

seen during the foregoing anaphases. There is therefore no evidence of a transverse division. McGregor ('99) describes a nearly similar process in *Amphiuma*, where the longitudinal division of the

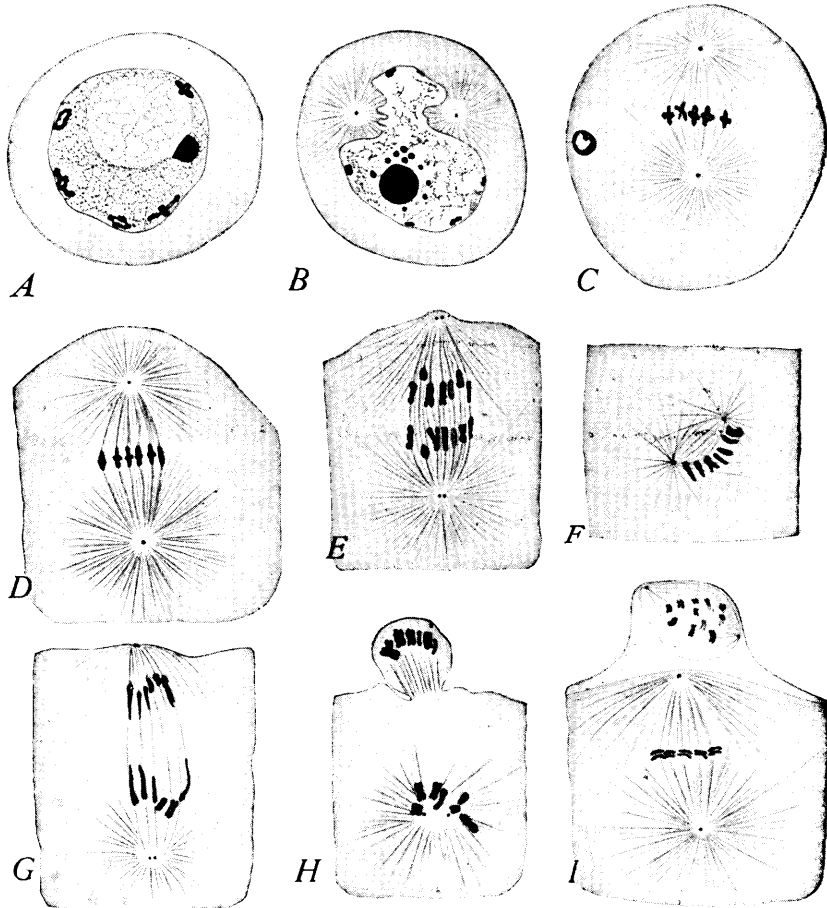


Fig. 130. — Maturation in the lamellibranch *Zirphæa* and in *Thalassema*. [GRIFFIN.]

A-E, Zirphæa; F-I, Thalassema.

A. Unfertilized egg, ring-shaped and cross-shaped chromosomes. *B.* Prophase of first polar mitosis. *C.* First polar spindle; double crosses. *D.* Slightly later stage. *E.* The double crosses have broken apart (equation-division). *G.* Ensuing stage; daughter-V's broken apart at the apex. *H.* Telophase of first, early prophase of second, division; limbs of the V's separate but closely opposed. *F.* Later prophase of second division. *I.* Second polar spindle in metaphase.

daughter-V's is seen with the greatest clearness throughout the anaphases.

The weak point in both the foregoing cases is the fact that all traces of the second longitudinal division are lost during the ensuing

resting period; and I do not think that even the observations of Flemming ('97), who has published the fullest evidence in the case, completely establish the occurrence of a subsequent longitudinal divi-

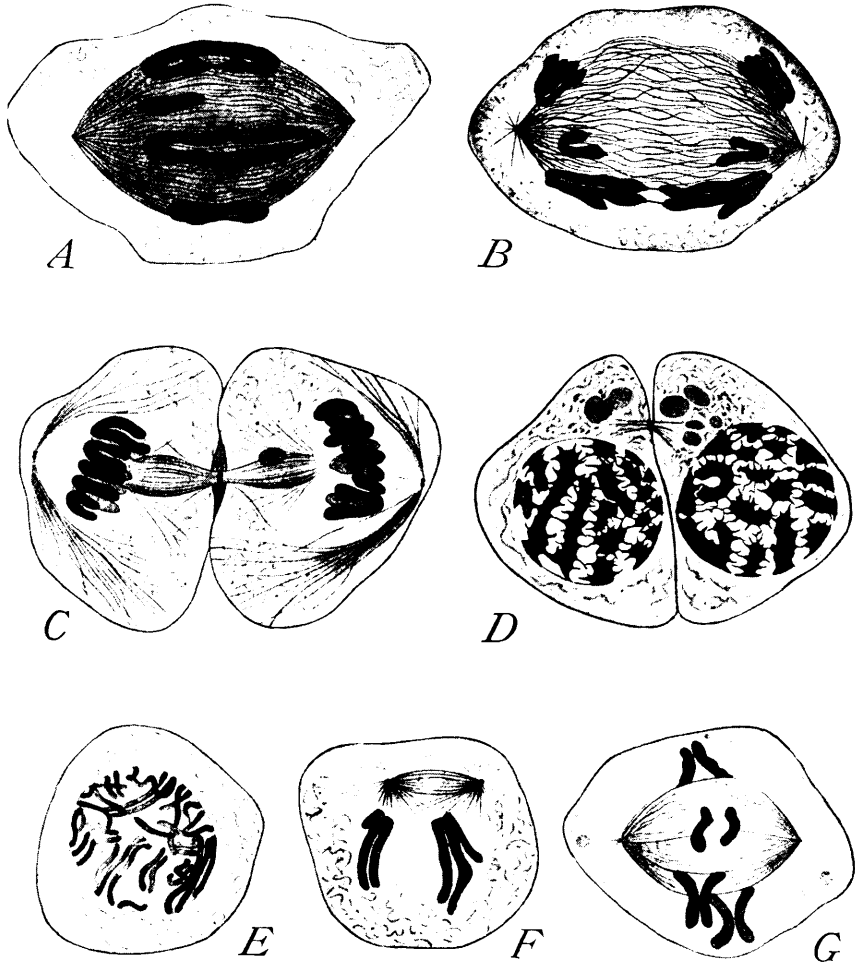


Fig. 131. — (Compare Fig. 27). Maturation-divisions in *Salamandra*. [*E* from FLEMMING, the others from MEVES.]

