

## CHAPTER V

### OÖGENESIS AND SPERMATOGENESIS. REDUCTION OF THE CHROMOSOMES

“Es kommt also in der Generationenreihe der Keimzelle irgendwo zu einer Reduktion der ursprünglich vorhandenen Chromosomenzahl auf die Hälfte, und diese *Zahlen*-reduktion ist demnach nicht etwa nur ein theoretisches Postulat, sondern eine Thatsache.”

BOVERI.<sup>1</sup>

VAN BENEDEN's epoch-making discovery that the nuclei of the conjugating germ-cells contain each one-half the number of chromosomes characteristic of the body-cells has now been extended to so many plants and animals that it may probably be regarded as a universal law of development. The process by which the reduction in number is effected, forms the most essential part of the phenomena of *maturat-ion* by which the germ-cells are prepared for their union. No phenomena of cell-life possess a higher theoretical interest than these. For, on the one hand, nowhere in the history of the cell do we find so unmistakable and striking an adaptation of means to ends or one of so marked a prophetic character, since maturation looks not to the present but to the future of the germ-cells. On the other hand, the chromatin-reduction suggests questions relating to the morphological constitution of nucleus and chromatin, which have an important bearing on all theories of the ultimate structure of living matter and now stand in the foreground of scientific discussion among the most debatable and interesting of biological problems.

Two fundamentally different views have been held of the manner in which the reduction is effected. The earlier and simpler view, which was suggested by Van Beneden and adopted in the earlier works of Weismann, Boveri, and others, assumed an actual degeneration or casting out of half of the chromosomes during the growth of the germ-cells—a simple and easily intelligible process. Later researches conclusively showed, however, that this view cannot be sustained, and that *reduction is effected by a rearrangement and redistribution of the nuclear substance* without loss of any of its essential constituents. It is true that a large amount of chromatin is lost during the growth of the egg.<sup>2</sup> It is nevertheless certain that this loss is not directly connected with the process of reduction; for, as Hertwig

<sup>1</sup> *Zellenstudien*, III., p. 62.

<sup>2</sup> Cf. Figs. 97, 116.

and others have shown, no such loss occurs during spermatogenesis, and even in the oögenesis the evidence is clear that an explanation must be sought in another direction. The attempts to find such an explanation have led to some of the most interesting researches of modern cytology; and though only partially successful, they have raised many new questions which promise to give in the end a deeper insight into some of the fundamental questions of cell-morphology. For this reason they deserve careful consideration, despite the fact that taken as a whole the subject still remains an unsolved riddle in the face of which we can only return again and again to Boveri's remark that whatever be its theoretical interpretation the numerical reduction of the chromosomes is itself not a theory but a fact.

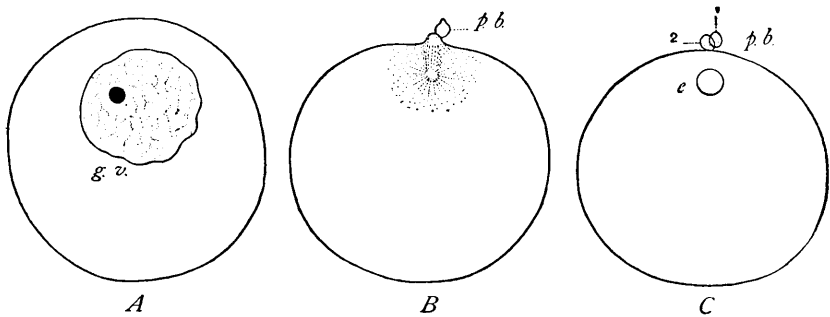


Fig. 114. — Formation of the polar bodies before entrance of the spermatozöon, as seen in the living ovarian egg of the sea-urchin, *Toxopneustes* ( $\times 365$ ).

*A.* Preliminary change of form in the germinal vesicle. *B.* The first polar body formed, the second forming. *C.* The ripe egg, ready for fertilization, after formation of the two polar bodies (*p. b. 1, 2*); *e.* the egg-nucleus. In this animal the first polar body fails to divide. For its division see Fig. 89.

## A. GENERAL OUTLINE

The general phenomena of maturation fall under two heads: viz. *oögenesis*, which includes the formation and maturation of the ovum, and *spermatogenesis*, comprising the corresponding phenomena in case of the spermatozöon. Recent research has shown that maturation conforms to the same type in both sexes, which show as close a parallel in this regard as in the later history of the germ-nuclei. Stated in the most general terms, this parallel is as follows:<sup>1</sup> In both sexes the final reduction in the number of chromosomes is effected in the course of the last two cell-divisions, or *maturation-divisions*, by which the definitive germ-cells arise, each of the four cells thus formed having but half the usual number of chromosomes. In the female but one

<sup>1</sup> The parallel was first clearly pointed out by Platner in 1889, and was brilliantly demonstrated by Oscar Hertwig in the following year.

of the four cells forms the "ovum" proper, while the other three, known as the *polar bodies*, are minute, rudimentary, and incapable of development (Figs. 89, 97, 114). In the male, on the other hand, all four of the cells become functional spermatozoa. This difference between the two sexes is probably due to the physiological division of labour between the germ-cells, the spermatozoa being motile and very small, while the egg contains a large amount of protoplasm and yolk, out of which the main mass of the embryonic body is formed. In the male, therefore, all of the four cells may become functional; in the female the functions of development have become restricted to but one

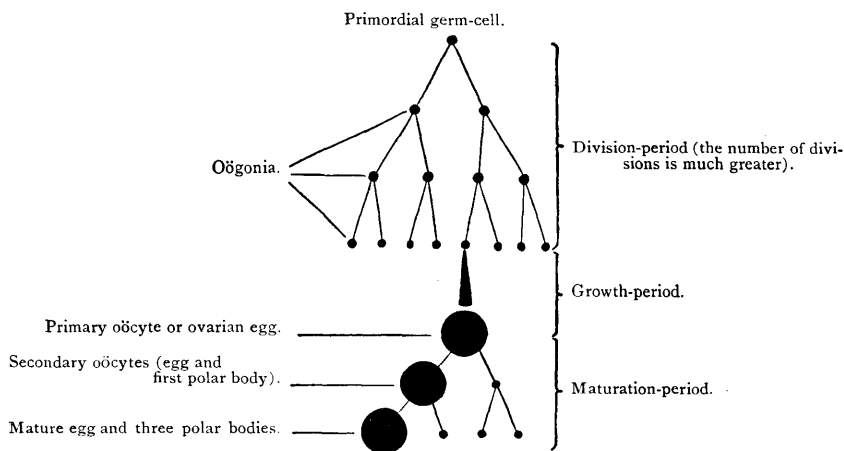


Fig. 115. — Diagram showing the genesis of the egg. [After BQVERI.]

of the four, while the others have become rudimentary (*cf.* p. 124). The polar bodies are therefore not only rudimentary cells (Giard, '76), but may further be regarded as *abortive eggs* — a view first put forward by Mark in 1881, and ultimately adopted by nearly all investigators.<sup>1</sup> The evidence is steadily accumulating that reduction is accomplished by two maturation-divisions throughout the animal kingdom, even in the unicellular forms; though in certain Infusoria an additional division occurs, while in some other Protozoa only one maturation-division has thus far been made out. Among plants, also, two maturation-

<sup>1</sup> A beautiful confirmation of this view is given by Francottes's ('97) observations on a turbellarian, *Prostheceraeus*. The first polar body is here often abnormally large, all gradations having been observed from the normal size up to cells nearly as large as the egg itself. *Such polar bodies are occasionally fertilized* and develop into small gastrulas, first forming a single polar body like the second polar body of the egg. Here, therefore, two of the four cells are exceptionally capable of development. It may be added that Fol long ago observed the penetration of the small polar bodies by spermatozoa in the echinoderms; and this has been more recently observed by Kostanecki in mollusks.

divisions occur in all the higher forms (Muscineæ, pteridophytes, and phanerogams), and in some, at least, of the lower ones. Here, however, the phenomena are complicated by the fact that the two divisions do not as a rule give rise directly to the four sexual germ-cells, but to four asexual spores which undergo additional divisions before the definitive germ-cells are produced. In the flowering plants there are only a few such divisions, which give rise to structures within the pollen-tube or embryo-sac. In the archegoniate cryptogams, on the other hand, each spore gives rise, by repeated divisions, to a "sexual generation" (prothallium, etc.) that intervenes between the process of reduction and that of fertilization. The following account deals primarily with reduction in animals, the plants being afterward considered.

### 1. *Reduction in the Female. Formation of the Polar Bodies*

As described in Chapter III., the egg arises by the division of cells descended from the primordial egg-cells of the maternal organism, and these may be differentiated from the somatic cells at a very early period, sometimes even in the cleavage-stages. As development proceeds, each primordial cell gives rise, by division of the usual mitotic type, to a number of descendants known as *oögonia* (Fig. 115), which are the immediate predecessors of the ovarian egg. At a certain period these cease to divide. Each of them then grows to form an ovarian egg, its nucleus enlarging to form the germinal vesicle, its cytoplasm becoming more or less laden with food-matters (yolk or deutoplasm), while egg-membranes may be formed around it. The ovum may now be termed the *oöcyte* (Boveri) or ovarian egg.

In this condition the egg-cell remains until near the time of fertilization, when the process of maturation proper — *i.e.* the formation of the polar bodies — takes place. In some cases, *e.g.* in the sea-urchin, the polar bodies are formed before fertilization, while the egg is still in the ovary. More commonly, as in annelids, gasteropods, nematodes, they are not formed until after the spermatozoön has made its entrance; while in a few cases one polar body may be formed before fertilization and one afterward, as in the lamprey-eel, the frog, and *Amphioxus*.<sup>1</sup> In all these cases the essential phenomena are the same. Two minute cells are formed, one after the other, near the upper or animal pole of the ovum (Figs. 97, 116); and in many cases the first of these divides into two as the second is formed (Fig. 89).

