quite satisfactorily. In treating of parthenogenesis, further on, I shall mention a fact which seems to me to furnish a real proof of the validity of this explanation; and, if we accept this fact for the present, it will be clear that the simple explanation now offered of phenomena which are otherwise so difficult to understand, would also largely support the theory of the continuity of the germ-plasm. Such an explanation would, above all, very clearly demonstrate the co-existence of two nucleoplasms with different qualities in one and the same nucleus. My theory must stand or fall with this explanation, for if the latter were disproved, the continuity of the germ-plasm could not be assumed in any instance, not even in the simplest cases, where, as in Diptera, the germ-cells are the first-formed products of embryonic development. For even in these insects the egg possesses a specific histological character which must depend upon a specifically differentiated nucleus. If then two kinds of nucleoplasm are not present, we must assume that in such cases the germ-plasm of the newly formed germ-cells, which has passed on unchanged from the segmentation nucleus, is at once transformed entirely into ovogenetic nucleoplasm, and must be re-transformed into germ-plasm at a later period when the egg is fully mature. We could not in any way understand why such a re-transformation requires the expulsion of part of the nuclear substance.

At all events, my explanation is simpler than all others, in that it only assumes a single transformation of part of the germ-plasm, and not the later re-transformation of ovogenetic nucleoplasm into germ-plasm, which is so improbable. The ovogenetic nucleoplasm must possess entirely different qualities from the germ-plasm; and, above all, it does not readily lead to division, and thus we can better understand the fact, in itself so remarkable, that egg-cells do not increase in number by division, when they have assumed their specific structure, and are controlled by the ovogenetic nucleoplasm. The tendency to nuclear division, and consequently to cell-division, is not produced until changes have to a certain extent taken place in the mutual relation between the two kinds of nucleoplasm contained in the germ-nucleus. This change is coincident with the attainment of maximum size by the body of the egg-cell. Strasburger, supported by his observations on *Spirogyra*, concludes that the stimulus towards cell-division emanates from the cell-body; but the so-called centres of attraction at the poles of the nuclear spindle obviously arise under the influence of the nucleus itself, even if we admit that they are entirely made up of cytoplasm. But this point has not been decided upon, and we may presume that the so-called 'Polkörperchen' of the spindle (Fol) are derived from the nucleus, although they are placed outside the nuclear membrane[1]. Many points connected with this subject are still in a

[1] E. van Beneden and Boveri have recently, quite independently of each other, made a more exact study of these 'Polkörperchen' ('Centrosoma,' Boveri). They show that nuclear division starts from these bodies, although the mode of origin of the latter is not yet quite clear.—A. W., 1888.

state of uncertainty, and we must abstain from general conclusions until it has been possible to demonstrate clearly the precise nature of certain phenomena attending indirect nuclear division, which still remain obscure in spite of the efforts of so many excellent observers. We cannot even form a decided opinion as to whether the chromatin or the achromatin of the nuclear thread is the real idioplasm. But although these points are not yet thoroughly understood, we are justified in maintaining that the cell enters upon division under the influence of certain conditions of the nucleus, although the latter are invisible until cell-division has already commenced.

I now pass on to examine my hypothesis as to the significance of the formation of polar bodies, in the light of those ascertained facts which bear upon it.

If the expulsion of the polar bodies means the removal of the ovogenetic nucleoplasm after the histological differentiation of the egg-cell is complete, we must expect to find polar bodies in all species except those in which the egg-cell has remained in a primitive undifferentiated condition, if indeed such species exist. Wherever the egg-cell assumes the character of a specialized cell, e.g. in the attainment of a particular size or constitution, in the admixture of food-yolk, or the formation of membranes, it must also contain ovogenetic nucleoplasm, which must ultimately be removed if the germ-plasm is to gain control over the egg-cell. It does not signify at all, in this respect, whether the egg is or is not destined for fertilization.

If we examine the Metazoa in regard to this question, we find that polar bodies have not yet been discovered in sponges [1], but this negative evidence is no proof that they are really absent. In all probability, no one has ever seriously endeavoured to find them, and there are perhaps difficulties in the way of the proofs of their existence, because the egg-cell lies free for a long time and even moves actively in the tissue of the mesogloea. We might expect that the formation of polar bodies takes place here, as in all other instances, when the egg becomes mature, that is, at a time when the eggs are already closely enveloped in the sponge tissue. At all events the eggs of sponges, as far as they are known, attain a specific

[1] The existence of polar bodies in sponges has been recently proved by Fiedler: Zool., Anzeiger., Nov. 28, 1887.—A. W., 1888.

nature, in the possession of a peculiar cell-body, frequently containing food-yolk, and of the nucleus which is characteristic of all animal eggs during the process of growth. Hence we cannot doubt the presence of a specific ovogenetic nucleoplasm, and must therefore also believe that it is ultimately removed in the polar bodies.

In other Coelenterata, in worms, echinoderms, and in molluscs polar bodies have been described, as well as in certain Crustacea, viz. in *Balanus* by Hoek and in *Cetochilus septentrionale* by Grobben. The latter instance appears to be quite trustworthy, but there is some doubt as to the former and also as regards *Moina* (a Daphnid), in which Grobben found a body, which he considered to be a polar body, on the upper pole of an egg which was just entering upon segmentation. In insects polar bodies have not been described up to the present time [1], and only in a few cases in Vertebrata, as in *Petromyzon* by Kupffer and Benecke.

It must be left to the future to decide whether the expulsion of polar bodies occurs in those large groups of animals in which they have not been hitherto discovered. The fact, however, that they have not been so discovered cannot be urged as an objection to my theory, for we do not know *a priori* whether the removal of the ovogenetic nucleoplasm has not been effected in the course of phylogeny in some other and less conspicuous manner. The cell-body of the polar globules is so minute in many eggs that it was a long time before the cellular nature of these structures was recognized [2]; and it is possible that their minute size may point to the fact that a phyletic process of reduction has taken place, to the end that the egg may be deprived of as little material as possible. It is at all events proved that in all Metazoan groups the nucleus undergoes changes during the maturation of the egg, which are entirely similar to those which lead to the formation of polar bodies in those eggs which possess them. In the former instances it is possible that nature has taken a shortened route to gain the same end.

It would be an important objection if it could be shown that no

[1] They have now been observed in many species, so that their general occurrence in insects is tolerably certain. Compare bibliography given in Weismann and Ischikawa, 'Weitere Untersuchungen zum Zahlengesetz der Richtungskörper,' 'Zoolog. Jahrbücher,' vol. iii. 1888, p. 593.—A. W., 1888.

[2] Van Beneden, even in his last work, considers these bodies to have only the value of nuclei; l. c., p. 394.

process corresponding to the expulsion of polar bodies takes place in the male germ-cells, for it is obvious that here also we should, according to my theory, expect such a process to occur. The great majority of sperm-cells differ so widely in character from the ordinary indifferent (i. e. undifferentiated) cells, that they are evidently histologically differentiated in a very high degree, and hence the sperm-cells, like the yolk-forming germ-cells, must possess a specific nuclear substance. The majority of sperm-cells therefore resemble the somatic cells in that they have a specific histological structure, but their characteristic form has nothing to do with their fertilizing power, viz. with their power of being the bearers of germ-plasm. Important as this structure is, in order to render it possible that the egg-cell may be approached and penetrated, it has nothing to *do with the property of the sperm-cell to transmit the qualities of* the species and of the individual to the following generation. The nuclear substance which causes such a cell to assume the appearance of a thread, or a stellate form (in Crustacea), or a boomerang form (present in certain Daphnids), or a conical bullet shape (Nematodes), cannot possibly be the same nuclear substance as that which, after conjugation with the egg-cell, contains in its molecular structure the tendency to build up a new Metazoon of the same kind as that by which it was produced. We must, therefore, conclude that the sperm-cell also contains two kinds of nucleoplasm, namely, germ-plasm and spermogenetic nucleoplasm.