A. First division in metaphase, showing heterotype rings. *B.* Anaphase; longitudinal splitting of the daughter-loops. *C.* Telophase. *D.* Ensuing pause. *E.* Early prophase of second division with longitudinally divided segmented spireme. *F.* Later prophase. *G.* Metaphase of second division.

sion of the chromosomes in the second mitosis. In *Desmognathus*, however, where the resting stage is less complete, Kingsbury ('99) finds the longitudinal split in the persistent chromosomes of the

pause following the first division; and he believes this to be the same division as that seen during the anaphase. Carnoy and Le Brun ('99) reach the same result in the formation of the polar bodies in *Triton*, though their general account of the heterotypical mitosis differs very considerably from that of other authors, the rings being stated to arise by a double instead of a single longitudinal split. These observers describe the rings of the early anaphase as having almost exactly the same double cross-form as those in *Thalassema* or *Zirphæa* (Griffin, '99), but believe them to arise in a manner nearly in accordance with Strasburger's abandoned view of 1895,¹ and with Guignard's ('98, 2) and Grégoire's ('99) latest results on the flowering plants, the ring being stated to arise by a double longitudinal splitting, as explained at page 265.

In the elasmobranch *Scyllium* Moore ('95) finds twelve (the reduced number) ring-shaped chromosomes at the first division. These closely resemble tetrads; but a resting stage follows, and the second division is likewise stated to be of the heterotypical form. Both divisions are stated to be equational-divisions—a conclusion well supported in case of the first, but so far from clear in the second that a careful reëxamination of the matter is highly desirable.

In mammals the first division is of the heterotypical form (Hermann, '89, Lenhossék, '98), though the rings are much smaller than in the salamander, recalling those seen in arthropods. No true tetrads are, however, formed, and the two divisions are separated by a resting period. The character of the second division is undetermined, though Lenhossék believes it to be heterotypical, like the first.

(b) *Plants*.—It is in the flowering plants, where reduction likewise occurs, as a rule, without true tetrad-formation, that the contradiction of results reaches its climax; and it must be said that until further research clears up the present confusion no definite result can be stated. The earlier work of Strasburger and Guignard indicated that no reducing division occurred, the numerical reduction being directly effected by a segmentation of the spireme-thread into half the somatic number of chromosomes. Thus these observers found in the male that the chromosomes suddenly appeared in the reduced number (twelve in the lily, eight in the onion) at the first division of the pollen-mother-cell, and in the female at the first division of the mother-cell of the embryo-sac. The subsequent phenomena differ in a very interesting way from those in animals, owing to the fact that the two maturation-divisions are followed in the female by one and in the male by two or more additional divisions, in both of which the reduced number of chromosomes persists. In the male the two maturation-divisions give rise to four pollen-grains, in the female to

¹ Cf. p. 269.

the four primary cells of the embryo-sac (Fig. 132); and these two divisions undoubtedly correspond to the two maturation-divisions in animals. In the female, as in the animals, only one of the four resulting cells gives rise to the egg, the other three corresponding to the polar bodies in the animal egg, though they here continue to divide, and thus form a rudimentary prothallium.¹ The first-men-

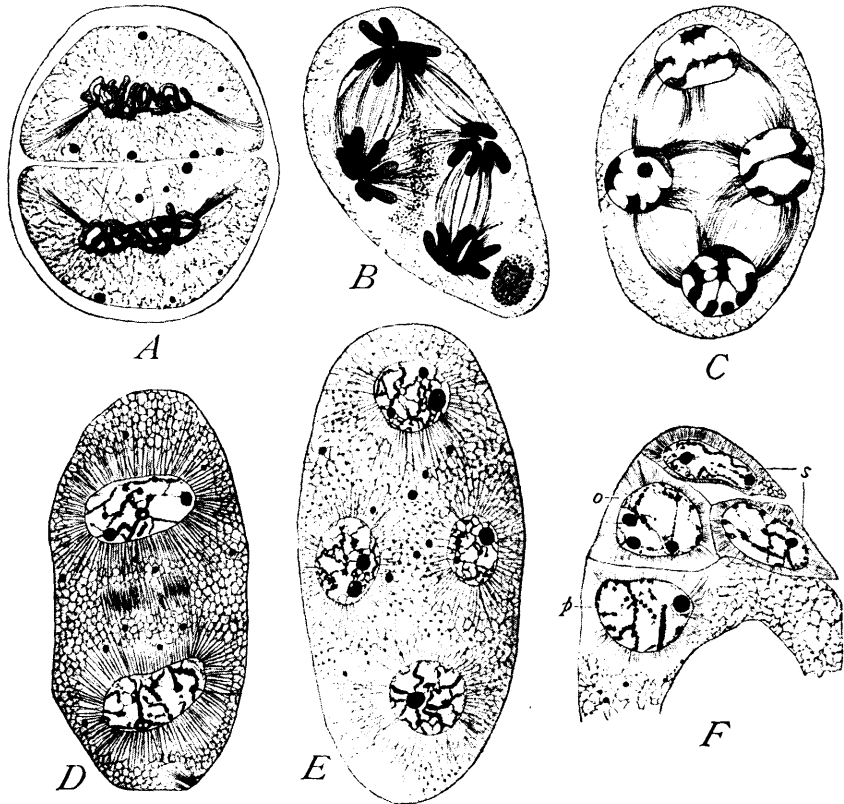


Fig. 132. — General view of the maturation-divisions in flowering plants. [MOTTIER.]

A-C, in the male; *D-F*, in the female. *A*. The two secondary spermatocytes (pollen-mother-cells) just after the first division (*Lilium*). *B*. Final anaphase of second division (*Podophyllum*). *C*. Resulting telophase, which by division of the cytoplasmic mass produces four pollen-grains. *D*. Embryo-sac after completion of the first nuclear division (*Lilium*). *E*. The same after the second division. *F*. The upper four cells resulting from the third division (cf. Fig. 106): *o*, ovum; *p*, upper polar cell; *s*, synergidæ. (For further details, see Figs. 133, 134.)

¹ Of these three cells one divides to form the "synergidæ," the other two divide to form three "antipodal cells" (which like the synergidæ finally degenerate) and a "lower polar cell." The latter sooner or later conjugates with the "upper polar cell" (the sister-cell of the egg) to form the "secondary embryo-sac-nucleus," by the division of which the endosperm-cells arise. Of the whole group of eight cells thus arising only the egg contributes

tioned cell, however, does not directly become the egg, but divides once, one of the products being the egg and the other the "upper polar cell" (Fig. 132, *F*), which contributes to the endosperm-formation (see footnote, and compare page 218).