A group of four cells thus arises, namely, the mature egg, which gives rise to the embryo, and three small cells or polar bodies which take no part in the further development, are discarded, and soon die

<sup>1</sup> *Cf.* p. 189.

without further change. The egg-nucleus is now ready for union with the sperm-nucleus.

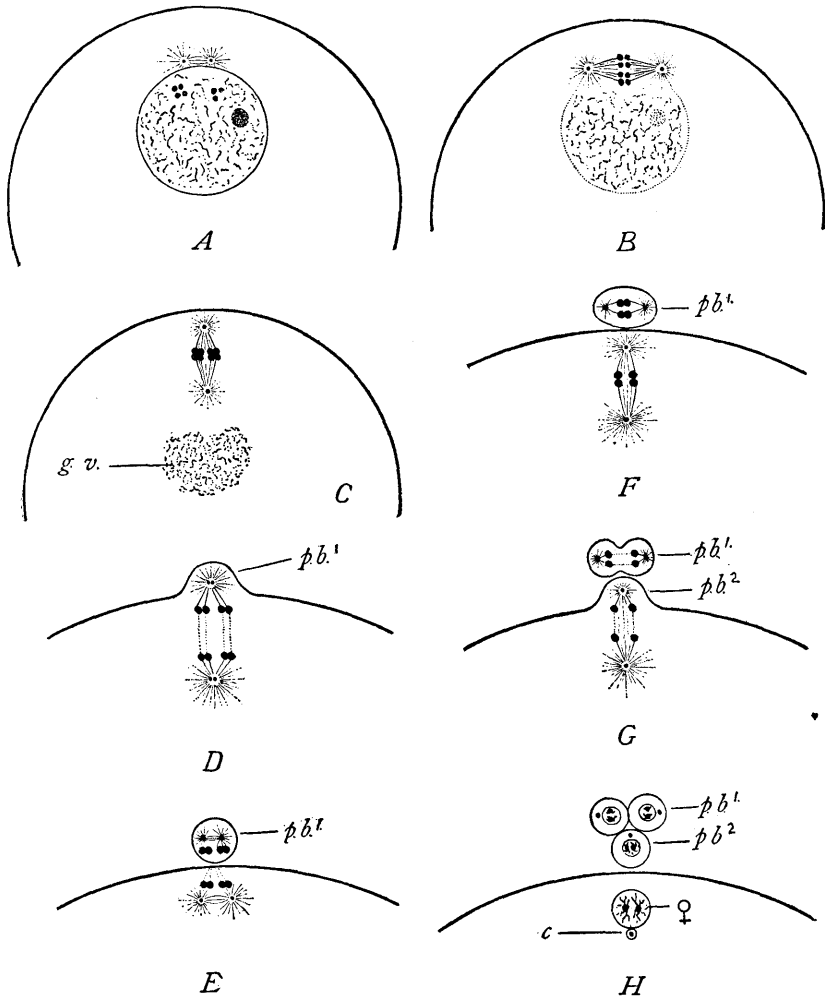


Fig. 116. — Diagrams showing the essential facts in the maturation of the egg. The somatic number of chromosomes is supposed to be four.

*A.* Initial phase; two tetrads have been formed in the germinal vesicle. *B.* The two tetrads have been drawn up about the spindle to form the equatorial plate of the first polar mitotic figure. *C.* The mitotic figure has rotated into position, leaving the remains of the germinal vesicle at *g.v.* *D.* Formation of the first polar body; each tetrad divides into two dyads. *E.* First polar body formed; two dyads in it and in the egg. *F.* Preparation for the second division. *G.* Second polar body forming and the first dividing; each dyad divides into two single chromosomes. *H.* Final result; three polar bodies and the egg-nucleus (♀), each containing two single chromosomes (half the somatic number); *c.* the egg-centrosome which now degenerates and is lost.

A study of the nucleus during these changes brings out the following facts. During the multiplication of the oögonia the number of chromosomes is the same as that occurring in the division of the somatic cells, and the same number enters into the formation of the chromatic reticulum of the germinal vesicle. During the formation of the polar bodies this number becomes reduced to one-half, the nucleus of each polar body and the egg-nucleus receiving the reduced number. In some manner, therefore, the formation of the polar bodies is connected with the process by which the reduction is effected. The precise nature of this process is, however, a matter which has been certainly determined in only a few cases.

We need not here consider the history of opinion on this subject further than to point out that the early observers, such as Purkinje, Von Baer, Bischoff, had no real understanding of the process and believed the germinal vesicle to disappear at the time of fertilization. To Bütschli ('76), Hertwig, and Giard ('76, '77) we owe the discovery that the formation of the polar bodies is through *mitotic division*, the chromosomes of the equatorial plate being derived from the chromatin of the germinal vesicle.<sup>1</sup> In the formation of the first polar body the group of chromosomes splits into two daughter-groups, and this process is immediately repeated in the formation of the second *without an intervening reticular resting stage*. The egg-nucleus therefore receives, like each of the polar bodies, one-fourth of the *mass* of chromatin derived from the germinal vesicle.

But although the formation of the polar bodies was thus shown to be a process of true cell-division, the history of the chromosomes was found to differ in some very important particulars from that of the tissue-cells. The essential facts, which were first carefully studied in *Ascaris* by Van Beneden ('83, '87), and especially by Boveri ('87, 1), are in a typical case as follows (Figs. 116, 117): As the egg prepares for the formation of the first polar body, the chromatin of the germinal vesicle groups itself in a number of masses, each of which splits up into a group of four bodies united by linin-threads to form a "quadruple group" or tetrad (Vierergruppe). *The number of tetrads is always one-half the usual number of chromosomes*. Thus in *Ascaris (megaloccephala, bivalens)* the germinal vesicle gives rise to two tetrads, the normal number of chromosomes in the earlier divisions being four; in the mole-cricket there are six tetrads, the somatic number of chromosomes being twelve; in *Cyclops* the respective numbers are twelve and twenty-four (one of the most frequent cases); while in *Artemia* there are eighty-four tetrads and one hundred and sixty-

<sup>1</sup>The early accounts asserting the disappearance of the germinal vesicle were based on the fact that in many cases only a small fraction of the chromatic network gives rise to chromosomes, the remainder disintegrating and being scattered through the yolk.

eight somatic chromosomes — the highest number thus far accurately counted. As the first polar body forms, each of the tetrads is halved to form two double groups, or *dyads*, one of which remains in the egg

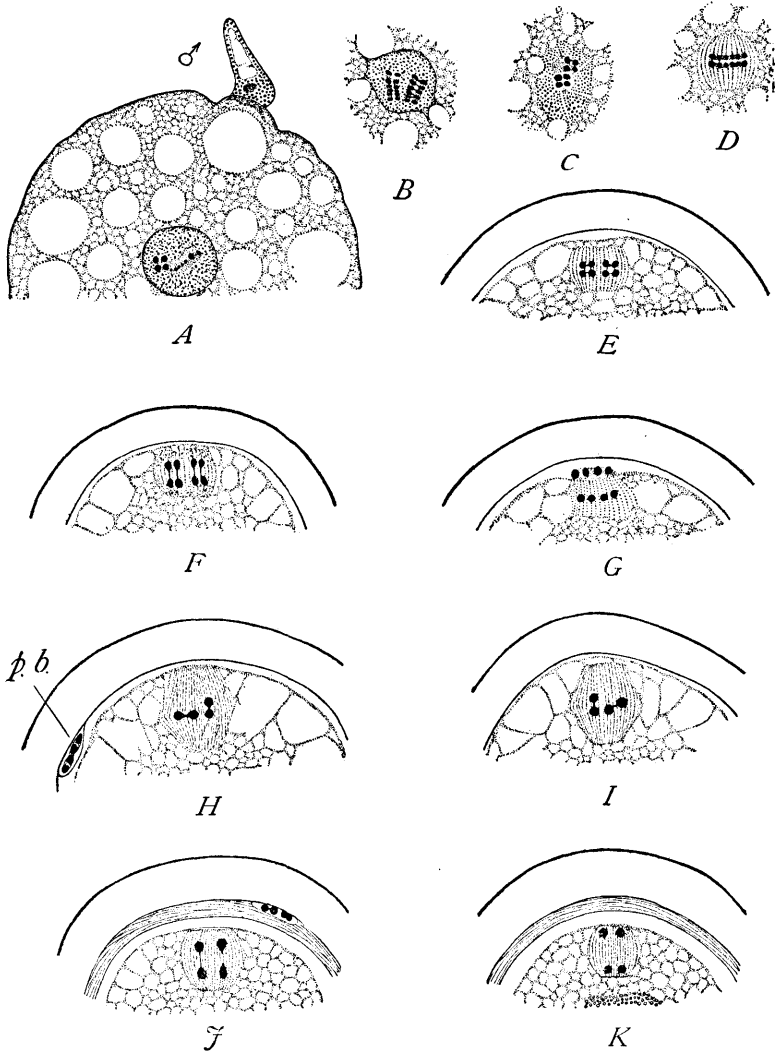


Fig. 117. — Formation of the polar bodies in *Ascaris megalocephala*, var. *bivalens*. [BOVERI]

A. The egg with the spermatozoön just entering at ♂; the germinal vesicle contains two rod-shaped tetrads (only one clearly shown), the number of chromosomes in earlier divisions having been four. B. The tetrads seen in profile. C. The same in end view. D. First spindle forming (in this case inside the germinal vesicle). E. First polar spindle. F. The tetrads dividing. G. First polar body formed, containing, like the egg, two dyads. H. I. The dyads rotating into position for the second division. J. The dyads dividing. K. Each dyad has divided into two single chromosomes, completing the reduction. (For later stages see Fig. 90.)