It is true that we cannot say a priori whether the influence exercised on the sperm-cell by the spermogenetic nucleoplasm might not be eliminated by some means other than its removal from the cell. It is conceivable, for instance, that this substance may be expelled from the nucleus, but may remain in the cell-body, where it is in some way rendered powerless. We do not yet really know anything of the essential conditions of nuclear division, and it is quite impossible to bring forward any facts in support of my previous suggestion. The germ-plasm is supposed to be present in the nucleus of the growing egg-cell in smaller quantity than the ovogenetic nucleoplasm, and the germ-plasm gradually increases in *quantity: thus when the egg has attained its maximum size,* the opposition between the two different kinds of nucleoplasm becomes so marked, in consequence of the alteration in their quantitative relations, that their separation, viz. nuclear division, results. But although we are not able to distinguish, by any visible characteristics, the different kinds of nucleoplasm which may be united in one nuclear thread, the assumption that the influence of each kind bears a direct proportion to its quantity is the most obvious and natural one. The tendency of the germ-plasm contained in the nucleus cannot make itself felt so long as an excess of ovogenetic nucleoplasm is also present. We may imagine that the effects of the two different kinds of nucleoplasm are combined to produce a resultant effect; but when the two influences exerted upon the cell are nearly opposed, only the stronger can make itself felt, and in such a case the latter must exceed the former in quantity, because part of it is as it were neutralized by the other nucleoplasm working in an opposite direction. This metaphorical representation may give us a clue to explain the fact that the ovogenetic nucleoplasm comes to exceed the germ-plasm in quantity. For obviously these two kinds of nucleoplasm exert opposite tendencies in at least one respect. The germ-plasm tends to effect the division of the cell into the two first segmentation spheres; the ovogenetic nucleoplasm, on the other hand, possesses a tendency towards the growth of the cell-body without division. Hence the germ-plasm cannot make itself felt, and is not able to expel the ovogenetic nucleoplasm until it has reached such a relative size as enables it to successfully oppose the latter.

Applying these ideas to the sperm-cells we must see whether the expulsion of part of the nuclear substance, viz. of the spermogenetic nucleoplasm, corresponding to the ovogenetic nucleoplasm, takes place in them also.

As far as we can judge from thoroughly substantiated observations such phenomena are indeed found in many cases, although they appear to be different from those occurring in the egg-cell, and cannot receive quite so certain an interpretation.

The attempt to prove that a process similar to the expulsion of polar bodies takes place in the formation of sperm-cells has already been made by those observers who regard such expulsion as the removal of the male element from the egg, thus leading to sexual differentiation; for such a theory also requires the removal of part of the nuclear substance from the maturing sperm-cell. Thus, according to E. van Beneden and Ch. Julin, the cells which, in *Ascaris*, produce the spermatogonia (mother-cells of the sperm-cells), expel certain elements from their nuclear plate, a phenomenon which has not been hitherto observed in any other animal, and even in this instance has only been inferred and not directly observed. Moreover the sperm-cells have not attained their specific form (conical bullet-shaped) at the time when this expulsion takes place from the spermatogonia, and we should expect that the spermogenetic nucleoplasm would not be removed until it has completed its work, viz. not until the specific shape of the sperm-cell has been attained. We might rather suppose that phenomena explicable in this way are to be witnessed in those sperm-blastophores (mother-cells of sperm-cells) which, as has been known for a long time, are not employed in the formation of the nuclei of sperm-cells, but for the greater part remain at the base of the latter and perish after their maturation and separation. In this case an influence might be exerted by these nuclei upon the specific form of the sperm-cells, for the former arise and develope in the form of bundles of spermatozoa in the interior of the mother-cell.

It has been already shown in many groups of animals that parts of the sperm-mother-cells[1] perish, without developing into sperm-cells, as in Selachians, in the frog, in many worms and snails, and also in mammals (Blomfield). But the attention of observers has been directed to that part of the cell-body which is not used in the formation of sperm-cells, rather than to the nucleus; and the proof that part of the nucleus also perishes is still wanting in many of these cases. Fresh investigation must decide whether the nucleus of the sperm-mother-cell perishes as a general rule, and whether part of the nucleus is rendered powerless in some other way, where such mother-cells do not exist. Perhaps the paranucleus (Nebenkern) of the sperm-cell, first described by La Valette St. George, and afterwards found in many animals of very different groups, is the analogue of the polar body. It is true that this so-called paranucleus is now considered as a condensed part of

[1] I purposely abstain from using a more precise term, for the complicated terminology employed in spermatogenesis hardly contributes anything to the elucidation of the phenomena themselves. Why do we not simply speak of sperm-cells and spermatoblasts, and distinguish the latter by numbers when they occur in successive generations of different form? Moreover, all the names which have been suggested for successive stages of development, can only be applied to the special group of animals upon which the observations have been made. Hence great confusion results from the use of such terms as spermatoblasts, spermatogonia, spermatomeres, spermatocysts, spermatocytes, spermatogemmae, etc.

the cell-body, but we must remember that it has been hitherto a question whether the head of the spermatozoon is formed from the nucleus of the cell or from the paranucleus; and that the observers who held the former view were in consequence obliged to regard the paranucleus as a product of the cell-body. But according to the most recent investigations of Fol[1], Roule[2], Balbiani[3], and Will[4], upon the formation of the follicular epithelium in the ovary of different groups, it is not improbable that parts of the nucleus may become detached without passing through the process of karyokinesis. Thus it is very possible that the paranucleus may be a product of the main nucleus and not a condensed part of the cell-body. This view is supported by its behaviour with staining reagents, while the other view, that it arises from the cell-substance, is not based upon direct observation. Consequently future investigation must decide whether the paranucleus is to be considered as the spermogenetic nucleoplasm expelled from the nucleus. But even if this question is answered in the affirmative, we should still have to explain why this nuclear substance, remaining in the cell-body, does not continue to exercise any control over the latter.

Strasburger has recently enumerated a large number of cases from different groups of plants, in which the maturation of both male and female germ-cells is accompanied by phenomena similar to the expulsion of polar bodies. In this respect the phenomena occurring in the pollen-grains of Phanerogams bear an astonishing resemblance to the maturation of the animal egg. For instance, in the larch, the sperm-mother-cell divides three times in succession, the products of division being very unequal on each occasion; and exactly as in the case of polar bodies, the three small so-called vegetative cells shrink rapidly after separation, and have no further physiological value. According to Strasburger, the so-called 'ventral canal-cell,' which, in mosses, ferns, and Conifers,

[1] Fol, 'Sur l'origine des cellules du follicule et de l'ovule chez les Ascidies.' Compt. rend., 28 mai, 1883.

[2] Roule, 'La structure de l'ovaire et la formation des œufs chez les Phallusiadées.' Ibid., 9 avril, 1883.

[3] Balbiani, 'Sur l'origine des cellules du follicule et du noyau vitellin de l'œuf chez les Géophiles.' Zool. Anzeiger, 1883, Nos. 155, 156.

[4] Will, 'Ueber die Entstehung des Dotters und der Epithelzellen bei den Amphibien und Insecten.' Ibid., 1884, Nos. 167, 168.

separates from the female germ-cell, reminds us, in every way, of the polar bodies of animal eggs. Furthermore, the spermatozoids in the mosses and vascular cryptogams throw off a small vesicle before performing their functions[1]. On the other hand the equivalents of 'polar bodies' (the 'ventral canal-cells') are said to be absent in the Cycads, although these are so nearly allied to Conifers. Furthermore, 'no phenomenon occurs in the oospheres (ova) of Angiosperms which can be compared to the formation of polar bodies.' Strasburger therefore concludes that the separation of certain parts from the germ-cells is not in all cases necessary for maturation, and that such phenomena are not fundamental, like those of fertilization, which must always take place along the same morphological lines. He further concludes that the former phenomena are only necessary in the case of the germ-cells of certain organisms, in order to bring the nuclei destined for the sexual act into the physiological condition necessary for its due performance.

I am unwilling to abandon the idea that the expulsion of the histogenetic parts of the nuclear substance, during the maturation of germ-cells, is also a general phenomenon in plants; for the process appears to be fundamental, while the argument that it has not been proved to occur universally is only of doubtful value. The embryo-sac of Angiosperms is such a complex structure that it seems to me to be possible (as it does to Strasburger) that 'processes which precede the formation of the egg-cell have borne relation to the sexual differentiation of the nucleus of the egg.' Besides, it is possible that the vegetable egg-cell may, in certain cases, possess so simple a structure and so small a degree of histological specialization, that it would not be necessary for it to contain any specific histogenetic nucleoplasm: thus it would consist entirely of germ-plasm from the first. In such cases, of course, its maturation would not be accompanied by the expulsion of somatic nucleoplasm.