In the male the two maturation-divisions are in the angiosperms followed by two others, one of which separates a "vegetative" from a "generative" cell, while the second divides the generative nucleus into two definite germ-nuclei. In the gymnosperms more than two such additional divisions take place. In these later divisions, both in the male and in the female (with the exception noted in the footnote below), the reduced number persists, and the principal interest centres in the first two or maturation-divisions. Strasburger and Guignard found in *Lilium* that while both these divisions differed in many respects from the mitosis of ordinary vegetative cells, neither involved a transverse or reducing division, the chromosomes undergoing a longitudinal splitting for each of the maturation-divisions. Further investigations by Farmer ('93), Belajeff ('94), Dixon ('96), Sargent ('96, '97), and others, showed that the first division is often of the heterotypical form, the daughter-chromosomes in the late-metaphase having the form of two V's united by their bases (<>). Despite the complication of these figures, due to torsion and other modifications, their resemblance to the ring-shaped bodies observed in the first maturation-division of so many animals is unmistakable, as was first clearly pointed out by Farmer and Moore ('95).

Botanists have differed, and still differ, widely in their interpretation both of the origin and subsequent history of these bodies upon which the question of reduction turns. According to Strasburger's ('95) first account their origin has nothing in common with that of the tetrad-rings, since they were described as arising by a *double* longitudinal splitting of a primary rod, the halves then separating first from one end along one of the division-planes, and then from the other end along the other plane, meanwhile opening out to form a ring such as is shown in Fig. 133. (This process, somewhat difficult to understand from a description, will be understood from the diagram, Fig. 135, *E-I*.) The four elements of the ring are then distributed without further division by the two ensuing maturation-divisions; and the process, except for the peculiar opening out of the ring, is

to the morphological formation of the embryo. It is a highly interesting fact that the number of chromosomes shown in the division of the lower of the two nuclei (*i.e.* the mother-nucleus of the antipodal cells and lower polar-cell) formed at the first division of the embryo-sac-nucleus is inconstant, varying in the lily from 12, 16, 20, to 24 (Guignard, '91, 1), in which respect they contrast with the descendants (egg, synergidae) of the upper nucleus, which always show the reduced number (Mottier, '97, 1), *i.e.* in *Lilium* twelve. This exception only emphasizes the rule of the constancy of the chromosome-number in general; for these cells are destined to speedy degeneration.

essentially in agreement with the facts described in *Ascaris*, and involves no reduction-division. Essentially the same result is reached by Guignard ('98) in his latest paper on *Naias*, and by Gregoire ('99) in the Liliaceae.

Strasburger twice shifted ground in rapid succession. First ('97, 2), with Mottier ('97, 1), he somewhat doubtfully adopted a view agreeing

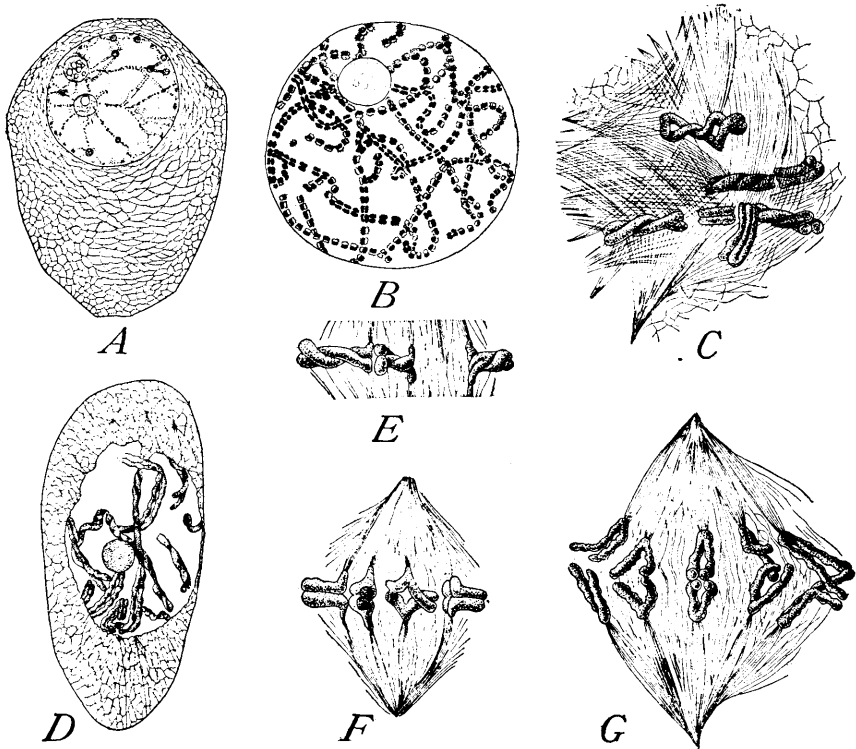


Fig. 133.—The first maturation-division in flowering plants. [F, STRASBURGER and MOTTIER; the others from MOTTIER.]

A. Mother-cell of the embryo-sac in *Lilium*; early prophase of first division; chromatin-threads already longitudinally divided. B. Slightly later stage (split spireme) in the nucleus of the pollen-mother-cell. C. A slightly later prophase (pollen-mother-cell, *Podophyllum*) with twisted split spireme. D. Earlier prophase (*Lilium*, female); split twisted chromosomes. E. Equatorial plate (*Lilium*, male). F. First maturation-spindle (*Fritillaria*, male). G. Divergence of the daughter-chromosomes (*Lilium*, male).

essentially with the interpretation of Vom Rath, Rückert, etc. (p. 247). The primary rods split once, and bend into a V, the branches of which often come close together, and may be twisted on themselves, thus giving the appearance of the second longitudinal split described in Strasburger's paper of 1895. The two halves of the split U then separate, opening out from the apex, to form the <>-figure. In the

second division the limbs of the daughter-V's again come close together, remaining, however, united at one end, where they were believed finally to break apart during the second division. The latter was, therefore, regarded as a true reduction-division, the apparent longitudinal split being merely the plane along which the halves of the V come into contact (Fig. 134, C, D).