while the other passes into the polar body. Both the egg and the first polar body therefore receive each a number of dyads equal to one-half the usual number of chromosomes. The egg now proceeds at once to the formation of the second polar body without previous reconstruction of the nucleus. Each dyad is halved to form two single chromosomes, one of which, again, remains in the egg while its sister passes into the polar body. Both the egg and the second polar body accordingly receive two single chromosomes (one-half the usual number), each of which is one-fourth of an original tetrad group. From the two remaining in the egg a reticular nucleus, much smaller than the original germinal vesicle, is now formed.<sup>1</sup>

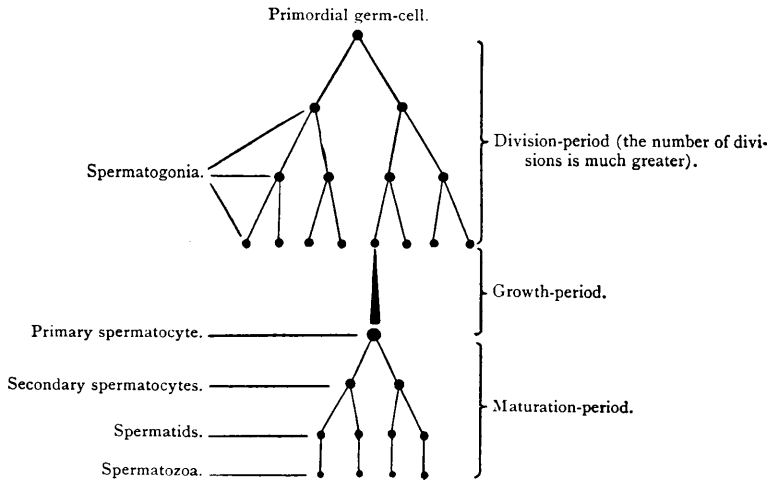


Fig. 118. — Diagram showing the genesis of the spermatozoön. [After BOVERI.]

Essentially similar facts have now been determined in a considerable number of animals, though, as we shall presently see, tetrad-formation is not of universal occurrence, nor is it always of the same type. For the moment we need only point out that the numerical reduction of chromatin-masses takes place before the polar bodies are actually formed, through processes which determine the number of tetrads within the germinal vesicle. The numerical reduction is therefore determined in the grandmother-cell of the egg. The actual divisions by which the polar bodies are formed merely distribute the elements of the tetrads.

<sup>1</sup> It is nearly certain that the division of the first polar body (which, however, may be omitted) is analogous to that by which the second is formed, *i.e.* each of the dyads is similarly halved. Cf. Griffin, '99.

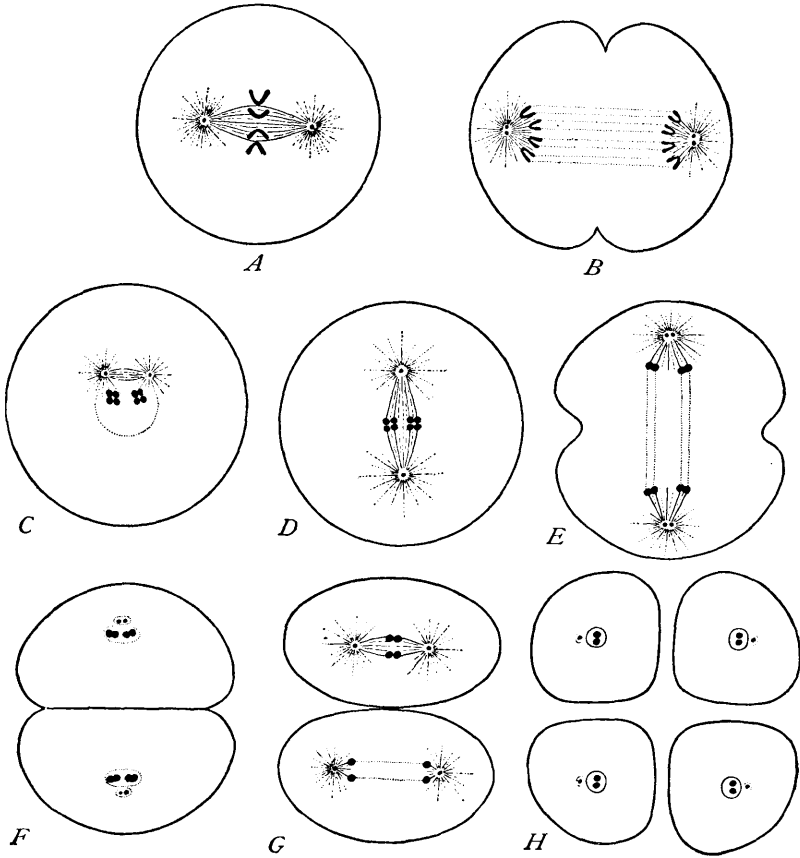


## 2. Reduction in the Male. Spermatogenesis

The researches of Platner ('89), Boveri, and especially of Oscar Hertwig ('90, 1) have demonstrated that reduction takes place in the male in a manner almost precisely parallel to that occurring in the female. Platner first suggested ('89) that the formation of the polar bodies is directly comparable to the last two divisions of the sperm mother-cells (spermatocytes). In the following year Boveri reached the same result in *Ascaris*, stating his conclusion that reduction in the male must take place in the "grandmother-cell of the spermatozoön, just as in the female it takes place in the grandmother-cell of the egg," and that the egg-formation and sperm-formation really agree down to the smallest detail ('90, p. 64). Later in the same year appeared Oscar Hertwig's splendid work on the spermatogenesis of *Ascaris*, which established this conclusion in the most striking manner. Like the ova, the spermatozoa are descended from primordial germ-cells which by mitotic division give rise to the *spermatogonia* from which the spermatozoa are ultimately formed (Fig. 118). Like the oögonia, the spermatogonia continue for a time to divide with the usual (somatic) number of chromosomes, *i.e.* four in *Ascaris megalocephala bivalens*. Ceasing for a time to divide, they now enlarge considerably to form *spermatocytes*, each of which is morphologically equivalent to an unripe ovarian ovum, or *oöcyte*. Each spermatocyte finally divides twice in rapid succession, giving rise first to two daughter-spermatocytes and then to four *spermatids*, each of which is directly converted into a single spermatozoön. *The history of the chromatin in these two divisions is exactly parallel to that in the formation of the polar bodies* (Figs. 119, 120). From the chromatin of the spermatocyte are formed a number of tetrads equal to one-half the usual number of chromosomes. Each tetrad is halved at the first division to form two dyads which pass into the respective daughter-spermatocytes. At the ensuing division, which occurs without the previous formation of a resting reticular nucleus, each dyad is halved to form two single chromosomes which enter the respective spermatids (ultimately spermatozoa). From each spermatocyte, therefore, arise four spermatozoa, and each sperm-nucleus receives half the usual number of single chromosomes. The parallel with the egg-reduction is complete.

These facts leave no doubt that the spermatocyte is the morphological equivalent of the oöcyte or immature ovarian egg, and that the group of four spermatozoa to which it gives rise is equivalent to the ripe egg plus the three polar bodies. Hertwig was thus led to the following beautifully clear and simple conclusion: "The polar bodies are abortive eggs which are formed by a final process of

division from the egg-mother-cell (oöcyte) in the same manner as the spermatozoa are formed from the sperm-mother-cell (spermatocyte). But while in the latter case the products of the division are all used as functional spermatozoa, in the former case one of the products



**Fig. 119.** — Diagrams showing the essential facts of reduction in the male. The somatic number of chromosomes is supposed to be four.

*A. B.* Division of one of the spermatogonia, showing the full number (four) of chromosomes. *C.* Primary spermatocyte preparing for division; the chromatin forms two tetrads. *D. E. F.* First division to form two secondary spermatocytes each of which receives two dyads. *G. H.* Division of the two secondary spermatocytes to form four spermatids. Each of the latter receives two single chromosomes and a centrosome which passes into the middle-piece of the spermatozoön.

of the egg-mother-cell becomes the egg, appropriating to itself the entire mass of the yolk at the cost of the others which persist in rudimentary form as the polar bodies.”<sup>1</sup>

<sup>1</sup> '90, 1, p. 126.

### 3. *Weismann's Interpretation of Reduction*

Up to this point the facts are clear and intelligible. Before coming to closer quarters with them it will be useful to make a digression in order to consider some of the theoretical aspects of reduction; though the reader must be warned that this will lead us into very uncertain ground traversed by a labyrinth of conflicting hypotheses from which no exit has yet been discovered.

The process of reduction is very obviously a provision to hold constant the number of chromosomes characteristic of the species; for if it did not occur, the number would be doubled in each succeeding generation through union of the germ-cells.<sup>1</sup> A number of writers have contented themselves with this simple interpretation, Oscar Hertwig, for example, regarding reduction as "merely a process to prevent a summation through fertilization of the nuclear mass and of the chromatic elements."<sup>2</sup> A moment's reflection reveals the entire inadequacy of such an explanation. As far as the chromatin-mass is concerned, it does not agree with the facts; for in reduction with tetrad-formation the chromatin-mass is reduced not to one-half, but to one-fourth. That reduction must mean more than mere mass-reduction is moreover proved by the fact that the bulk of the nucleus may enormously increase or decrease at different periods in the same cell, irrespective of the number of chromosomes. The real problem is why the number of chromosomes should be held constant. The

<sup>1</sup> Of the many earlier attempts to interpret the meaning of the polar bodies, we need only consider at this point the very interesting suggestion of Minot ('77), afterward adopted by Van Beneden ('83), that the ordinary cell is hermaphrodite, and that maturation is for the purpose of producing a unisexual germ-cell by dividing the mother-cell into its sexual constituents, or "genoblasts." Thus, the male element is removed from the egg in the polar bodies, leaving the mature egg a female. In like manner he believed the female element to be cast out during spermatogenesis (in the "Sertoli cells"), thus rendering the spermatozoa male. By the union of the germ-cells in fertilization, the male and female elements are brought together so that the fertilized egg or oöperm is again hermaphrodite or neuter. This ingenious view was independently advocated by Van Beneden in his great work on *Ascaris* ('83). A fatal objection to it, on which both Strasburger and Weismann have insisted, lies in 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-cells are therefore non-sexual. The researches of many observers show, moreover, that all of the four spermatids derived from a spermatocyte become functional spermatozoa. Minot's hypothesis must, therefore, in my opinion, be abandoned.