I have hitherto abstained from discussing the question as to whether the process of the formation of polar bodies may require an interpretation which is entirely different from that which I have given it, whether it may receive a purely morphological inter-

[[1] It is almost certain that this vesicle is not derived from the nucleus, but from the cytoplasm of the sperm-mother-cell. See Douglas H. Campbell, 'Zur Entwicklungsgeschichte der Spermatozoiden' in Berichte der deutschen botanischen Gesellschaft, vol. v, 1887, p. 122.—S. S.]

pretation. In former times it could only be regarded as of purely phyletic significance: it could only be looked upon as the last remnant of a process which formerly possessed some meaning, but which is now devoid of any physiological importance. We are indeed compelled to admit that a process does occur in connexion with the true polar bodies of animal eggs, which we cannot explain on physiological grounds; I mean the division of the polar bodies after they have been expelled from the egg. In many animals the two polar bodies divide again after their expulsion, so as to form four bodies, which distinctly possess the structure of cells, as Trinchese observed in the case of gastropods. But, in the first place, this second division does not always take place, and, secondly, it is very improbable that a process which occurs during the first stage of ontogeny, or more properly speaking, before the commencement of ontogeny, and which is, therefore, a remnant of some excessively ancient phyletic stage, would have been retained up to the present day unless it possessed some very important physiological significance. We may safely maintain that it would have disappeared long ago if it had been without any physiological importance. Relying on our knowledge of the slow and gradual, although certain, disappearance, in the course of phylogeny, of organs which have lost their functions, and of processes which have become meaningless, we are compelled to regard the process of the formation of polar bodies as of high physiological importance. But this view does not exclude the possibility that the process possessed a morphological meaning also, and I believe that we are quite justified in attempting (as Bütschli [1] has recently done) to discover what this morphological meaning may have been.

Should it be finally proved that the expulsion of polar bodies is nothing more than the removal of histogenetic nucleoplasm from the germ-cell, the opinion (which is so intimately connected with the theory of the continuity of the germ-plasm) that a re-transformation of specialised idioplasm into germ-plasm cannot occur, would be still further confirmed; for we do not find that any part of an organism is thrown away simply because it is useless: organs that have lost their functions are re-absorbed, and their material is thus employed to assist in building up the organism.

[1] Bütschli, 'Gedanken über die morphologische Bedeutung der sogenannten Richtungskörperchen,' Biolog. Centralblatt, Bd. VI. p. 5, 1884.

III. On the Nature of Parthenogenesis.

It is well known that the formation of polar bodies has been repeatedly connected with the sexuality of germ-cells, and that it has been employed to explain the phenomena of parthenogenesis. I may now, perhaps, be allowed to develope the views as to the nature of parthenogenesis at which I have arrived under the influence of my explanation of polar bodies.

The theory of parthenogenesis adopted by Minot and Balfour is distinguished by its simplicity and clearness, among all other interpretations which had been hitherto offered. Indeed, their explanation follows naturally and almost as a matter of course, if the assumption made by these observers be correct, that the polar body is the male part of the hermaphrodite egg-cell. An egg which has lost its male part cannot develope into an embryo until it has received a new male part in fertilization. On the other hand, an egg which does not expel its male part may develope without fertilization, and thus we are led to the obvious conclusion that parthenogenesis is based upon the non-expulsion of polar bodies. Balfour distinctly states 'that the function of forming polar cells has been acquired by the ovum for the express purpose of preventing parthenogenesis[1].'

It is obvious that I cannot share this opinion, for I regard the expulsion of polar bodies as merely the removal of the ovogenetic nucleoplasm, on which depended the development of the specific histological structure of the egg-cell. I must assume that the phenomena of maturation in the parthenogenetic egg and in the sexual egg are precisely identical, and that in both, the ovogenetic nucleoplasm must in some way be removed before embryonic development can begin.

Unfortunately the actual proof of this assumption is not so complete as might be desired. In the first place, we are as yet uncertain whether polar bodies are or are not expelled by parthenogenetic eggs[2]; for in no single instance has such expulsion been established beyond doubt. It is true that this deficiency does not afford any

[1] F. M. Balfour, 'Comparative Embryology,' vol. i. p. 63.

[2] The formation of a polar body in parthenogenetic eggs has now been proved: see note at the end of this Essay; see also Essay VI.—A. W., 1888.

support to the explanation of Minot and Balfour, for in all cases in which polar bodies have not been found in parthenogenetic eggs, these structures are also absent from the eggs which require fertilization in the same species. But although the expulsion of polar bodies in parthenogenesis has not yet been proved to occur, we must assume it to be nearly certain that the phenomena of maturation, whether connected or unconnected with the expulsion of polar bodies, are the same in the eggs which develope parthenogenetically and in those which are capable of fertilization, in one and the same species. This conclusion depends, above all, upon the phenomena of reproduction in bees, in which, as a matter of fact, the same egg may be fertilized or may develope parthenogenetically, as I shall have occasion to describe in greater detail at a later period.

Hence when we see that the eggs of many animals are capable of developing without fertilization, while in other animals such development is impossible, the difference between the two kinds of eggs must rest upon something more than the mode of transformation of the nucleus of the germ-cell into the first segmentation nucleus. There are, indeed, facts which distinctly point to the conclusion that the difference is based upon quantitative and not qualitative relations. A large number of insects are exceptionally reproduced by the parthenogenetic method, e. g. in Lepidoptera. Such development does not take place in all the eggs laid by an unfertilized female, but only in part, and generally a small fraction of the whole, while the rest die. But among the latter there are some which enter upon embryonic development without being able to complete it, and the stage at which development may cease also varies. It is also known that the eggs of higher animals may pass through the first stages of segmentation without having been fertilized. This was shown to be the case in the egg of the frog by Leuckart [1], in that of the fowl by Oellacher [2], and even in the egg of mammals by Hensen [3].

Hence in such cases it is not the impulse to development, but the

[1] R. Leuckart, — article 'Zeugung,' in R. Wagner's 'Handwörterbuch der Physiologie,' 1853, Bd. IV. p. 958. Similar observations were made by Max Schultze. These observations appear however to be erroneous, for Pflüger has since shown that the eggs of frogs never develope if the necessary precautions are taken to prevent the access of any spermatozoa to the water.—A. W., 1888.

[2] Oellacher, 'Die Veränderungen des unbefruchteten Keims des Hühncheneies. 'Zeitschrift für wissenschaftliche Zoologie,' Bd. XXII. p. 181. 1872.

[3] Hensen, 'Centralblatt,' 1869, No. 26.

power to complete it, which is absent. We know that force is always bound up with matter, and it seems to me that such instances are best explained by the supposition that too small an amount of that form of matter is present, which, by its controlling agency, effects the building-up of the embryo by the transformation of mere nutritive material. This substance is the germ-plasm of the segmentation nucleus, and I have assumed above that it is altered in the course of ontogeny by changes which arise from within, so that, when sufficient nourishment is afforded by the cell-body, each succeeding stage necessarily results from the preceding one. I believe that changes arise in the constitution of the nucleoplasm at each cell-division which takes place during the building-up of the embryo, changes which either correspond or differ in the two halves of each nucleus. If, for the present, we neglect the minute amount of unchanged germ-plasm which is reserved for the formation of the germ-cells, it is clear that a great many different stages in the development of somatic nucleoplasm are thus formed, which may be denominated as stages 1, 2, 3, 4, &c., up to *n*. In each of these stages the cells differ more as development proceeds, and as the number by which the stage is denominated becomes higher. Thus, for instance, the two first segmentation spheres would represent the first stage of somatic nucleoplasm, a stage which may be considered as but slightly different in its molecular structure from the nucleoplasm of the segmentation nucleus; the four first segmentation spheres would represent the second stage; the succeeding eight spheres the third, and so on. It is clear that at each successive stage the molecular structure of the nucleoplasm must be further removed from that of the germ-plasm, and that, at the same time, the cells of each successive stage must also diverge more widely among themselves in the molecular structure of their nucleoplasm. Early in development each cell must possess its own peculiar nucleoplasm, for the further course of development is peculiar to each cell. It is only in the later stages that equivalent or nearly equivalent cells are formed in large numbers, cells in which we must also suppose the existence of equivalent nucleoplasm.