The two accounts just given represent two extremes, the first agreeing essentially with *Ascaris*, the second with the copepods or insects. When we compare them with others, we encounter a truly bewildering confusion. Strasburger and Mottier ('97) themselves soon abandoned their acceptance of the reducing division, returning to the conclusion that in both sexes (*Lilium*, *Podophyllum*) both divisions involve a longitudinal splitting of the chromosomes (Figs. 133, 134). In the first division the longitudinally split spireme segments into twelve double rods, which bend at the middle to form double V's, with closely approximated halves. Becoming attached to the spindle by the apex, the limbs of each separate to form a <>-figure. At telophase the daughter-V's shorten, thicken, and join together to form a daughter-spireme consisting of a single contorted thread. *This splits lengthwise throughout its whole extent*, and then segments into double chromosomes, the halves of which separate at the second division (Fig. 135, L-M). The latter, therefore, like the first, involves no reducing division. This result agrees in substance with the slightly earlier work of Dixon ('96) and of Miss Sargant ('96, '97), whose account of the origin of the <>-figure of the first division differs, however, in some interesting details. It is also in harmony with the general results of Farmer and Moore ('95), of Grégoire ('99), and of Guignard ('98), who, however, describes the first division nearly in accordance with Strasburger's account of 1895, as stated above. On the other hand, Ishikawa (pollen-mother-cells of *Allium*, '97) and especially Belajeff (pollen-mother-cells of *Iris*, '98) conclude that the second division is a true transverse or reducing division.¹ Ishikawa described the first division as being nearly similar to the ring-formation in copepods, the four elements of the ring being often so condensed as nearly to resemble an actual tetrad. In the early anaphases the daughter-V's break at the apex; and, although in the later anaphases the limbs reunite, Ishikawa is inclined to regard the transverse division as being a preparation for the second mitosis. Belajeff's earlier work ('94) on *Lilium* gave an indecisive result, though one on the whole favourable to a reducing division. In his latest paper, however ('98, 1), Belajeff takes more positive ground, stating that after the examination of a large number of forms he has found

¹ Schaffner ('97, 2) reaches exactly the reverse result in *Lilium philadelphicum*, i.e. the first division is transverse, the second longitudinal.

in the pollen-mother-cells of *Iris* a much more favourable object of investigation than *Lilium*, *Fritillaria*, and the other forms on which most of the work thus far has been done, and one in which the second division takes place with "admirable clearness"; he also gives interesting additional details of the first division in this and other forms. In the first division the spireme splits lengthwise, and then breaks into chromosomes, which assume the shape of a V, Y, or X (Fig. 135, N-Q). The two limbs of these bodies do not, as might be

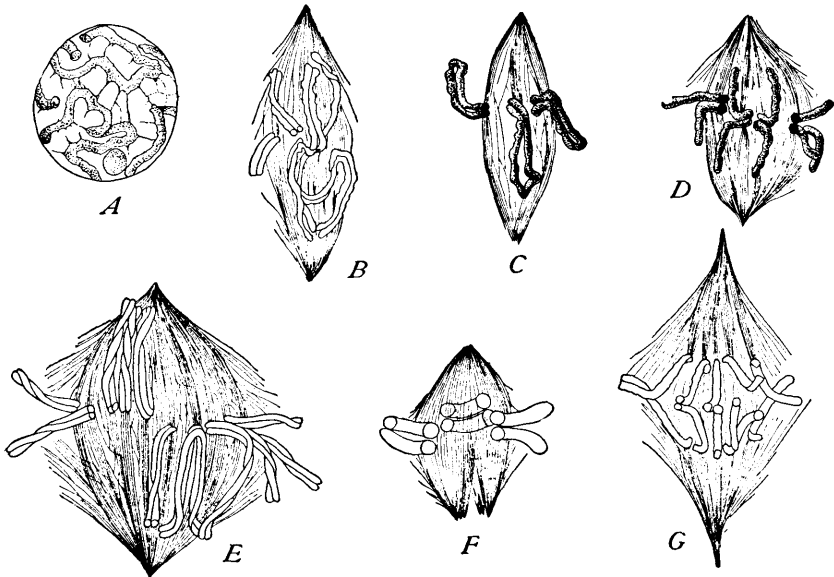


Fig. 134.—The second maturation-division in flowering plants. [B. STRASBURGER and MOTTIER; the others from MOTTIER.]

A. Nucleus of secondary spermatocyte (*Podophyllum*). B. Prophase of second division (*Lilium*, male) with longitudinally divided chromatin-threads. E. Corresponding stage in the female. F. Metaphase of second division (*Podophyllum*, male). G. Initial anaphase (*Lilium*, female). C. D. illustrate Mottier's earlier conclusions. C. Second division (*Lilium*, male), with chromosomes bent together so as to simulate a split. D. Slightly later stage (*Fritillaria*, male), showing stage supposed to result from breaking apart of the limbs of the U at point of flexure.

supposed, represent sister-chromosomes (resulting from the longitudinal division of the spireme) attached by one end or at the middle, since each X, Y, or V is double, consisting of two similar superimposed halves. Belajeff, therefore, regards these figures as longitudinally divided bivalent chromosomes, having the value of tetrads, each limb being a longitudinally split single chromosome. The double V's, Y's, and X's take up a position with the apex (or one end of the X) attached to the spindle, and the longitudinal division in the equatorial plane. The halves then progressively diverge from the

point of attachment, thus giving rise to $\langle \rangle$ -shaped, $\langle \rangle$ -shaped, or \times -shaped figures, all of which in the end assume the $\langle \rangle$ -shape. This part of the process is in the main similar to that described by Strasburger and Mottier, and the daughter-V's diverge in the same way as these authors describe. The second division, however, differs radically from their account, since no splitting of the spireme-thread occurs. The chromosomes reappear in the V-, Y-, and X-forms, but are *undivided*, and only half as thick as in the first division. Passing to the equator of the spindle, the V- and Y-forms break apart at the apex, while the X-forms separate into the two branches of the X, the daughter-chromosomes having the form of rods slightly bent at the outer end to form a J-figure (Fig. 135, R-T). This division is, accordingly, a transverse or reducing one, which "corresponds completely to the reduction-division in the animal organism" ('98, 2, p. 33.) Atkinson ('99) reaches the same general result in *Trillium*, stating very positively that no longitudinal division occurs in the second mitosis, and believing that the daughter-V's of the first (heterotypical) mitosis retain their individuality throughout the ensuing pause, and break apart at the apex (reducing division) in the second mitosis. This observer finds further that in *Arisæma* the heterotypical rings of the first mitosis *condense into true tetrads*, by one longitudinal and one transverse division, but believes that in this case it is the *first* division that effects the reduction, as in the insects.