Balfour doubtless approximated more nearly to the truth when he said, "In the formation of the polar cells part of the constituents of the germinal vesicle, which are requisite for its functions as a complete and independent nucleus, is removed to make room for the supply of the necessary parts to it again by the spermatic nucleus" ('80, p. 62). He fell, however, into the same error as Minot and Van Beneden in characterizing the germ-nuclei as "male" and "female"; and, as shown at pages 194, 353, it has been found that a single germ-nucleus is able to carry out development of an embryo without union with another.

<sup>2</sup> '90, I, p. 112. Cf. Hartog, '91, p. 57.

deeper meaning of the phenomena was first seriously considered by Weismann in his essays of 1885 and 1887; and, although his conclusions were of a highly speculative character, they nevertheless gave so

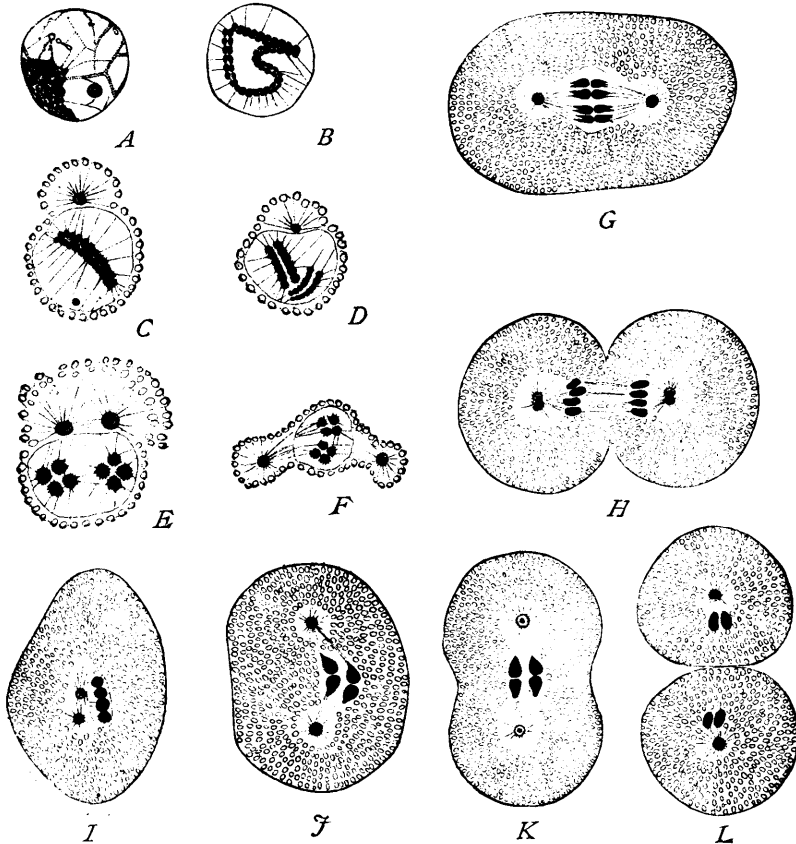


Fig. 120. — Reduction in the spermatogenesis of *Ascaris megalocephala*, var. *bivalens*. [BRAUER.]<sup>1</sup>

A-G. Successive stages in the division of the primary spermatocyte. The original reticulum undergoes a very early division of the chromatin-granules which then form a doubly split spireme-thread, B. This shortens (C), and breaks in two to form the two tetrads (D in profile, E viewed endwise). F, G, H. First division to form two secondary spermatocytes, each receiving two dyads. I. Secondary spermatocyte. J, K. The same dividing. L. Two resulting spermatids, each with two single chromosomes and a centrosome.

great a stimulus to the study of the entire problem that his views deserve special attention. Weismann's interpretation was based on a remarkable paper published by Wilhelm Roux in 1883,<sup>2</sup> in which are

<sup>1</sup> For division of the spermatogonia see Fig. 55; for the corresponding phenomena in var. *univalens* see Fig. 148.

<sup>2</sup> *Über die Bedeutung der Kerntheilungsfiguren.*

developed certain ideas which afterward formed the foundation of Weismann's whole theory of inheritance and development. Roux argued that the facts of mitosis are only explicable under the assumption that chromatin is not a uniform and homogeneous substance, but differs qualitatively in different regions of the nucleus; that the collection of the chromatin into a thread and its accurate division into two halves is meaningless unless the chromatin in different regions of the thread represents different *qualities* which are to be divided and distributed to the daughter-cells according to some definite law. He urged that if the chromatin were qualitatively the same throughout the nucleus, direct division would be as efficacious as indirect, and the complicated apparatus of mitosis would be superfluous. Roux and Weismann, each in his own way, subsequently elaborated this conception to a complete theory of inheritance and development, but at this point we may confine our attention to the views of Weismann. The starting-point of his theory is the hypothesis of De Vries that the chromatin is a congeries or colony of invisible self-propagating vital units or *biophores* somewhat like Darwin's "gemmules" (p. 12), each of which has the power of determining the development of a particular quality. Weismann conceives these units as aggregated to form units of a higher order known as "determinants," which in turn are grouped to form "ids," each of which, for reasons that need not here be specified,<sup>1</sup> is assumed to possess the complete architecture of the germ-plasm characteristic of the species. The "ids" finally, which are identified with the visible chromatin-granules, are arranged in linear series to form "idants" or chromosomes. It is assumed further that the "ids" differ slightly in a manner corresponding with the individual variations of the species, each chromosome therefore being a particular group of slightly different germ-plasms and differing qualitatively from all the others.

We come now to the essence of Weismann's interpretation. The end of fertilization is to produce new combinations of variations by the mixture of different ids. Since, however, their number, like that of the chromosomes which they form, is doubled by the union of two germ-nuclei, an infinite complexity of the chromatin would soon arise did not a periodic reduction occur. Assuming, then, that the "ancestral germ-plasms" (ids) are arranged in a linear series in the spireme-thread or the chromosomes derived from it, Weismann ventured the prediction ('87) that two kinds of mitosis would be found to occur. The first of these is characterized by a longitudinal splitting of the thread, as in ordinary cell-division, "by means of which all the ancestral germ-plasms are equally distributed in each of the daughter-nuclei after having been divided into halves." This form of division, which

<sup>1</sup> Cf. the Germ-plasm, p. 60.

he called *equal division* (Aequationstheilung), was then a known fact. The second form, at that time a purely theoretical postulate, he assumed to be of such a character that each daughter-nucleus should receive only half the number of ancestral germ-plasms possessed by the mother-nucleus. This he termed a *reducing division* (Reduktionstheilung), and suggested that this might be effected either by a *transverse* division of the chromosomes, or by the elimination of entire chromosomes without division.<sup>1</sup> By either method the number of "ids" would be reduced; and Weismann argued that such reducing divisions must be involved in the formation of the polar bodies, and in the parallel phenomena of spermatogenesis.

The fulfilment of Weismann's prediction is one of the most interesting results of recent cytological research. It has been demonstrated, in a manner which seems to be incontrovertible, that the reducing divisions postulated by Weismann actually occur, though not precisely in the manner conceived by him. Unfortunately for the general theory, however, transverse divisions have been certainly determined in only a few types, while in others, of which *Ascaris* is the best-known example, the facts thus far known seem clearly opposed to the assumption. On the whole, the evidence of reducing divisions, *i.e.* such as involve a transverse and not a longitudinal division of the chromatin-thread, has steadily increased; but it remains quite an open question whether they have the significance attributed to them by Weismann.

## B. ORIGIN OF THE TETRAIDS

### I. *General Sketch*

In considering the origin of the tetrads or their equivalents, it should be borne in mind that true tetrad-formation, as described above, has only been certainly observed in a few groups (most clearly in the nematodes and arthropods). But even in cases where the chromatin does not condense into actual tetrads these bodies are represented by chromosomes in the form of rings, crosses, and the like, which are closely similar, and doubtless equivalent, to those from which actual tetrads arise, and present us with the same problems. With a few apparent exceptions, described hereafter, the tetrads of their equivalents always arise by a double division of a single primary chromatin-rod or mass. Nearly all observers agree further that the number of primary rods at their first appearance in the germinal vesicle or in the spermatocyte-nucleus is *one-half the usual number of chromosomes*, and that this numerical reduction is due to the fact that the spireme-thread segments into one-half the

<sup>1</sup> Essay VI., p. 375.

usual number of pieces. Apparently, however, there are two radically different types of tetrad-formation as follows.

In the first type the tetrad arises by *one longitudinal and one transverse division of each primary chromatin-rod*, the latter effecting the reduction demanded by Weismann's hypothesis (Fig. 121, I). To give the usual graphic representation, let us, for the sake of discussion, assume the somatic number of chromosomes to be four, designating the spireme-thread as  $a b c d$ ,

*I* each letter representing a chromosome, each of which we may in turn assume to consist of a series of four granules or "ids" (Fig. 121). In ordinary mitosis the spireme would segment into  $a - b - c - d$ , which then would divide lengthwise to form pairs of identical sister chromosomes  $\frac{a}{a} - \frac{b}{b} - \frac{c}{c} - \frac{d}{d}$ .