If we may assume that a certain amount of germ-plasm must be contained in the segmentation nucleus in order to complete the whole process of the ontogenetic differentiation of this substance;

if we may further assume that the quantity of germ-plasm in the segmentation nucleus varies in different cases; then we should be able to understand why one egg can only develope after fertilization, while another can begin its development without fertilization, but cannot finish it, and why a third is even able to complete its development. We should also understand why one egg only passes through the first stages of segmentation and is then arrested, while another reaches a few more stages in advance, and a third developes so far that the embryo is nearly completely formed. These differences would depend upon the extent to which the germ-plasm, originally present in the egg, was sufficient for the development of the latter; development will be arrested as soon as the nucleoplasm is no longer capable of producing the succeeding stage, and is thus unable to enter upon the following nuclear division.

From a general point of view such a theory would explain many difficulties, and it would render possible an explanation of the phyletic origin of parthenogenesis, and an adequate understanding of the strange and often apparently abrupt and arbitrary manner of its occurrence. In my works on *Daphnidae* I have already laid especial stress upon the proposition that parthenogenesis in insects and Crustacea certainly cannot be an ancestral condition which has been transmitted by heredity, but that it has been derived from a sexual condition. In what other way can we explain the fact that parthenogenesis is present in certain species or genera, but absent in others closely allied to them; or the fact that males are entirely wanting in species of which the females possess a complete apparatus for fertilization? I will not repeat all the arguments with which I attempted to support this conclusion[1]. Such a conclusion may be almost certainly accepted for the *Daphnidae*, because parthenogenesis does not occur in their still living ancestors, the Phyllopods, and especially the *Estheridae*. In *Daphnidae* the cause and object of the phyletic development of parthenogenesis may be traced more clearly than in any other group of animals. In *Daphnidae* we can accept the conclusion with greater certainty than in all other groups, except perhaps the *Aphidae*, that parthenogenesis is extremely advantageous to species in certain conditions of life; and that it has only been adopted when, and as far as, it has been

[1] Weismann, 'Beiträge zur Naturgeschichte der Daphnoiden,' Leipzig, 1876-79, Abhandlung VII, and 'Zeitschrift für wissenschaftliche Zoologie,' Bd. XXXIII.

beneficial; and further, that at least in this group parthenogenesis became possible, and was adopted, in each species as soon as it became useful. Such a result can be easily understood if it is only the presence of more or less germ-plasm which decides whether an egg is, or is not, capable of development without fertilization.

If we now examine the foundations of this hypothesis we shall find that we may at once accept one of its assumptions, viz. that fluctuations occur in the quantity of germ-plasm in the segmentation nucleus; for there can never be absolute equality in any single part of different individuals. As soon therefore as these fluctuations become so great that parthenogenesis is produced, it may become, by the operation of natural selection, the chief mode of reproduction of the species or of certain generations of the species. In order to place this theory upon a firm basis, we have simply to decide whether the quantity of germ-plasm contained in the segmentation nucleus is the factor which determines development; although for the present it will be sufficient if we can render this view to some extent probable, and show that it is not in contradiction with established facts.

At first sight this hypothesis seems to encounter serious difficulties. It will be objected that neither the beginning nor the end of embryonic development can possibly depend upon the quantity of nucleoplasm in the segmentation nucleus, since the amount may be continually increased by growth; for it is well known that during embryonic development the nuclear substance increases with astonishing rapidity. By an approximate calculation I found[1] that, in the egg of a *Cynips*, the quantity of nuclear substance present at the time when the blastoderm was about to be formed, and when there were twenty-six nuclei, was even then seven times as great as the quantity which had been contained in the segmentation nucleus. How then can we imagine that embryonic development would ever be arrested from want of nuclear substance, and if such deficiency really acted as an arresting force, how then could development begin at all? We might suppose that when germ-plasm is present in sufficient quantity to start segmentation, it must also be sufficient to complete the development; for it grows continuously, and must presumably always possess a power

[1] Weismann, 'Beiträge zur Kenntniss der ersten Entwicklungsvorgänge im Insectenei,' Bonn, 1882, p. 106.

equal to that which it possessed at the beginning, and which was just sufficient to start the process of segmentation. If at each ontogenetic stage, the quantity of nucleoplasm is just sufficient to produce the following stage, we might well imagine that the whole ontogeny would necessarily be completed.

The flaw in this argument lies in the erroneous assumption that the growth of nuclear substance is, when the quality of the nucleus and the conditions of nutrition are equal, unlimited and uncontrolled. The intensity of growth must depend upon the quantity of nuclear substance with which growth and the phenomena of segmentation commenced. There must be an optimum quantity of nucleoplasm with which the growth of the nucleus proceeds most favourably and rapidly, and this optimum will be represented in the normal size of the segmentation nucleus. Such a size is just sufficient to produce, in a certain time and under certain external conditions, the nuclear substance necessary for the construction of the embryo, and to start the long series of cell-divisions. When the segmentation nucleus is smaller, but large enough to enter upon segmentation, the nuclei of the two first embryonic cells will fall rather more below the normal size, because the growth of the segmentation nucleus during and after division will be less rapid on account of its unusually small size. The succeeding generations of nuclei will depart more and more from the normal size in each respective stage, because they do not pass into a resting-stage during embryonic development, but divide again immediately after their formation. Hence nuclear growth would become less vigorous as the nuclei fell more and more below the optimum size, and at last a moment would arrive when they would be unable to divide, or would be at least unable to control the cell-body in such a manner as to lead to its division.

The first event of importance for embryonic development is the maturation of the egg, i. e. the transformation of the nucleus of the germ-cell into a nuclear spindle and the removal of the ovogenetic nucleoplasm by the separation of polar bodies, or by some analogous process. There must be some cause for this separation, and I have already tried to show that it may lie in the quantitative relations which obtain between the two kinds of nucleoplasm contained in the nucleus of the egg. I have suggested that the germ-plasm, at first small in quantity, undergoes a gradual increase, so that it can finally oppose the ovogenetic nucleoplasm. I will not further elaborate this suggestion, for the ascertained facts are insufficient for the purpose. But the appearances witnessed in nuclear division indicate that there are opposing forces, and that such a contest is the motive cause of division; and Roux [1] may be right in referring the opposition to electrical forces. However this may be, it is perfectly certain that the development of this opposition is based upon internal conditions arising during growth in the nucleus itself. The quantity of nuclear thread cannot by itself determine whether the nucleus can or cannot enter upon division; if so, it would be impossible for two divisions to follow each other in rapid succession, as is actually the case in the separation of the two polar bodies, and also in their subsequent division. In addition to the effects of quantity, the internal conditions of the nucleus must also play an important part in these phenomena. Quantity alone does not necessarily produce nuclear division, or the nucleus of the egg would divide long before maturation is complete, for it contains much more nucleoplasm than the female pronucleus, which remains in the egg after the expulsion of the polar bodies, and which is in most cases incapable of further division. But the fact that segmentation begins immediately after the conjugation of male and female pronuclei, also shows that quantity is an essential requisite. The effect of fertilization has been represented as analogous to that of the spark which kindles the gunpowder. In the latter case an explosion ensues, in the former segmentation begins. Even now, many authorities are inclined to refer the polar repulsion manifested in the nuclear division which immediately follows fertilization, to the antagonism between male and female elements. But, according to the important discoveries of Flemming and van Beneden, the polar repulsion in each nuclear division is not based on the antagonism between male and female loops, but depends upon the antagonism and mutual repulsion between the two halves of the same loop. The loops of the father and those of the mother remain together and divide together throughout the whole ontogeny.