Such confusion in the results of the most competent observers of reduction in the flowering plants is itself a sufficient commentary on the very great difficulty and uncertainty of the subject; and it would be obviously premature to draw any positive conclusions until further research shall have cleared up the matter.¹

¹ Strasburger's new book, entitled *Über Reduktionsteilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich* (Jena, 1900), is received while this work is in press, too late for analysis in the text. In this treatise the author gives an exhaustive review of the entire subject, contributing also many new and important observations on *Lilium*, *Iris*, *Podophyllum*, *Tradescantia*, *Allium*, *Larix*, and several other forms. The general result of these renewed researches leads Strasburger to return, in the main, to his conclusions of 1895, with which agree, as stated above, the results of Guignard and Grégoire; and, in a careful critique of Belajeff's work, he shows how the results of this observer may be reconciled with his own. The essence of Strasburger's interpretation is as follows. In the prophase of the first division the chromosomes first undergo a longitudinal division, shorten to form double rods, and then again split lengthwise in a plane at right angles to the first. The following stages vary even in the same species (*Lilium*); and here lies the explanation of much of the divergence between the accounts of different observers. (1) In the typical case, the chromosomes are placed radially, with one end next the spindle; and, during the metaphase, they open apart along the first division-plane, from the spindle outwards, to form \vdash -shaped figures. These figures meanwhile open apart from the free end inwards along the second division-plane. Thus arise the characteristic $\langle \rangle$ -shaped figures, the daughter-V's having separated along the first (equatorial) division-plane, while the two limbs of each V have resulted, not through bending, but from a second (axial) split (Fig. 135, E-H). The

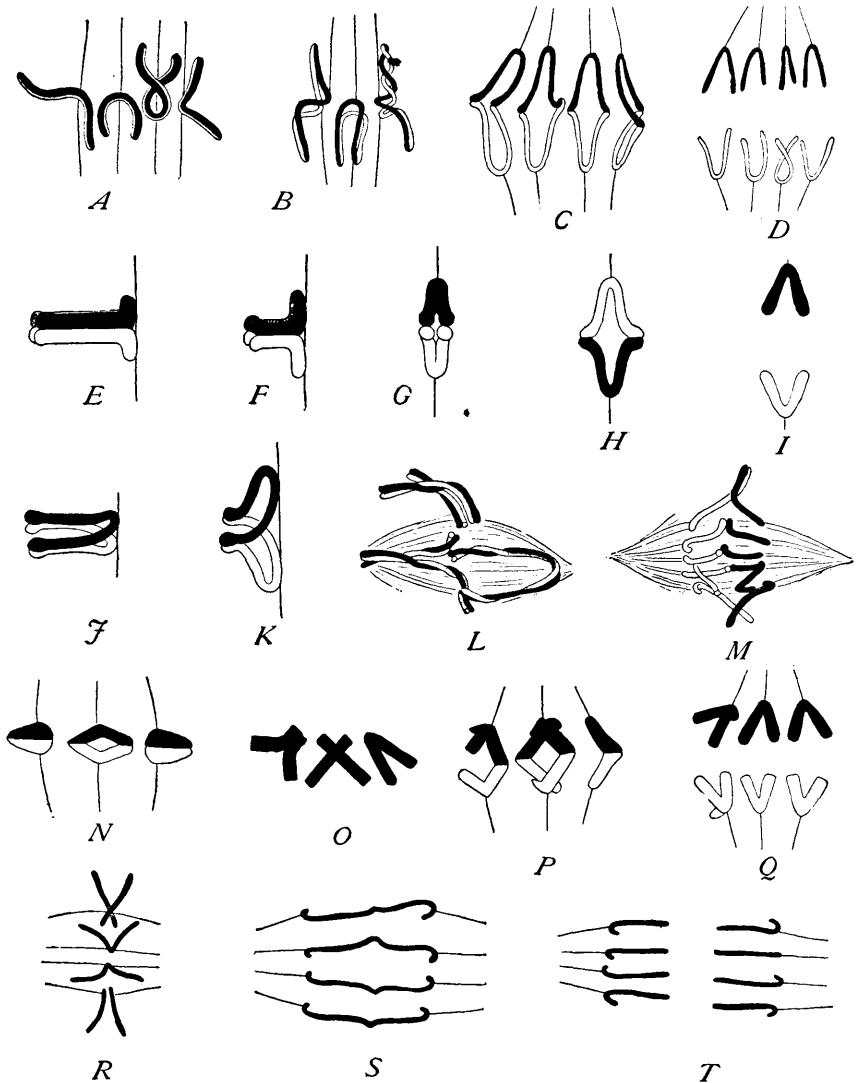


Fig. 135. — Diagrams illustrating different accounts of reduction in the flowering plants.

A-D. Vegetative mitoses (heterotypical form) in *Picea*. [BELAJEFF.]

E-I. Illustrate Straszburger's earlier account ('95) and the later one of Guignard, of the first maturation-division. E. Doubly split rod. F. Metaphase, in profile. G. The same *en face*, showing the heterotype ring. H, I. Opening out and breaking apart of the ring.

J-M. Later account of Straszburger and Mottier (*cf.* Figs. 133, 134). J. Longitudinally split, V-shaped chromosome of first division. K. Opening out of the ring. L. Prophase of second division, showing longitudinally split segmented spireme. M. Initial anaphase of second division.

N-Q. First division. [BELAJEFF.] N. Longitudinally split chromosome, viewed in the equatorial plane. O. The same viewed in the axis of the spindle. P. Separation of the daughter-chromosomes. Q. Anaphase, all the chromosomes assuming the V-form.

R-T. Second division in *Iris*. [BELAJEFF.] R. Equatorial plate, limbs of X's and V's breaking apart (reducing division). S. Slightly later stage, with daughter-chromosomes still united at one end. T. Anaphase.

Résumé. In reduction without tetrad-formation the spireme segments into half the somatic number of chromosomes, which split lengthwise and open out to form rings for the first (heterotypical) mitosis. According to one set of observers, including Flemming, Meves, McGregor, Kingsbury, Moore, Klinckowström, Van der Stricht, Francotte, Griffin, Belajeff, Farmer, Dixon, Strasburger, Sargant, Mottier, Ishikawa, and Atkinson, the ring arises by a single longitudinal division. According to another group, including Carnoy, Le Brun, Guignard, and Grégoire, the ring arises through a double longitudinal division, one representing the axial and the other the equatorial plane of the $\langle \rangle$ -figure. The second group of observers regard both maturation-divisions as longitudinal. Among the first group, Flemming, Meves, McGregor, Kingsbury, Moore, Farmer, Dixon, Strasburger, Sargant, and Mottier likewise believe both divisions to be longitudinal, the daughter-V's or their products again splitting lengthwise for the second division; while Klinckowström, Van der Stricht, Francotte, Griffin, Belajeff, Ishikawa, and Atkinson believe one of them to be transverse, the daughter-V's breaking apart at the apex, and thus giving the reducing division of Weismann.¹