To form the tetrad, on the other hand, the spireme first segments into two rods  $ab$  and  $cd$ , each of which, in view of its subsequent history, may be regarded as bivalent, representing two chromosomes united end to end (Vom Rath, Rückert, Häcker). Each of these divides once longitudinally, giving the identical pairs or

dyads  $\frac{ab}{ab} - \frac{cd}{cd}$ , and once transversely, giving the tetrads  $\frac{a}{a} \mid \frac{b}{b} - \frac{c}{c} \mid \frac{d}{d}$ . Inspection of Fig. 121, I, shows that through the second or transverse division, each member of the tetrad receives only half the number of ids contained in the original segment. This number, four, is the same as that assumed for a single chromosome; and, since each of the two tetrads contributes one chromosome to the germ-cell, the latter receives

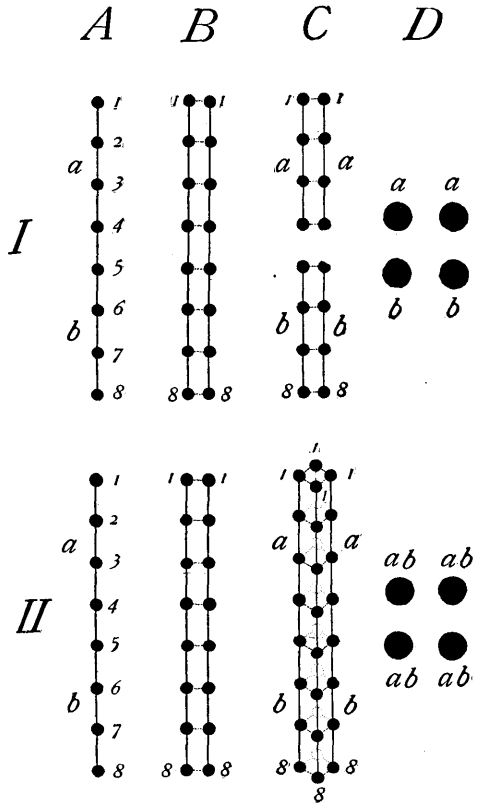


Fig. 121.—Diagrams of tetrad-formation; I, with one transverse and one longitudinal division (copepod type); II, with two longitudinal divisions (*Ascaris* type). A-D, successive stages; chromatin-granules numbered from 1 to 8. The two types diverge at C. In D the granules of each constituent of the tetrad fuse to form a homogeneous sphere.

but half the usual number both of chromosomes and of ids. This mode of tetrad-formation has been most clearly demonstrated in insects and copepods, and an equivalent process occurs also in mollusks, annelids, turbellarians, and some other animals, as described beyond.

In the second type, illustrated especially by *Ascaris*, the tetrad is apparently formed by *two longitudinal divisions* of each primary chromatin-rod, and no reducing division occurs. If, therefore, we adopt the same terminology as before, we have first  $ab$  and  $cd$ , then  $\frac{ab}{ab} - \frac{cd}{cd}$ , and finally  $\frac{ab}{ab} | \frac{ab}{ab} - \frac{cd}{cd} | \frac{cd}{cd}$ , by two longitudinal divisions. In this case, according to Brauer's careful studies, each chromatin-granule ("id") divides at each longitudinal division of the primary rod. The four chromosomes of the tetrad are therefore exactly equivalent, being derived from the same region of the spireme-thread, and containing the undiminished number of "ids" (Fig. 121, II).

The contradiction may be stated in a different way. In the first type of tetrad formation, the number both of granules and of chromosomes is first *doubled* (*i.e.* in the assumed case, through the formation of two tetrads, each consisting of four chromosomes, or eight in all), and then reduced to half that number by the two successive maturation-divisions. In the second type, on the other hand, the number of chromosomes is likewise doubled, but that of the granules is *quadrupled*, so that, although in both types the two maturation-divisions reduce the number of *chromosomes* to one-half, only in the first type do they reduce the number of granules or "ids," as Weismann's hypothesis demands. We must therefore distinguish sharply between the reduction of the chromosomes and that of the "ids." The former is primarily effected by the segmentation of the primary spireme-thread, or the resolution of the nuclear reticulum, into one-half the usual number of segments (*i.e.* the "pseudo-reduction" of Rückert); and *here the real secret of the reduction of the chromosomes lies*. The reduction of the "ids," if they have any real existence, is a distinct, and as yet unsolved, question.

## 2. Detailed Evidence

We may now consider some of the phenomena in detail, though the limits of this work will only allow the consideration of a few typical cases.

(a) *Tetrad-formation with one Longitudinal and one Transverse Division*. — In many of the cases of this type the tetrads arise from ring-shaped bodies which are analogous to the ring-shaped chromosomes occurring in heterotypical mitosis (p. 86). First observed by Henking ('91) in *Pyrrhocoris*, tetrad-origin of this type has since been found in other insects by Vom Rath, Toyama, Paulmier, and others,



in copepods by Rückert, Häcker, and Vom Rath, in pteridophytes by Calkins and Osterhout, in the onion, *Allium*, by Ishikawa, and in various other forms where their history has been less clearly made out. The genesis of the ring was first determined by Vom Rath in the mole cricket (*Gryllotalpa*, '92), and has been thoroughly elucidated by the later work of Rückert ('94), Häcker ('95, 1), and Paulmier ('99). All these observers have reached the same conclusion; namely, that the ring arises by the longitudinal splitting of a primary chromatin-rod, the two halves remaining united by their ends, and opening out to form a ring. The ring-formation is, in fact, a form of

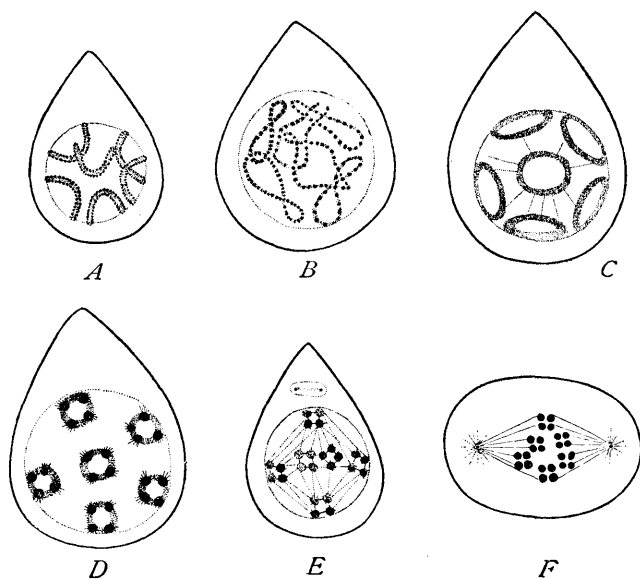


Fig. 122.—Origin of the tetrads by ring-formation in the spermatogenesis of the mole-cricket *Gryllotalpa*. [VOM RATH.]

A. Primary spermatocyte, containing six double rods, each of which represents two chromosomes united end to end and longitudinally split except at the free ends. B. C. Opening out of the double rods to form rings. D. Concentration of the rings. E. The rings broken up into tetrads. F. First division-figure established.

heterotypical mitosis (p. 86). The breaking of the ring into four parts involves, first, the separation of these two halves (corresponding with the original longitudinal split), and second, the *transverse* division of each half, the latter being the reducing division of Weismann. The number of primary rods, from which the rings arise, is one-half the somatic number. Hence each of them is conceived by Vom Rath, Häcker, and Rückert as bivalent or double; *i.e.* as representing two chromosomes united end to end. This appears with the greatest clearness in the spermatogenesis of *Gryllotalpa* (Fig. 122). Here

the spireme-thread splits lengthwise before its segmentation into rods. It then divides transversely to form six double rods (half the usual number of chromosomes), which open out to form six closed rings. These become small and thick, break each into four parts, and thus

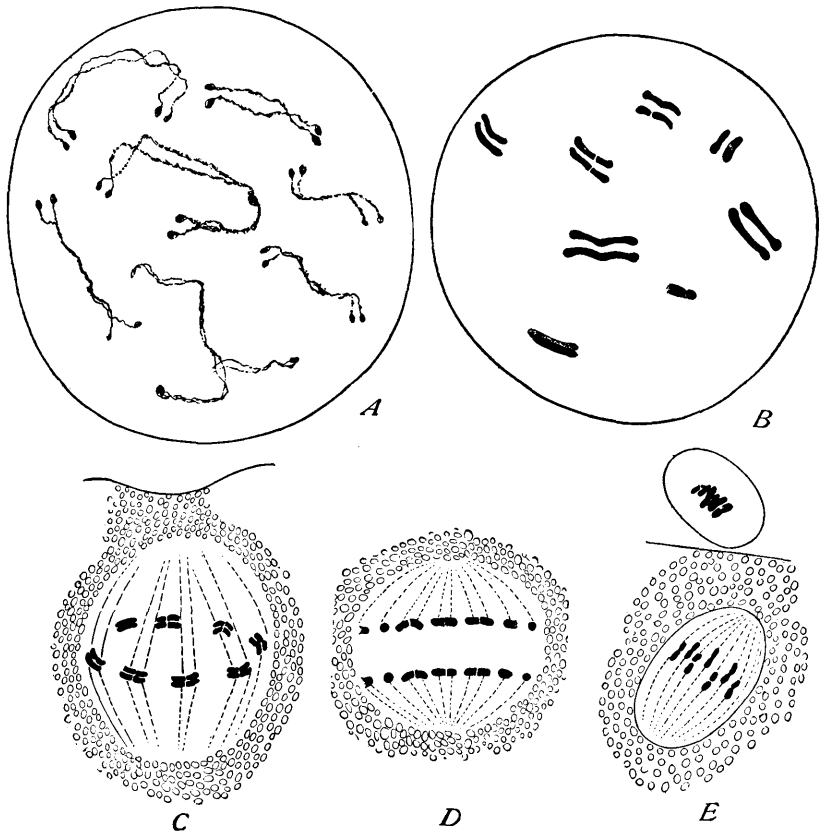


Fig. 123. — Formation of the tetrads and polar bodies in *Cyclops*, slightly schematic. (The full number of tetrads is not shown.) [RÜCKERT.]