What can be the explanation of the fact that nuclear division follows immediately after fertilization, but that without fertilization

[1] W. Roux, 'Ueber die Bedeutung der Kerntheilungsfiguren.' Leipzig, 1883.

it does not occur in most cases? There is only one possible explanation, viz. the fact that the quantity of the nucleus has been suddenly doubled, as the result of conjugation. The difference between the male and female pronuclei cannot serve as an explanation, even though the nature of this difference is entirely unknown, because polar repulsion is not developed between the male and female halves of the nucleus, but within each male and each female half. We are thus forced to conclude that increase in the quantity of the nucleus affords an impulse for division, the disposition towards it being already present. It seems to me that this view does not encounter any theoretical difficulties, and that it is an entirely feasible hypothesis to suppose that, besides the internal conditions of the nucleus, its quantitative relation to the cell-body must be taken into especial account. It is imaginable, or perhaps even probable, that the nucleus enters upon division as soon as its idioplasm has attained a certain strength, quite apart from the supposition that certain internal conditions are necessary for this end. As above stated, such conditions may be present, but division may not occur because the right quantitative relation between nucleus and cell-body, or between the different kinds of nuclear idioplasm, has not been established. I imagine that such a quantitative deficiency exists in an egg, which, after the expulsion of the ovogenetic nucleoplasm in the polar bodies, requires fertilization in order to begin segmentation. The fact that the polar bodies were expelled proves that the quantity of the nucleus was sufficient to cause division, while afterwards it was no longer sufficient to produce such a result.

This suggestion will be made still clearer by an example. In *Ascaris megalocephala* the nuclear substance of the female pronucleus forms two loops, and the male pronucleus does the same; hence the segmentation nucleus contains four loops, and this is also the case with the first segmentation spheres. If we suppose that in embryonic development, the first nuclear division requires such an amount of nuclear substance as is necessary for the formation of four loops,—it follows that an egg, which can only form two or three loops from its nuclear reticulum, would not be able to develope parthenogenetically, and that not even the first division would take place. If we further suppose that, while four loops are sufficient to start nuclear division, these loops must be of a certain size and quantity in order to complete the whole ontogeny (in a certain species), it follows that eggs possessing a reticulum which contains barely enough nuclear substance to divide into four segments, would be able to produce the first division and perhaps also the second and third, or some later division, but that at a certain point during ontogeny, the nuclear substance would become insufficient, and development would be arrested. This will occur in eggs which enter upon development without fertilization, but are arrested before its completion. One might compare this retardation leading to the final arrest of development, to a railway train which is intended to meet a number of other trains at various junctions, and which can only travel slowly because of some defect in the engine. It will be a little behind time at the first junction, but it may just catch the train, and it may also catch the second or even the third; but it will be later at each successive junction, and will finally arrive too late for a certain train; and after that it will miss all the trains at the remaining junctions. The nuclear substance grows continuously during development, but the rate at which it increases depends upon the nutritive conditions together with its initial quantity. The nutritive changes during the development of an egg depend upon the quantity of the cell-body which was present at the outset, and which cannot be increased. If the quantity of the nuclear substance is rather too small at the beginning, it will become more and more insufficient in succeeding stages, as its growth becomes less vigorous, and differs more from the standard it would have reached if the original quantity had been normal. Consequently it will gradually fall more and more short of the normal quantity, like the train which arrives later and later at each successive junction, because its engine, although with the full pressure of steam, is unable to attain the normal speed.

It will be objected that four loops cannot be necessary for nuclear division in *Ascaris,* since such division takes place in the formation of the polar bodies, resulting in the appearance of the female pronucleus with only two loops. But this fact only shows that the quantity of nuclear substance necessary for the formation of four loops is not necessary for all nuclear divisions; it does not disprove the assumption that such a quantity is required for the division of the segmentation nucleus. In addition to these considerations we must not leave the substance of the cell-body altogether out of account, for, although it is not the bearer of the tendencies of heredity, it must be necessary for every change undergone by the nucleus, and it surely also possesses the power of influencing changes to a large extent. There must be some reason for the fact that in all animal eggs with which we are acquainted, the nucleus moves to the surface of the egg at the time of maturation, and there passes through its well-known transformation. It is obvious that it is there subjected to different influences from those which would have acted upon it in the centre of the cell-body, and it is clear that such an unequal cell-division as takes place in the separation of the polar bodies could not occur if the nucleus remained in the centre of the egg.

This explanation of the necessity for fertilization does not exclude the possibility, that, under certain circumstances, the substance of the egg-nucleus may be larger, so that it is capable of forming four loops. Eggs which thus possess sufficient nucleoplasm, viz. germ-plasm, for the formation of the requisite four loops of normal size, (namely, of the size which would have been produced by fertilization), can and must develope by the parthenogenetic method.

Of course the assumption that four loops must be formed has only been made for the sake of illustration. We do not yet know whether there are always exactly four loops in the segmentation nucleus[1]. I may add that, although the details by which these considerations are illustrated are based on arbitrary assumptions, the fundamental view that the development of the egg depends, *ceteris paribus*, upon the quantity of nuclear substance, is certainly right, and follows as a necessary conclusion from the ascertained facts. It is not unlikely that such a view may receive direct proof in the results of future investigations. Such proof might for instance be forthcoming if we were to ascertain, in the same species, the number of loops present in the segmentation nucleus of fertilization, as compared with those present in the segmentation nucleus of parthenogenesis.

The reproductive process in bees will perhaps be used as an argument against my theory. In these insects, the same egg will develope into a female or male individual, according as fertilization

[1] We now know that the number of loops varies considerably in different species, even when they belong to the same group of animals (e.g. Nematodes).—A.W., 1888.

has or has not taken place, respectively. Hence, one and the same egg is capable of fertilization, and also of parthenogenetic development, if it does not receive a spermatozoon. It is in the power of the queen-bee to produce male or female individuals: by an act of will she decides whether the egg she is laying is to be fertilized or unfertilized. She 'knows beforehand'[1] whether an egg will develope into a male or a female animal, and deposits the latter kind in the cells of queens and workers, the former in the cells of drones. It has been shown by the discoveries of Leuckart and von Siebold that all the eggs are capable of developing into male individuals, and that they are only transformed into 'female eggs' by fertilization. This fact seems to be incompatible with my theory as to the cause of parthenogenesis, for if the same egg, possessing exactly the same contents, and above all the same segmentation nucleus, may develope sexually or parthenogenetically, it appears that the power of parthenogenetic development must depend on some factor other than the quantity of germ-plasm.

Although this appears to be the case, I believe that my theory encounters no real difficulty. I have no doubt whatever, that the same egg may develope with or without fertilization. From a careful study of the numerous excellent investigations upon this point which have been conducted in a particularly striking manner by Bessels[2] (in addition to the observers quoted above), I have come to the conclusion that the fact is absolutely certain. It must be candidly admitted that the *same* egg will develope into a drone when not fertilized, or into a worker or queen when fertilized. One of Bessels' experiments is sufficient to prove this assertion. He cut off the wings of a young queen and thus rendered her incapable of taking 'the nuptial flight.' He then observed that all the eggs which she laid developed into male individuals. This experiment was made in order to prove that drones are produced by unfertilized eggs; but it also proves that the assertion mentioned above is correct, for the eggs which ripen first and are therefore first laid, would have

[1] This expression is used by bee-keepers, for instance by the well-known Baron Berlepsch. Of course, it would be more accurate to say that the queen, seeing the cell of a drone, is stimulated to lay an unfertilized egg, and that, on the other hand, she is stimulated to lay a fertilized egg when she sees the cell of a worker, or that of a queen.

[2] E. Bessels, 'Die Landois'sche Theorie widerlegt durch das Experiment.' Zeitschrift für wissenschaftliche Zoologie, Bd. XVIII. p. 124. 1868.

been fertilized had the queen been impregnated. The supposition that, at certain times, the queen produces eggs requiring fertilization, while at other times her eggs develope parthenogenetically, is quite excluded by this experiment; for it follows from it, that the eggs must all be of precisely the same kind, and that there is no difference between the eggs which require fertilization and those which do not.