D. SOME PECULIARITIES OF REDUCTION IN THE INSECTS

We may here briefly consider some interesting observations which show that in some cases the nuclear substance may be unequally distributed to the germ-nuclei. Henking ('90) discovered that in the second spermatocyte-division of *Pyrrochoris* one of the "chromosomes" passes undivided into one of the daughter-cells (spermatids) which receives twelve chromatin-elements while its sister receives but eleven. (The number of chromosomes in the spermatogonia, and of rings in the first spermatocyte-division is twenty-four). This anomalous process is confirmed with interesting additional details by Paulmier ('99) in *Anasa*, and obviously related phenomena are described by Montgomery ('99, 1) in *Pentatoma*, and by McClung ('99) in *Xiphidium*.

breaking apart of the V's at the apex, as described by Belajeff, is, therefore, not a transverse division, but merely the completion of the second longitudinal division. (2) In a second and exceptional type, the chromosomes are placed *tangentially* to the spindle, and the halves separate from the middle, again producing $\langle \rangle$ -shaped figures. These, however, are not of the same nature as those arising in the first case, since they are formed by a bending out of each daughter-chromosome at the middle to form the V, and not by the second longitudinal split. The effect of the latter is in this case to render each daughter-V in itself double, precisely as in the salamander. The difference between the two types results merely from the difference of position of the chromosome with respect to the spindle, and the final result is the same in both, *i.e.* two longitudinal divisions and no reducing one.

This highly important work brings very strong evidence against the occurrence of transverse or reducing divisions in the higher plants, and seems to explain satisfactorily most of the differences of interpretation given by other observers. It will be interesting to see whether a similar interpretation is possible in the case of mollusks, annelids, and arthropods, where the early stages, in many cases, so strikingly resemble those occurring in the plants.

¹ Cf. footnote on page 269.

In *Pentatoma* the number of chromosomes in the spermatocyte is fourteen. During the final anaphases of the last division, one of the fourteen daughter-chromosomes assumes a different staining-capacity from the others, and becomes a "chromatin-nucleolus" which fragments into several smaller bodies during the ensuing resting-stage. During each of the succeeding spermatocyte-divisions appear seven chromosomes and a single small chromatin-nucleolus, and both of these kinds of bodies are halved at each division, so that each spermatid receives seven chromosomes and a single chromatin-nucleolus.¹ In *Xiphidium* a body called by McClung the "accessory chromosome," and believed by him to correspond to the "chromatin-nucleolus" of *Pentatoma*, appears in the early prophases of the last spermatogonium-division while the remaining chromatin still forms a reticulum. In the equatorial plate this lies outside the ring of chromosomes, but divides like the latter. The same body appears in the ensuing resting-stage, and during both of the spermatocyte-divisions. In these it lies, as before, outside the chromosome-ring, and differs markedly from the other chromosomes, but divides like the latter, each of the halves passing into one of the spermatids, where it appears to form an important part of the sperm-nucleus.

Despite the peculiarities described above, the chromatin, as a whole, seems to be equally distributed in both *Pentatoma* and *Xiphidium*. In *Anasa*, however, Paulmier's studies ('98, '99), made in my laboratory, give a result agreeing with that of Henking, and suggest some very interesting further questions. The spermatogonia-nuclei contain two nucleolus-like bodies, and give rise to twenty-two chromosomes, of which two are smaller than the others (Fig. 126). In the first spermatocyte-division appear eleven tetrads. Ten of these arise from rings like those of *Grylotalpa*, etc. The eleventh, which is much smaller than the others, seems to arise from a single nucleolus-like body of the spermatocyte-nucleus, and by a process differing considerably from the others. All of these bodies are halved to form dyads at the first division. In the second spermatocyte-division (Fig. 127) the larger dyads divide to form single chromosomes in the usual manner. *The small dyad, however, fails to divide, passing over bodily into one of the spermatids.* In this case, therefore, half of the spermatids receive ten single chromosomes, while the remainder receive in addition a small dyad.

A comparison of the foregoing results indicates that the small tetrad (dyad) corresponds to the extra chromosome observed by Henking in *Pyrrochoris*, and perhaps also to the "accessory chromosome" of *Xiphidium*. Whether it corresponds to the "chromatin-nucleolus" of *Pentatoma* is not yet clear. The most remarkable of these strange phenomena is the formation of the small tetrad, which seems to be a non-essential element, since it does not contribute to all the spermatozoa. Paulmier is inclined to ascribe to it a vestigial significance, regarding it as a "degenerating" chromosome which has lost its functional value, though still undergoing in some measure its original morphological transformation; in this connection it should be pointed out that the spermatocyte-nucleolus, from which it seems to be derived, is represented in the spermatogonia by *two* such nucleoli, just as the single small tetrad is represented by two small chromosomes in the spermatogonia-mitoses. The real meaning of the phenomenon is, however, wholly conjectural.

E. THE EARLY HISTORY OF THE GERM-NUCLEI

There are many peculiarities in the early history of the germ-nuclei, both in plants and animals, that have a special interest in con-

¹ On this latter point Montgomery's observations do not seem quite decisive.

nection with the reduction-problem; and some of these have raised some remarkable questions regarding the origin of reduction. A large number of observers are now agreed that during the growth-period preceding the maturation-division (p. 236), in both sexes, the nucleus of the mother-cell (spermatogonium, oögonium), both in plants and in animals, passes through some of the changes preparatory to reduction at a very early period. Thus, in the egg the primary chromatin-rods are often present in the very young ovarian eggs, and from their first appearance are already split longitudinally.¹ Häcker ('92, 2) made the interesting discovery that in some of the copepods (*Canthocamptus*, *Cyclops*) these double rods could be traced

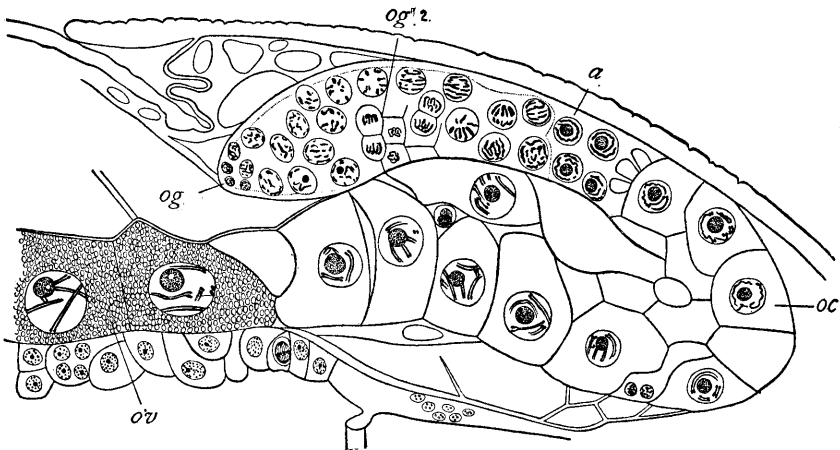


Fig. 136. — Longitudinal section through the ovary of the copepod *Canthocamptus*. [HÄCKER.]
og. The youngest germ-cells or oögonia (dividing at *og*.²); *a*. upper part of the growth-zone; *oc*. oöcyte, or growing ovarian egg; *ov*. fully formed egg, with double chromatin-rods.