*A.* Germinal vesicle containing eight longitudinally split chromatin-rods (half the somatic number). *B.* Shortening of the rods; transverse division (to form the tetrads) in progress. *C.* Position of the tetrads in the first polar spindle, the longitudinal split horizontal. *D.* Anaphase; longitudinal divisions of the tetrads. *E.* The first polar body formed; second polar spindle with the eight dyads in position for the ensuing division, which will be a *transverse* or reducing division.

give rise to six typical tetrads. An essentially similar account of the ring-formation is given by Vom Rath in *Euchæta* and *Calanus*, and by Rückert in *Hetercope* and *Diaptomus*.

That the foregoing interpretation of the rings is correct, is beautifully demonstrated by the observations of Häcker, and especially of

Rückert, on a number of other copepods (*Cyclops*, *Canthocamptus*), in which rings are not formed, since the splitting of the primary chromatin-rods is complete. The origin of the tetrads has here been traced with especial care in *Cyclops strenuus*, by Rückert ('94), whose observations, confirmed by Häcker, are quite as convincing as those

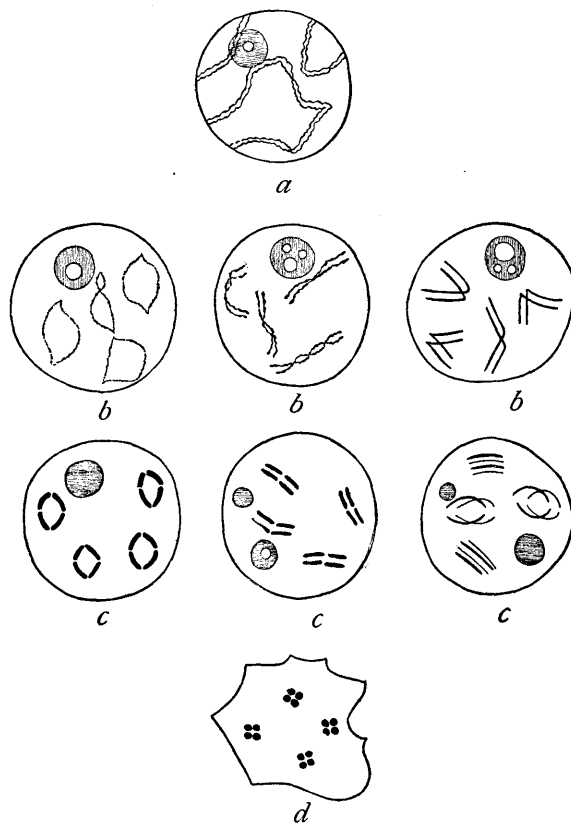


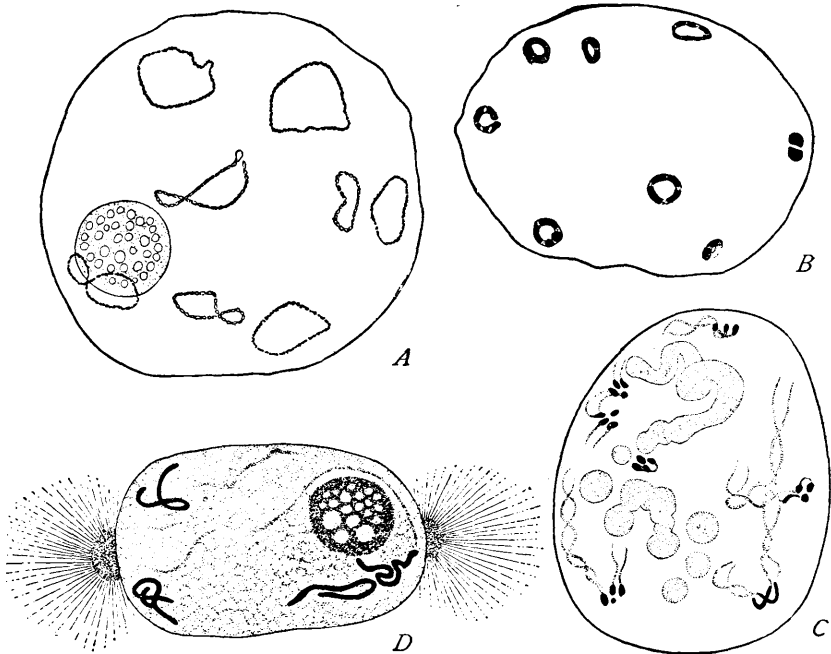
Fig. 124. — Diagrams of various modes of tetrad-formation. [HÄCKER.]

*a.* Common starting-point, a double spireme-thread in the germinal vesicle; *d.* common result, the typical tetrads; *b. c.* intermediate stages: at the left the ring-formation (as in *Diaptomus*, *Grylloalpa*, *Heterocope*); middle series, complete splitting of the rods (as in *Cyclops* according to Rückert, and in *Canthocamptus*); at the right by breaking of the V-shaped rods (as in *Cyclops strenuus*, according to Häcker.

of Brauer on *Ascaris*, though they led to a diametrically opposite result.

The normal number of chromosomes is here twenty-two. In the germinal vesicle arise eleven threads, which split lengthwise (Fig. 123), and finally shorten to form double rods, manifestly equivalent to the closed rings of *Diaptomus*. Each of these now segments *transversely*

to form a tetrad group, and the eleven tetrads then place themselves in the equator of the spindle for the first polar body (Fig. 123, *C*), in such a manner that the *longitudinal split* is transverse to the axis of the spindle. As the polar body is formed, the longitudinal halves of the tetrad separate, and the formation of the first polar body is thus demonstrated to be an "equal division" in Weismann's sense. The eleven dyads remaining in the eggs now rotate (as in *Ascaris*),



**Fig. 125.** — Germinal vesicles of various eggs, showing chromosomes, tetrads, and nucleoli.  
*A.* A copepod (*Heterocope*) showing eight of the sixteen ring-shaped tetrads and the nucleolus. [RÜCKERT.]  
*B.* Later stage of the same, condensation and segmentation of the rings. [RÜCKERT.]  
*C.* "*Cyclops strenuus*," illustrating Häcker's account of the tetrad-formation from elongate double rods; a group of "accessory nucleoli." [HÄCKER.]  
*D.* Germinal vesicle of an annelid (*Ophryotrocha*) showing nucleolus and four chromosomes. [KORSCHÉLT.]

so that the transverse division lies in the equatorial plane, and are halved during the formation of the second polar body. The division is accordingly a "reducing division," which leaves eleven single chromosomes in the egg. Paulmier's work on *Anasa* and other Hemiptera ('99) gives the same result as the above in regard to the origin of the tetrads (Figs. 126, 127). The process is, however, slightly complicated by the fact that no continuous spireme-thread is formed, while the rings are often bent or twisted and never open out to a

circular form. They finally condense into true tetrads which are successively divided into dyads and monads by the two divisions; but it is an interesting fact that the order of division occurring in the copepods appears here to be reversed, the first division being the transverse and the second the longitudinal one—a result agreeing with Henking's earlier conclusion in the case of *Pyrrhochoris*. Osterhout ('97) and Calkins ('97) independently discovered tetrads in the vascular cryptogams (*Equisetum*, *Pteris*), and the last-named observer finds that in *Pteris* they may arise either from rings, as in *Gryllotalpa* or *Heterocope*, or from double rods as in *Cyclops*, the halves in the latter case being either parallel or forming a cross. This longitudinal split, occurring in the spireme, is followed by a transverse division by which the tetrad is formed. Tetrads having an essentially similar mode of origin are also described by Atkinson ('99) in *Arisæma*, and tetrad-formation is nearly approached in *Allium* according to Ishikawa ('99).<sup>1</sup> These cases are considered at page 263.

*Résumé.* In all the foregoing cases the tetrads arise from a spireme which splits lengthwise, segments into one-half the somatic number of rods (each longitudinally divided) and each of the latter divides transversely to form the tetrad. When the ends of the daughter-chromosomes resulting from the longitudinal split remain united (as in insects) ring-forms result, and the earlier phases of tetrad-formation are thus identical with those of heterotypical mitosis. When the split is complete, so that the ends remain free, double rods result; while, if the daughter-chromosomes remain temporarily united at the middle or at the end, X-, Y-, and V-shaped figures may arise. In all these forms tetrad-formation is completed by the complete separation of the daughter-rods, the transverse division of each in the middle, and the condensation of the four resulting bodies into a quadruple mass. As will be shown in Section C (p. 258) the transverse division is in many forms delayed until after separation of the longitudinal halves. In such cases no actual tetrads are formed, though the result is the same.

(b) *Second Type. Tetrad-formation with two Longitudinal Divisions.*—The only accurately known case of this type is *Ascaris*, the object in which tetrads were first discovered by Van Beneden in 1883. Carnoy ('86, 2) reached the conclusion that the tetrads in some other nematodes (*Ophiostomum*, *Ascaris clavata*, *A. lumbricoides*) arose by a double longitudinal splitting of the primary chromatin-rods.

<sup>1</sup> Vom Rath ('93, '59) has endeavoured to show that a process involving the formation of true tetrads occurs in the salamander and the frog, but the later and more accurate studies of Meves ('96) seem to leave little doubt that this was an error, and that the tetrads observed in these forms are not of normal occurrence, as Flemming ('87) had earlier concluded. Cf. p. 259.