But does it therefore follow that the quantity of germ-plasm in the segmentation nucleus is not the factor which determines the beginning of embryonic development? I believe not. It can be very well imagined that the nucleus of the egg, having expelled the ovogenetic nucleoplasm, may be increased to the size requisite for the segmentation nucleus in one of two ways: either by conjugation with a sperm-nucleus, or by simply growing to double its size. There is nothing improbable in this latter assumption, and one is even inclined to inquire why such growth does not take place in all unfertilized eggs. The true answer to this question must be that nature generally pursues the sexual method of reproduction, and that the only way in which the general occurrence of parthenogenesis could be prevented, was by the production of eggs which remained sterile unless they were fertilized. This was effected by a loss of the capability of growth on the part of the egg-nucleus after it had expelled the ovogenetic nucleoplasm.

The case of the bee proves in a very striking manner that the difference between eggs which require fertilization, and those which do not, is not produced until after the maturation of the egg, and the removal of the ovogenetic nucleoplasm. The increase in the quantity of the germ-plasm cannot have taken place at any earlier period, or else the nucleus of the egg would always start embryonic development by itself, and the egg would probably be incapable of fertilization. For the relation between egg-nucleus and sperm-nucleus is obviously based upon the fact that each of them is insufficient by itself, and requires completion. If such completion had taken place at an early stage the egg-nucleus would either cease to exercise any attractive force upon the sperm-nucleus, or else conjugation would be effected, as in Fol's interesting experiments upon fertilization by many spermatozoa; and, as in these experiments, malformation of the embryo would result. In *Daphnidae*

I believe I have shown [1] that the summer-eggs are not only developed parthenogenetically, but also that they are never fertilized; and the explanation of this incapacity for fertilization may perhaps be found in the fact that their segmentation nucleus is already formed.

We may therefore conclude that, in bees, the nucleus of the egg, formed during maturation, may either conjugate with the sperm-nucleus, or else if no spermatozoon reaches the egg may, under the stimulus of internal causes, grow to double its size, thus attaining the dimensions of the segmentation nucleus. For our present purpose we may leave out of consideration the fact that in the latter case the individual produced is a male, and in the former case a female.

It is clear that such an increase in the germ-plasm must depend, to a certain extent, upon the nutrition of the nucleus, and thus indirectly upon the body of the egg-cell; but the increase must chiefly depend upon internal nuclear conditions, viz. upon the capability of growth. We must further assume that the latter condition plays the chief part in the process, for everywhere in the organic world the limit of growth depends upon the internal conditions of the growing body, and can only be altered to a small extent by differences of nutrition. The phyletic acquisition of the capability of parthenogenetic development must therefore depend upon an alteration in the capability of growth possessed by the nucleus of the egg.

This theory of parthenogenesis most nearly approaches Strasburger's views upon the subject, for he also explains the non-occurrence of parthenogenetic development by the insufficient quantity of nucleoplasm remaining in the egg after the expulsion of polar bodies. The former theory differs however in that the occurrence of parthenogenesis is supposed to be only due to an increase of this nucleoplasm to the normal size of the segmentation nucleus. Strasburger assumes that 'specially favourable conditions of nutrition counteract the deficiency of nuclear idioplasm,' while it seems to me that nutrition must be considered as only of secondary importance. Thus in bees, as above stated, the same egg may develope parthenogenetically or after fertilization, the nucleus being subject to the same conditions of nutrition in both cases. Strasburger[2]

[1] 'Daphniden,' Abhandlung, vi. p. 324. [2] l. c., p. 150.

considers that parthenogenesis may be interpreted by one of three possible explanations. First, he suggests that especially favourable nutrition may lead to the completion of the nuclear idioplasm. But if this assumption be made, we must ask why a part of the idioplasm should be previously expelled, when immediately afterwards the presence of an equal amount becomes necessary. Such a view can only be explained by the above-made assumption that the expelled nucleoplasm has a different constitution from that possessed by the nucleoplasm which is afterwards formed. It is true that we do not yet certainly know whether a polar body is expelled in eggs in which parthenogenesis occurs, but we do know that the egg of the bee passes through the same stages of maturation whether it is to be fertilized or not. I can hardly accept Strasburger's second suggestion, 'that under some favourable conditions of nutrition half [or perhaps better, a quarter] of the idioplasm of the egg-nucleus is sufficient to start the processes of development in the cyto-idioplasm.' Finally, his third suggestion, 'that the cyto-idioplasm, nourished by its surroundings and thus increased in quantity, compels the nucleus of the egg to enter upon division,' presupposes that the cell-body gives the impulse for nuclear division, a supposition which up to the present time remains at least unproved. The ascertained facts appear to me to indicate rather that the cell-body serves only as a medium for the nutrition of the nucleus, and Fol's recently mentioned observations, which have been especially quoted by Strasburger in support of his theories, seem to me to rather confirm my conclusions. If supernumerary sperm-nuclei penetrate into the egg, they may, under the nutritive influence of the cell-body, become centres of attraction, and may take the first step towards nuclear and cell-division by forming amphiasters. Such nuclei cannot control the whole cell-body and force it to divide, but each one of them, having grown to a certain size at the expense of the cell-body, makes its influence felt over a certain area. Strasburger is quite right in considering this process as a 'partial parthenogenesis.' Such partial parthenogenesis presumably occurs in all egg-nuclei, but the latter cannot attain to complete parthenogenesis when, as in Fol's supernumerary sperm-nuclei, their powers of assimilation are insufficient to enable them to reach the requisite size. As before stated, the cell-body does not force the nucleus to divide, but *vice versa*. It would, moreover, be quite erroneous to suppose that parthenogenetic eggs must contain a larger amount of nutritive material in order to facilitate the growth of the nucleus. The parthenogenetic eggs of certain *Daphnidae* (*Bythotrephes*, *Polyphemus*) are very much smaller than the winter-eggs, which require fertilization, in the same species. It is also an error for Strasburger to conclude that 'it has been established with certainty that favourable conditions of nutrition cause parthenogenetic development in *Daphnidae*, while unfavourable conditions cause the formation of eggs requiring fertilization.' It is true that Carl Düsing[1], in his notable work upon the origin of sex, has attempted, in a most ingenious manner, to prove, from my observations and experiments on the reproduction of *Daphnidae*, 'that winter or summer-eggs are formed according to the nutritive condition of the ovary.' I do not, however, believe that he has succeeded in this attempt, and at all events it is quite clear that the validity of such conclusions is not fully established. I have observed that the maturing eggs break up in the ovaries and are absorbed in those *Daphnidae* (*Sida*) which are starved because sufficient food cannot be provided in captivity. Hence such animals live, as it were, at the expense of their descendants; but it would be quite erroneous to conclude with Düsing, from the similarity which such disappearing egg-follicles bear to the groups of germ-cells which normally break up in the formation of winter-eggs, that with a less degree of starvation winter-eggs would have been formed. Düsing further quotes my incidental remark that the formation of resting-eggs in *Daphnia* has been especially frequent in aquaria 'which had been for some time neglected, and in which it was found that a great increase in the number of individuals had taken place.' He is entirely wrong in concluding that there was any want of food in these neglected aquaria; and if I had foreseen that such conclusions would have been drawn, I might have easily guarded against them by adding that in these very aquaria an undisturbed growth of different algae was flourishing, so that there could have been no deficiency, but, on the contrary, a great abundance of nutritive material. I may add that since that time I have conducted some experiments directly bearing upon this question, by bringing virgin females as near to the verge of

[1] Carl Düsing, 'Die Regulirung des Geschlechtsverhältnisses.' Jena, 1884.

starvation as possible, but in no case did they enter upon sexual reproduction [1].