back continuously to a double spireme-thread, following immediately upon the division of the last generation of oögonia, and that *at no period is a true reticulum formed in the germinal vesicle* (Fig. 136). In the following year Rückert ('93, 2) made a precisely similar discovery in the case of selachians. After division of the last generation of oögonia the daughter-chromosomes do not give rise to a reticulum, but split lengthwise, and persist in this condition throughout the entire growth-period of the egg. Rückert therefore concluded that the germinal vesicle of the selachians is to be regarded as a "daughter-spireme of the oögonium (*Ur-ei*) grown to enormous dimensions, the chromosomes of which are doubled and arranged in

¹ Häcker, Vom Rath, Rückert, in copepods; Rückert in selachians; Born and Fick in Amphibia; Holl in the chick; Rückert in the rabbit.

pairs.”¹ In this case their number seems to be at first the somatic number (thirty-six), which is afterward halved by conjugation of the elements two and two (Rückert), as in *Lumbricus* (Calkins). It is, however, certain that in many cases (insects, copepods) the double rods first appear in the reduced number, and the observations of Vom Rath ('93) and Häcker ('95, 3) give some reason to believe that the reduced number may in some forms be present in the earlier progenitors of the germ-cells, the former author having found but half the normal number in some of the embryonic cells of the salamander, while Häcker ('95, 3) finds that in *Cyclops brevicornis* the reduced number of chromosomes (twelve) appears in the primordial germ-cells which are differentiated in the blastula-stage (Fig. 74). He adds the interesting discovery that in this form the *somatic* nuclei of the cleavage-stages show the same number, and hence concludes that all the chromosomes of these stages are bivalent. As development proceeds, the germ-cells retain this character, while the somatic cells acquire the usual number (twenty-four)—a process which, if the conception of bivalent chromosomes be valid, must consist in the division of each bivalent rod into its two elements. We have here a wholly new light on the historical origin of reduction; for the pseudo-reduction of the germ-nuclei seems to be in this case a persistence of the embryonic condition, and we may therefore hope for a future explanation of the process by which it has in other cases been deferred until the penultimate cell-generation, as is certainly the fact in *Ascaris*.²

This leads to the consideration of some very interesting recent discoveries regarding the relation of reduction to the alternation of generations in the higher plants. As already stated (p. 263), Strasburger, Guignard, and other observers have found that in the angiosperms the two maturation-divisions are in both sexes followed by one or more divisions in which the reduced number persists. The cells thus formed are generally recognized as belonging to the vestiges of the sexual generation (prothallium) of the higher cryptogams, the pollen-grains (or their analogues in the female) corresponding to the asexual spores of the archegoniate cryptogams. We should, therefore, expect to find reduction in the latter forms occurring in the two corresponding divisions, by which the “tetrad” of spores is formed (as was first pointed out by Hartog, '91). Botanists were thus led to the surmise, first expressed by Overton in 1892, that the reduced number would be found to occur in the prothallium-cells derived from those spores.

¹ '92, 2, p. 51.

² It may be recalled that in *Ascaris* Boveri proved that the primordial germ-cells have the full number of chromosomes, and Hertwig clearly showed that this number is retained up to the last division of the spermatogonia. Ishikawa ('97) finds that in *Allium* the reduced number (eight) appears in the mitosis of the “Urpollenzellen” preceding the pollen-mother-cells. This is, however, contradicted by Mottier ('97, 2).

This surmise quickly became a certainty. Overton himself discovered ('93) that the cells of the endosperm in the gymnosperm *Ceratozamia* divide with the reduced number, namely eight; and Dixon observed the same fact in *Pinus* at the same time. In the following year Strasburger brought the matter to a definite conclusion in the case of a fern (*Osmunda*), showing that *all the cells of the prothallium, from the original spore-mother-cell onwards to the formation of the germ-cells, have one-half the number of chromosomes found in the asexual generation*, namely twelve instead of twenty-four; in other words, the reduction takes place in the formation of the spore from which the sexual generation arises, many cell-generations before the germ-cells are formed, indeed before the formation of the body from which these cells arise. Similar facts were determined by Farmer in *Pallavicinia*, one of the Hepaticæ, where all of the nuclei of the asexual generation (sporogonium) show eight chromosomes during division, those of the sexual generation (thallus) four. It now seems highly probable that this will be found a general rule.

The striking point in these, as in Häcker's observations, is that the numerical reduction takes place so long before the fertilization for which it is the obvious preparation. Speculating on the meaning of this remarkable fact, Strasburger advances the hypothesis that the reduced number is *the ancestral number* inherited from the ancestral type. The normal, *i.e.* somatic, number arose through conjugation by which the chromosomes of two germ-cells were brought together. Strasburger does not hesitate to apply the same conception to animals, and suggests that the four cells arising by the division of the oögonium (egg plus three polar bodies) represent the remains of a separate generation, now a mere remnant included in the body in somewhat the same manner that the rudimentary prothallium of angiosperms is included in the embryo-sac. This may seem a highly improbable conclusion, but it must not be forgotten that so able a zoölogist as Whitman expressed a nearly related thought, as long ago as 1878: "I interpret the formation of polar globules as *a relic of the primitive mode of asexual reproduction.*"¹ Strasburger's view is exactly the reverse of this in identifying the polar bodies as the remains of a sexual generation; and as Häcker has pointed out ('98, p. 102), it is difficult to reconcile with the fact that true reduction appears to occur already in the unicellular organisms (p. 277). The hypothesis is nevertheless highly suggestive and one which suggests a quite new point of view for the study not only of maturation but also of the whole problem of sexuality.