In the first of his classical cell-studies Boveri ('87, 1) reached the same result through a careful study of *Ascaris megalocephala*, showing that each tetrad appears in the germinal vesicle in the form of four parallel rods, each consisting of a row of chromatin-granules (Fig. 117, A-C). He believed these rods to arise by the double longitudinal splitting of a single primary chromatin-rod, each cleavage being a

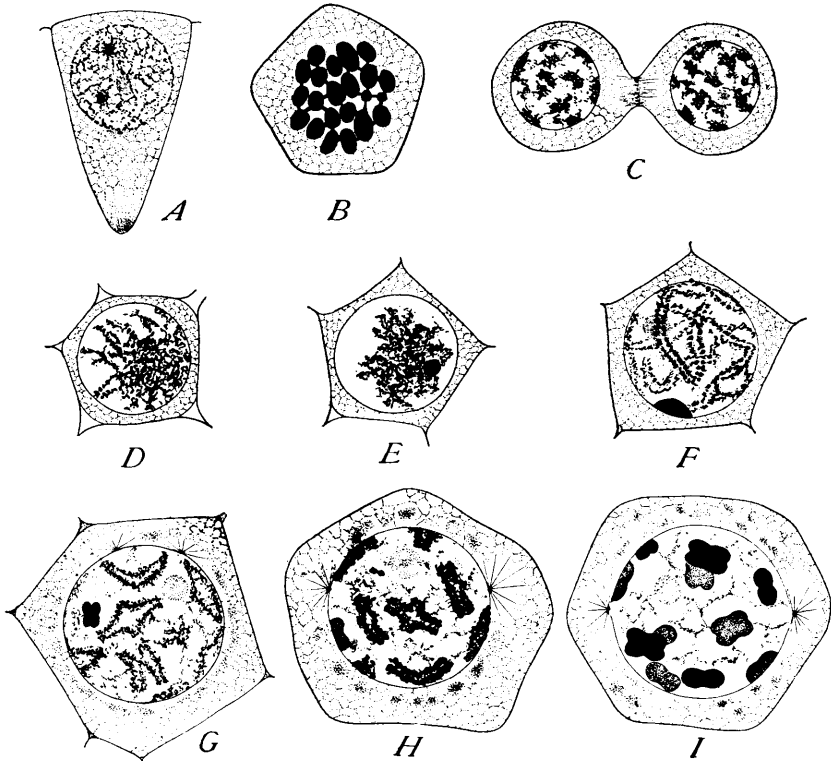


Fig. 126.—Tetrad-formation in an insect, *Anasa*. [PAULMIER.]

A. Resting spermatogonium with single plasmosome and two chromatin-nucleoli. B. Equatorial plate of dividing spermatogonium; twenty large and two small chromosomes. C. Final spermatogonium-division. D-I. Prophases of first maturation-division. D, E. Synapsis, with single chromatin-nucleolus. F. Segmented split spireme. G, H. Formation of the tetrad-rings. H, I. Concentration of the rings to form tetrads.

preparation for one of the polar bodies. In his opinion, therefore, the formation of the polar bodies differs from ordinary mitosis only in the fact that the chromosomes split very early, and not once, but twice, in preparation for two rapidly succeeding divisions without an intervening resting period. He supported this view by further observations in 1890 on the polar bodies of *Sagitta* and several gasteropods, in which he again determined, as he believed, that the tetrads

arose by double longitudinal splitting. An essentially similar view of the tetrads was taken by Hertwig in 1890, in the spermatogenesis of *Ascaris*, though he could not support this conclusion by very convincing evidence. In 1893, finally, Brauer made a most thorough and apparently exhaustive study of their origin in the spermatogenesis of *Ascaris*, which seemed to leave no doubt of the correctness of Boveri's result. Every step in the origin of the tetrads from the reticulum of the resting spermatocytes was traced with the most painstaking care. In the early prophases of the first division the nuclear reticulum breaks up more or less completely into granules, which

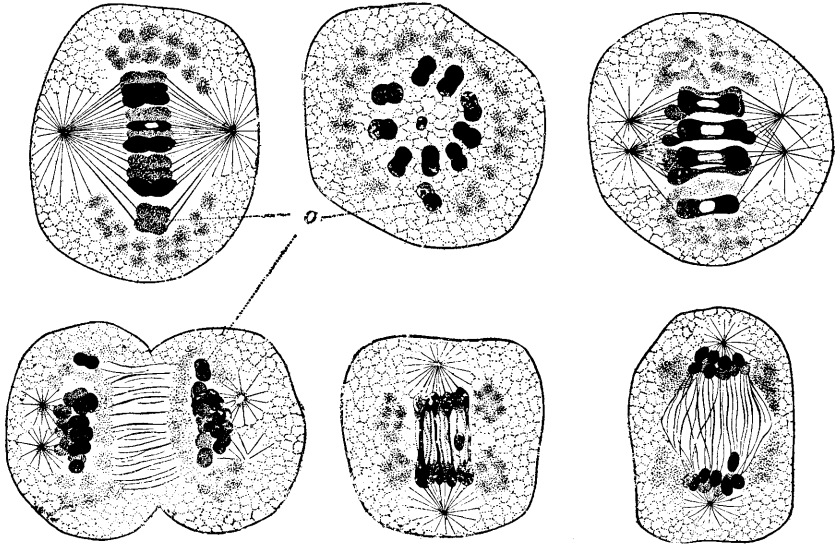


Fig. 127. — Maturation-divisions in an insect, *Anasa*. [PAULMIER.]

A. Primary spermatocyte in metaphase. B. Equatorial plate, showing ten large tetrads and one small one; "odd chromosome" at *o*. C. Separation of the dyads. D. Telophase, which is also a prophase of the second division. E. Secondary spermatocyte; division of the dyads; small dyad shown undivided. F. Final anaphase; small dyad near the lower chromosome-group. (The figures are numbered from left to right. For later states, see Fig. 82.)

become in part aggregated in a mass at one side of the nucleus ("synapsis," p. 276), from which delicate threads extend through the remaining nuclear space (Fig. 120, A). Even at this period the granules of the threads are divided into four parts. As the process proceeds the chromatin resolves itself into a single spireme-thread, consisting of four parallel rows of granules, which break in two to form the two tetrads (var. *bivalens*), or is directly converted into a single tetrad (var. *univalens*) (Fig. 120). From these observations Brauer concludes that each tetrad arises from a rod, doubly split lengthwise by a process initiated at a very early period through the

double fission of the chromatin-granules. If this be correct, there can be no reduction in Weismann's sense; for the four products of each primary chromatin-granule are equally distributed among the four daughter-cells. A similar conclusion, based on much more incomplete evidence, was reached by Brauer ('92) in the phyllopod *Branchipus*.

Brauer's evidently conscientious figures very strongly sustain his conclusion, which, reinforced by the earlier work of Hertwig and Boveri, has until now seemed to rest upon an unassailable basis. The recent work of Sabaschnikoff ('97) nevertheless raises the possibility of a different interpretation. Brauer himself justly urges that the essence of the process lies in the double fission of the chromatin-granules to which the formation of chromosomes is secondary.<sup>1</sup> Everything, therefore, turns on the manner in which the quadruple granules arise; and Sabaschnikoff's work gives some ground for the view that they may arise, not by a double fission, but in some other way.

According to this author there is a period (in the oögenesis) at which the nuclear threads wholly disappear, the entire chromatin being broken up into granules. From this state the granules emerge in quadruple form to arrange themselves in the doubly split spireme exactly as Brauer describes: and a few observations are given (regarding the size and arrangement of the granules) which suggest the possibility that the quadruple granules may arise by the *conjugation* either of four separate granules or of two pairs of double granules. Since there is ground for the view that tetrads may arise by the conjugation of chromosomes (see following section), there is no *a priori* objection to such a conclusion. Could it be sustained, the maturation-divisions of *Ascaris* would in fact involve a true reduction in Weismann's sense; for despite the fact that the chromosomes are only longitudinally divided, the four longitudinal constituents of each tetrad would not be equivalent with respect to the granules, and it is the reduction of the latter ("ids") that forms the essence of Weismann's hypothesis (p. 245). Another consideration, suggested to me by Professor T. H. Morgan, opens still another possibility, which seems well worthy of test by further research. As already stated (p. 88), the long chromosomes of *Ascaris* are plurivalent, since in all but the germ-cells each breaks up into a much larger number of smaller chromosomes (Fig. 73, p. 148). If, therefore, the latter correspond to the chromosomes of other forms in which tetrads occur (*e.g.* *Cyclops* or *Artemia*), the so-called "tetrad" of *Ascaris* is a compound body: and the true process of reduction must be sought in the origin of the smaller elements of which it is composed, which are, perhaps, directly comparable with Sabaschnikoff's "granules." Until the questions thus opened have been further studied, the case for *Ascaris* must remain open: and it is perhaps worth suggesting that a new point of view may here be found for further study also of reduction in the vertebrates.<sup>2</sup>

<sup>1</sup> Cf. p. 113.

<sup>2</sup> Bodies closely resembling tetrads are sometimes formed in mitosis, where no reduction should occur. Thus, R. Hertwig ('95) has observed tetrads in the first cleavage-spindle of echinoderm-eggs after treatment with dilute poisons (p. 306). Klinckowström figures them in the *second* polar spindle of *Prostheceranus* eggs, while Moore ('95) describes in the elasmobranchs small ring-shaped chromosomes, not only in the first but also in the *second* spermatocyte-divisions, concluding that no reduction occurs in either division.