An author must have been to some extent misled by preconceived ideas when he is unable to see that the manner in which the two kinds of eggs are respectively formed, directly excludes the possibility of the origin of sexual eggs from the effects of deficient or poor nutrition. The resting eggs, which require fertilization, are always larger, and require for their formation far more nutritive material, than the parthenogenetic summer-eggs. In *Moina*, for instance, forty large food-cells are necessary for the formation of a resting egg, while a summer-egg only requires three. And Düsing is aware of these facts, and quotes them. How can the formation of resting eggs depend upon the effects of poor nutrition when food is most abundant at the very time of their formation? In all those species which inhabit lakes, sexual reproduction occurs towards the autumn, and in such cases the resting eggs are true winter-eggs, destined to preserve the species during the winter. But at no time of the year is the food of the *Daphnidae* so abundant as in September and October, and frequently even until late in November (in South Germany). At this period of the year, the water is filled with flakes of animal and vegetable matter in a state of partial decomposition, thus affording abundant food for many species. It also swarms with a large number of species of Crustacea, Radiolaria, and Infusoria; and thus such Daphnids as the *Polyphemidae* are also well provided for. Hence there is no deficiency in the supply of food. Any one who has used a fine net in our fresh waters at this time of the year must have been at first astonished at the enormous abundance of the lower forms of animal life; and he must have been much more astonished if he has been able to compare such results with the scanty population of the same localities in spring. But it is during the spring and summer that these very *Daphnidae* reproduce themselves parthenogenetically. I am far from believing that my experiments on *Daphnidae* are exhaustive and final, and I have stated this in my published writings on the subject; but it seems to me that I have established the fact that direct influences, whether of food or of temperature, acting upon single individuals, do not determine the kind of eggs

[1] I intend to publish these experiments elsewhere in connexion with other observations.

which are to be produced; but that such a decisive influence is to be found in the indirect conditions of life, and especially in the average frequency of the recurrence of adverse circumstances which kill whole colonies at once, such as the winter cold, or the drying-up of small ponds in summer. It is unnecessary for me to controvert Düsing in detail, as I have already taken this course in the case of Herbert Spencer[1], who had also formed the hypothesis that diminished nutrition causes sexual reproduction.

One of my observations seems, indeed, to support such a view, but only when it is considered as an isolated example. I refer to the behaviour of the genus *Moina*. Females of this genus which possess sexual eggs in their ovaries, and which would have continued to produce such eggs if males had been present, enter in the absence of the latter upon the formation of parthenogenetic summer-eggs, that is, if the sexual eggs have not all been extruded, but have been re-absorbed in the ovary. At first sight, indeed, such a result appears to indicate that the increase in nutrition, produced by the breaking-up of the large winter-egg in the ovary, determines the formation of parthenogenetic eggs. This apparent conclusion seems to be further confirmed by the following fact. The transition from sexual to parthenogenetic reproduction only occurs in one species of *Moina* (*M. rectirostris*), but in this species it occurs always and without exception, while in the other species which I have investigated (*M. paradoxa*), winter-eggs, when once formed, are always laid, and such females can never produce summer-eggs. But in spite of this fact, Düsing is mistaken when he explains the continuous formation of sexual eggs in the latter species as due to the absence of any great increase in the amount of nutrition, such as would have followed if the egg had broken up in the ovary. In many other *Daphnidae* which have come under my notice, the females frequently enter again upon the formation of parthenogenetic summer-eggs, after having laid fertilized resting eggs, upon one or more occasions. This is the case, for instance, in all the species of *Daphnia* with which I am acquainted, and such a fact at once proves that the abnormal increase in nutrition produced by the absorption of winter-eggs cannot be the cause of the succeeding parthenogenesis. It also supports the proof that

[1] Weismann, 'Daphniden,' Abhandlung, VII. p. 329; Herbert Spencer, 'The Principles of Biology,' 1864, vol. i. pp. 229, 230.

a high or low nutritive condition of the whole animal can have nothing to do with the kind of eggs which are produced, for in the above-quoted instance, the nutrition has remained the same throughout, or at all events has not been increased. It is erroneous to always look for the explanation of the mode of egg-formation in the direct action of external causes. Of course there must be direct causes which determine that one germ shall become a winter-egg, and another a summer-egg; but such causes do not lie outside the animal, and have nothing to do with the nutritive condition of the ovary: they are to be found in those conditions which we are not at present able to analyze further, and which we must, in the meantime, call the specific constitution of the species. In the young males of *Daphnidae* the testes have precisely the same appearance as the ovaries of the young females[1], but the former will, nevertheless, produce sperm-cells and not ova. In such cases the sex of the young individual can always be identified by the form of the first antenna and of the first thoracic appendage, both of which are always clawed in the male. But who can point to the direct causes which determine that the sexual cells shall become sperm-cells in this case, and not egg-cells? Does the determining cause depend on the conditions of nutrition? Or, again, in the females, can the state of nutrition determine that the third out of a group of four germ-cells shall become an egg-cell, and that the others shall break up to serve as its food?

It is, I think, clear that these are obvious instances of the general conclusion that the direct causes determining the direction of development in each case are not to be looked for in external conditions, but in the constitution of the organs concerned.

We arrive at a like conclusion when we consider the quality of the eggs which are produced. The constitution of one species of *Moina* contains the cause which determines that each individual shall produce winter-eggs only, or summer-eggs only; while in another species the transition from the formation of sexual eggs to the formation of summer-eggs can take place, but only when the winter-egg remains unfertilized. The latter case appears to me to be notably a special adaptation, in this and other species, to the deficiency of males, which is apt to occur. *At all events, it is*

[1] The same fact has since been ascertained in species belonging to several groups of animals.

obvious that it is an advantage that an unfertilized sexual egg shall not be lost to the organism. The re-absorption of the winter-egg is an arrangement which, without being the cause, is favourable to the production of summer-eggs.

This subject is by no means a simple one, as is proved by the behaviour of the small group of *Daphnidae*. Thus in some species, the winter-eggs are produced by purely sexual females, which never enter upon parthenogenesis; in others, the sexual females may take the latter course, but only when males are absent; in others, again, they regularly enter upon parthenogenesis. In my work on *Daphnidae*, I have attempted to show that their behaviour in this respect is associated with the various external conditions under which the different species live; and also that the ultimate occurrence of the sexual period, and finally the whole cyclical alternation of sexual and parthenogenetic reproduction, depend upon adaptation to certain external conditions of life.

With the aid of my hypothesis that the egg-nucleus is composed of ovogenetic nucleoplasm and germ-plasm, I can now attempt to give an approximate explanation of the nature and origin of the direct causes which determine the production, at one time of parthenogenetic summer-eggs, and at another time of winter-eggs, requiring fertilization. But in such an explanation I should also wish to include a consideration of the causes which determine the formation of the nutritive cells of the egg and of the sperm-cells to which I have alluded above.

I believe that the direct cause which determines why the apparently identical cells of the young testis and ovary in the *Daphnidae* develope in such different directions, is to be found in the fact, that their nuclei possess different histogenetic nucleoplasms, while, if we neglect individual differences, the germ-plasm remains precisely the same. In the sperm-cells the histogenetic nucleoplasm is spermogenetic, in the egg-cells it is ovogenetic. This must be conceded if our fundamental view is correct, that the specific nature of the cell-body is determined by the nature of its nucleus.

Similarly, the germ-cells of female *Daphnidae*, which at first do not exhibit the smallest differences, must really differ in that their nuclei must contain different kinds of nucleoplasm, which are present in different proportions. Germ-cells which are to produce a finely granular, brick-red, winter yolk (*Moina rectirostris*) must possess an ovogenetic nucleoplasm of a somewhat different molecular structure from those germ-cells which have only to form a few large blue fat-globules, as in the summer-eggs of the same species. It is further probable that different proportions obtain between germ-plasm and ovogenetic nucleoplasm, in these two kinds of germ-cells; and it would be a very simple explanation of the otherwise obscure part played by the food-cells, if we were to suppose that they do not contain any germ-plasm at all, and on this account do not enter upon embryonic development, but are arrested after growing to a certain size. Such an explanation, however, would not by itself show why they subsequently undergo gradual solution in the surrounding fluids. But since we know that egg-cells also begin to undergo solution as soon as the parent Daphnid is poorly nourished, we can hardly help also referring the solution of the food-cells to insufficient nourishment, occurring as soon as the egg-cell, after the attainment of a certain size, exercises a superior power of assimilation. But hitherto we could not in any way understand why the third out of a group of germ-cells should always gain this superior power and become an egg-cell. If it could be shown that its position is more highly favoured in respect of nutrition, we could understand why it outstrips the other three in development, and thus prevents them from further growth. But nothing of the kind can be shown to occur with any degree of probability, as I have previously mentioned in my works on the subject. At that time, having no better explanation, I adopted the view in question, although only as a provisional interpretation. It was not possible for me to seek in the substance of those four apparently identical cells for the cause of their different development; but now I am justified in offering the supposition that during the division of a primitive germ-cell into two, and afterwards into four germ-cells, an unequal division of the nucleoplasms takes place, in that one of the four cells receives germ-plasm as well as ovogenetic nucleoplasm, while the other three receive the latter alone. Similarly, the fact that the second cell of the group may occasionally become an egg is also intelligible, although this fact remained quite inexplicable by my former interpretation. The fact that true egg-cells, or even the whole ovary with all its germ-cells, may break up and become absorbed when the animal has been starved for a certain period of time, seems to me to be no objection to our present view, any more than the fact that an Infusorian may die from starvation would be an objection to the supposition of the immortality of unicellular organisms. The growth of an organism is not only arrested by its constitution, but also by absolute want of food; but it would be very foolish to explain the differences in size of the various species of animals as results of the different conditions of nutrition to which they were subject. Just as a sparrow, however highly nourished, could never attain the size or form of an eagle, so a germ-cell destined to become a summer-egg could never attain the size, form, or colour of a winter-egg. It is by internal constitutional causes that the course of development is determined in both these cases; and in the latter, the cause can hardly be anything more than the different constitution of the nucleoplasms.