(c) *The Formation of Tetrads by Conjugation.*—A considerable number of observers have maintained that reduction may be effected by the union or conjugation of chromosomes that were previously separate. This view agrees in principle with that of Rückert, Häcker, and Vom Rath; for the bivalent chromosomes assumed by these authors may be conceived as two conjugated chromosomes. It seems to be confirmed by the observations of Born and Fick on Amphibia and those of Rückert on selachians (*Pristiurus*); for in all these cases the number of chromatin-masses at the time the first polar body is formed is but half the number observed in younger stages of the germinal vesicle. In *Pristiurus* there are at first thirty-six double segments in the germinal vesicle. At a later period these give rise to a close spireme, which then becomes more open, and is found to form a double thread segmented into eighteen double segments; *i.e.* the reduced number. In this case, therefore, the preliminary pseudo-reduction is almost certainly effected by the union of the original thirty-six double chromosomes, two by two. The most specific accounts of such a mode of origin have, however, been given by Calkins (earthworm) and Wilcox (grasshopper). The latter author asserts ('95) that in *Caloptenus* the spireme of the first spermatocyte gives rise without longitudinal division to twenty-four chromosomes (double the somatic number). These then become associated in pairs, and still later the twelve pairs conjugate two and two to form six tetrads. There is, therefore, no longitudinal splitting of the chromosomes. The *a priori* improbability of such a conclusion is increased by the studies of Paulmier on the Hemiptera, which demonstrate the occurrence of a longitudinal division in a number of these forms and confirm the original studies of Vom Rath on *Grylotalpa*.<sup>1</sup>

The second case, which is perhaps better founded, is that of the earthworm (*Lumbricus terrestris*), as described by Calkins ('95, 2), whose work was done under my own direction. Calkins finds that the spireme splits longitudinally and then divides transversely into 32 double segments. These then unite, two by two, to form 16 tetrads. The 32 primary double segments therefore represent chromosomes of the normal number that have split longitudinally, *i.e.*  $\frac{a}{a} - \frac{b}{b}$  etc., and the formula for a tetrad is  $\frac{a|b}{a|b}$  or  $\frac{a|x}{a|x}$ . Such a tetrad, therefore, agrees as to its composition with the formulas of Häcker, Vom Rath, and Rückert, and agrees in mode of origin with the process described by Rückert in the eggs of *Pristiurus*. While these observations are not absolutely conclusive, they never-

<sup>1</sup> Montgomery, who has denied the occurrence of a longitudinal division in *Pentatoma* ('98, 1), has subsequently found such a division in the nearly related if not identical genus *Euchistis* ('99).

theless rest on strong evidence, and they do not stand in actual contradiction of what is known in the copepods and vertebrates. The possibility of such a mode of origin in other forms must, I think, be held open.

Under the same category must be placed Korschelt's unique results in the egg-reduction of the annelid *Ophryotrocha* ('95), which are very difficult to reconcile with anything known in other forms. The typical somatic number of chromosomes is here four. The *same number* of chromosomes appear in the germinal vesicle (Fig. 125, *D*). They are at first single, then double by a longitudinal split, but afterward single again by a reunion of the halves. The four chromosomes group themselves in a single tetrad, two passing into the first polar body, while two remain in the egg, but meanwhile each of them again splits into two. Of the four chromosomes thus left in the egg two are passed out into the second polar body, while the two remaining in the egg give rise to the germ-nucleus. From this it follows that the formation of the *first* polar body is a reducing division—a result which agrees with the earlier conclusions of Henking on *Pyrrhochoris*, and with those of Paulmier on the Hemiptera.

### C. REDUCTION WITHOUT TETRAD-FORMATION

As already stated (p. 246), the formation of actual tetrads is of relatively rare occurrence, being thus far certainly known only in the arthropods, nematodes, and some annelids. In the greater number of cases the two divisions of the primary chromatin-masses (*i.e.* of the primary oöcyte or spermatocyte) are separated by a considerable interval, during which the first maturation cell-division takes place or is initiated, and hence no actual tetrads are formed. This obviously differs only in degree from tetrad-formation, the latter occurring only when the two divisions are simultaneous or occur in rapid succession.

In the cases now to be considered the length of the pause between the maturation-divisions varies considerably, and in some forms (vertebrates, flowering plants) it is so prolonged that the nucleus is partially reconstructed. In all, or nearly all, these cases the *first maturation-division is of the heterotypical form*, the chromosomes having the form of rings and arising by a process that agrees in most of its features with that leading to tetrad-formation. There is here, however, exactly the same contradiction of results as in the case of tetrad-formation described at page 247, and a bewildering confusion of the subject still exists. In brief, it may be stated that most observers of reduction of this type in the lower animals (flat-worms, annelids, mollusks) have found one transverse and one longitudinal division; most of those

who have studied the vertebrates find two longitudinal divisions; while opinion regarding the plants is still divided.

(a) *Animals*.—In the gephyrean *Thalassema* and the mollusk *Zirphæa* (Figs. 128–130) Griffin ('99) finds that the rings, arising as described above, place themselves in the equator of the spindle with the longitudinal division in the equatorial plane. They are then drawn out toward the spindle-poles from the middle point, first assuming the form of a double cross, then of elongated ellipses, and finally break into two daughter-U's or -V's. The first division is therefore longitudinal. During the late anaphase the V's break at the apex, the two limbs come close together, so as to give the decep-

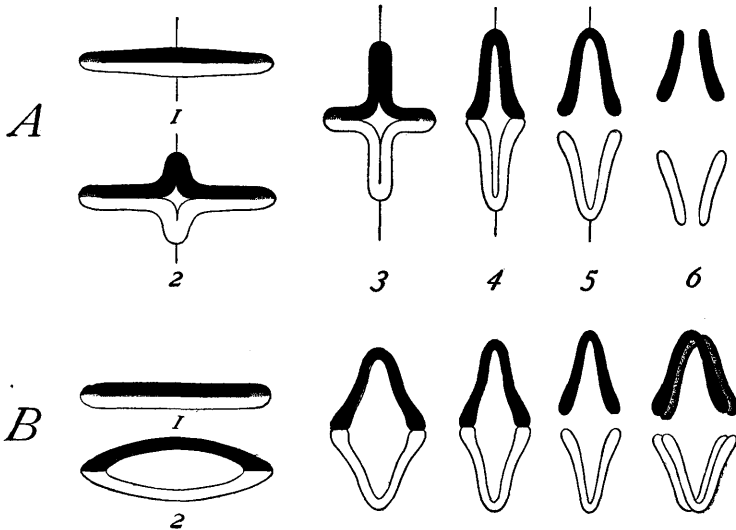


Fig. 128.—Diagrams of reduction in the types represented by *Thalassema* (A) and *Salamandra* (B). In both the first division is heterotypical. The second division (6) is transverse in the first and longitudinal in the second.

tive appearance of a longitudinal split, and are separated by the second division (following immediately upon the first without intervening resting stage). The latter is therefore a transverse division (Fig. 130). An essentially similar result, though less completely worked out, is independently reached by Bolles Lee ('97) in *Helix*; by Klinckowström ('97) in the turbellarian *Prostheceræus*; and by Francotte ('97) and Van der Stricht ('98, 1) in *Thysanozoon*. Klinckowström shows that there is much variation in the way in which the rings open out and break apart, though the result is the same in all.

In case of the vertebrates, Flemming ('87) long since described and figured typical tetrads in the salamander, but regarded them as "anomalies." Vom Rath's later conclusion ('93, '95) that they are

normal tetrads has not been sustained by the still more recent work of Meves ('96), whose careful studies, together with those of Moore, Lenhossék, and others, thus far give no evidence of tetrad-formation, and seem opposed to the occurrence of reducing divisions in the vertebrates. Meves's work in the main confirms the earlier results of Flemming, except that he shows that, as in so many other animals, only two generations of spermatocytes exist. At the first division the nuclear reticulum resolves itself into twelve (the reduced number) segments, which split lengthwise, the halves remaining united to form elongated rings (Figs. 27, 37). These do not, however, con-

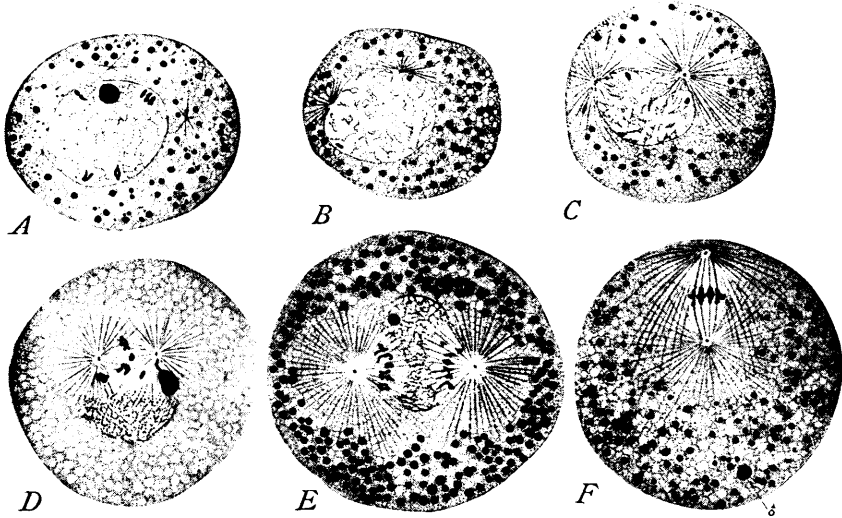


Fig. 129. — Maturation and fertilization in an annelid (armed gephyrean) *Thalassema*. [GRIFFIN.]

*A.* A few moments after entrance of the spermatozoon, showing accessory asters; tetrads forming. *B.* Early prophase of first polar mitosis with centrosomes. *C.* In-pushing of nuclear wall. *D.* Central spindle established; elimination of nucleolus and nuclear reticulum. *E.* Slightly later stage viewed from above. *F.* First polar spindle established, cross-shaped tetrads, crossing of astral rays; sperm-head at  $\sigma$ .

dense into tetrads, but break apart during the first division at the points corresponding with the ends of the united halves. The first division is therefore an equation-division. As the V-shaped halves separate they again split lengthwise (Fig. 131), each of the secondary spermatocytes receiving twelve double V's or dyads. In the telophases and ensuing resting stage, however, all traces of this splitting are lost, the nuclei partially returning to the resting stage, but retaining traces of a spireme-like arrangement (Fig. 131). In the second division twelve double V's reappear, showing a longitudinal division which Flemming and Meves believe to be directly related to that