All these considerations depend upon the supposition that the egg-nucleus contains two kinds of idioplasm, viz. germ-plasm and ovogenetic nucleoplasm. I have not hitherto brought forward any direct evidence in favour of this assumption, but I believe that such proofs can be obtained.

It is well known that there are certain eggs in which the polar bodies are not expelled until after the entrance of spermatozoa. Brooks[1] has already made use of this fact as evidence against Minot's and Balfour's theory; for he quite rightly concludes that if the polar bodies really possess the significance of male cells, we cannot understand why such eggs are unable to develope without fertilization, when they still possess the male half of the nucleus necessary for development. But such eggs (e.g. that of the oyster) do not develope, but always die if they remain unfertilized.

This argument can only be met by a new hypothesis, the construction of which I must leave to the defenders of the above-mentioned theory. But the observation in question seems to me to furnish at the same time a proof of the co-existence of two different nucleoplasms in the egg-nucleus. If the nucleoplasm of the polar bodies was also germ-plasm, we could not understand why such eggs are unable to develope parthenogenetically, for at least as much germ-plasm is contained in the unfertilized egg as would have been present after fertilization.

[1] Brooks, 'The Law of Heredity.' Baltimore, 1883, p. 73.

The only objection which can be raised against this conclusion depends upon the supposition that the nucleoplasm of the sperm-cell is qualitatively different from that of the egg-cell. I have already dealt with this view, but I should wish to refer to it again rather more in detail. Some years ago I expressed the opinion [1] that the physiological values of the sperm-cell and of the egg-cell must be identical; that they stand in the ratio of 1 : 1. But Valaoritis [2] has brought forward the objection that if we consider the function of a cell as the measure of its physiological value, it is only necessary to point to the respective functions of ovum and spermatozoon in order to show that their physiological values must be different. 'The egg-cell alone, by passing more or less completely through the phyletic stages of the female parent, developes into a similar organism; and although the presence of the spermatozoon is in most cases required in order to render possible such a result, the cases of parthenogenesis prove nevertheless that the egg can do without this stimulus.' This objection appeared to be fully justified as long as fertilization was looked upon as the 'vitalization of the germ,' and so long as the sperm-cell was considered as merely 'the spark that kindles the gunpowder,' and further so long as the germ-substance was believed to be contained in the cell-body. But now we can hardly give to the body of the egg-cell a higher significance than that of the common nutritive soil of the two nuclei which conjugate in fertilization. But these two nuclei 'are not different in nature,' as Strasburger says, and as I fully believe. They cannot differ in kind, for they both consist of germ-plasm belonging to the same species of animal or plant; and there cannot be any deeper contrast between them such as would correspond to the differences between mature individuals. They cannot, from their essential nature, exercise any special attraction upon each other, and when we see that sperm-cell and egg-cell do nevertheless attract each other, as has been shown in both plants and animals, such a property must have been secondarily acquired, and has no other significance than to favour the union of sexual cells—an arrangement which may be compared to the vibrating flagellum of the spermatozoon or the micropyle of the egg, but which is not fundamental, and is not based upon the molecular

[1] 'Zeitschrift für wissenschaftliche Zoologie,' Bd. XXXIII. p. 107. 1873.
[2] Valaoritis, l. c., p. 6.

structure of the germ-plasm. In lower plants, Pfeffer has proved that certain chemical stimuli emanate from the egg and attract the spermatozoid; and according to Strasburger, the synergidae in the upper part of the embryo-sac of Phanerogams secrete a substance which is capable of directing the growth of the pollen-tube towards the egg-cell. In animals it is only known as yet that spermatozoa and ova do attract each other, so that the former find the latter and bore their way through its membranes. It has also been shown that the substance of the egg-body moves towards the penetrating spermatozoon ('*cones d'exsudation*' in *Asteridae*: Fol); and that it sometimes enters upon convulsive movements (*Petromyzon*). Here therefore a mutual stimulation and attraction must exist; and perhaps we must also assume that there is an attraction between the two conjugating nuclei, for we cannot readily understand how the cytoplasm alone could direct the one to the other, as Strasburger supposes. According to Strasburger's hypothesis, we must suppose that part of the specific cytoplasm of the sperm-cell continues to surround the nucleus after it has penetrated into the body of the egg. But however this may be, the assumed attraction between the conjugating nuclei certainly cannot depend upon the molecular structure of their germ-plasm, which is the same in both, but it must be due to some accessory circumstance. 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. Unfortunately the practical difficulties are so great that it is hardly possible that the experiment can ever be made; but such want of experimental proof is partially compensated for by the fact, ascertained by Berthold, that in certain Algae (*Ectocarpus* and *Scytosiphon*) there is not only a female, but also a male parthenogenesis; for he shows that in these species the male germ-cells may sometimes develope into plants, which however are very weakly[1]. Furthermore

[1] I quote from Falkenberg, in Schenk's 'Handbuch der Botanik,' Bd. II. p. 219. He further states that these are the only instances hitherto known in which undoubted male cells have proved to be capable of further development when they have been unable to exercise their powers of fertilization. It must be added that the two kinds of germ-cells do not differ in appearance, but only in behaviour; the female

the process of conjugation may be considered as a proof that this view as to the secondary importance of sexual differentiation is the true one. At the present time there can hardly be any hesitation in accepting the view that conjugation is the sexual reproduction of unicellular organisms. In these the two conjugating cells are almost always identical in appearance, and there is no evidence in favour of the assumption that they are not also identical in molecular structure, at least so far as one individual of the same species may be identical with another. But there are also forms in which the conjugating cells are distinctly differentiated into male and female, and these are connected with the former by a gradual transition: thus in *Pandorina*, a genus of *Volvocineae*, we are unable to make out any differences between the conjugating cells, while large egg-cells and minute sperm-cells exist in the closely allied *Volvox*. If we must suppose that the conjugation of two entirely identical Infusoria has the same physiological effect as the union of two sexual cells in higher animals and plants, we cannot escape the conclusion that the process is essentially the same throughout: and that therefore the differences, which are perhaps already indicated in *Pandorina* and are very distinct in *Volvox* and in all higher organisms, have nothing to do with the nature of the process, but are of quite secondary importance. If we further take into account the extremely different constitution of the two kinds of sexual cells in size, appearance, membranes, motile power, and finally in number, no doubt remains that these differences are only adaptations which secure the meeting of the two kinds of conjugating cells: that in each species they are adaptations to the peculiar conditions under which fertilization takes place.

germ-cells becoming fixed, and withdrawing one of their two flagella, while the male cells continue to swarm. But even this slight degree of differentiation requires the supposition of internal molecular differentiation.

NOTE.

It is of considerable importance for the proper appreciation of the views advanced in the present essay, to ascertain whether a polar body is or is not expelled from eggs which develope parthenogenetically. I wish therefore to briefly state that I have recently succeeded in proving the formation of a polar body of distinctly cellular structure in the summer-eggs of *Daphnidae*. I propose to publish a more detailed account in a future paper.

A. W.

June 22, 1885.