We may now return to the consideration of some details. In a considerable number of forms, though not in all, the early prophase is

¹'78, p. 262.

characterized, especially in the male, by a more or less complete concentration of the chromatin-substance at one side of the nucleus. This stage, to which Moore has given the name *synapsis* (Fig. 120, *A*), sometimes occurs when the spireme thread is already split (*Ascaris*, *Lilium*), sometimes before the division is visible (insects). In either case the chromatin-segments emerge from the synapsis stage longitudinally divided and in the reduced number, a fact which gives ground for the conclusion that the synapsis is in some way concerned with the rearrangement of the chromatin-substance involved in the numerical reduction. During the synapsis the nucleolus remains quite distinct from the chromatin, and in many cases it afterward persists beside the tetrads, in the formation of which it takes no part, to be cast out into the cytoplasm (Fig. 124) or to degenerate *in situ* during the first maturation-division.

A suggestive phenomena, described by several observers,¹ is the casting out of a large part of the nuclear reticulum of the germinal

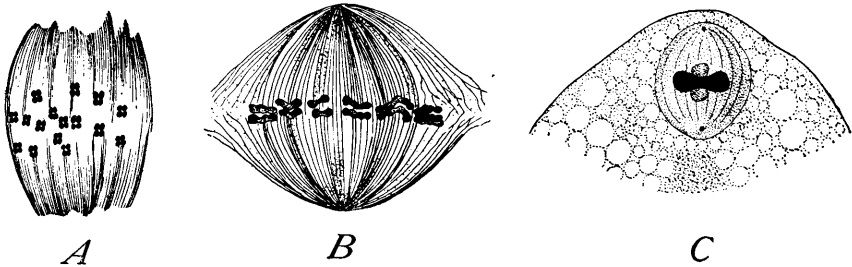


Fig. 137. — Types of maturation-spindles in the female.

A. First polar spindle with tetrads, in *Heterocope*. [HÄCKER]. *B.* Second polar spindle in *Triton*. [CARNOY and LEBRUN.] *C.* First polar spindle of *Ascaris*. [FÜRST.]

vesicle at the time the polar bodies are formed (Figs. 97, 128). In these cases (*Asterias*, *Polychærus*, *Thalassema*, *Nereis*) only a small fraction of the chromatin-substance is preserved to form the chromosomes, the remainder degenerating in the cytoplasm.²

As a final point we must briefly consider the varying accounts of the achromatic maturation-figures in the female already briefly referred to at page 85. In many forms (*e.g.* in turbellarians, nemertines, annelids, mollusks, echinoderms) the polar amphiasters are of quite typical form, with large asters and distinct centrosomes nearly similar to those of the cleavage-figures. In others, however (nematodes, arthropods, tunicates, vertebrates), the polar spindles differ markedly from those of the cleavage-figures, being described by many authors as *entirely devoid of asters* and even in some cases of centrosomes (Fig. 137).

¹ Cf. Mathews (Wilson and Mathews, '95), Gardiner ('98), Griffin ('99).

² Cf. the enormous reduction of the chromatin-substance in the elasmobranch egg, p. 338.

There can be no doubt that these polar spindles differ from the usual type, and that they approach those recently described in the mitosis of the higher plants, but it is doubtful whether the apparent absence of asters and centrosomes is normal. In *Ascaris*, the first polar spindle arising by a direct transformation of the germinal vesicle (Fig. 117) has a barrel-shape, with no trace of asters. At the poles of the spindle, however, are one or two deeply staining granules (Fig. 137), which have been identified as centrosomes by Häcker ('94) and Erlanger ('97, 4), but by Fürst ('98) are regarded as central granules, the whole spindle being conceived as an enlarged centrosome.¹ For the reasons stated at page 314, I believe the former to be the correct interpretation.² Spindles without centrosomes have been described in the eggs of tunicates (Julin, Hill, Crampton), in *Amphioxus* (Sobotta), in some species of copepods (Häcker), and in some vertebrates (*Diemyctylus*, Jordan; mouse, Sobotta). In *Amphioxus* (Sobotta) and *Triton* (Carnoy and LeBrun) complete asters are not formed, but fibrillæ apparently corresponding to astral rays and converging to the spindle-poles are found outside the limits of the spindle (Fig. 137). In the guinea-pig, according to Montgomery ('98), centrosomes and asters are present in the first polar spindle, but absent in the second. The evidence is on the whole rather strong that the achromatic figure in these cases approaches in form that seen in the higher plants; but it is an open question whether the appearances described may not be a result of imperfect fixation.

F. REDUCTION IN UNICELLULAR FORMS

Although the one-celled and other lower forms have not yet been sufficiently investigated, we have already good ground for the conclusion that a process analogous to the reduction of higher types regularly recurs in them. In the conjugation of Infusoria, as already described (p. 223), the original nucleus divides several times before union, and only one of the resulting nuclei becomes the conjugating germ-nucleus, while the others perish, like the polar bodies. The numerical correspondence between the rejected nuclei or "corpuscules de rebut" has already been pointed out (p. 227). Hertwig could not count the chromosomes with absolute certainty, yet he states ('89) that in *Paramæcium caudatum*, during the final division, the number of spindle-fibres and of the corresponding chromatic elements is but 4-6, while in the

¹ Cf. p. 312.

² Sala ('94) and Fürst have shown that occasionally the polar spindles of *Ascaris* are provided with large typical asters, and thus resemble those of annelids or mollusks. Sala believed this to be an effect of lowered temperature, but Fürst's observations are unfavourable to this conclusion.

earlier divisions the number is approximately double this (8-9). This observation makes it nearly certain that a numerical reduction of chromosomes occurs in the Protozoa in a manner similar to that of the higher forms; but the reduction here appears to be deferred until

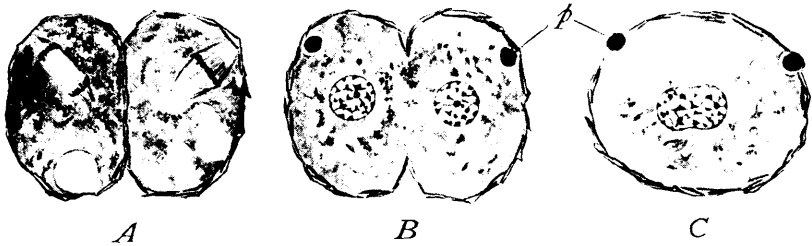


Fig. 138. — Conjugation and formation of the polar bodies in *Actinophrys*. [SCHAUDINN.]

A. Union of the gametes; first polar spindle. B. Fusion of the cell-bodies; a single polar body near the periphery of each. C. Fusion of the nuclei.

the final division. In the gregarines Wolters ('91) has observed the formation of an actual polar body as a small cell segmented off from each of the two conjugating animals soon after their union; but the

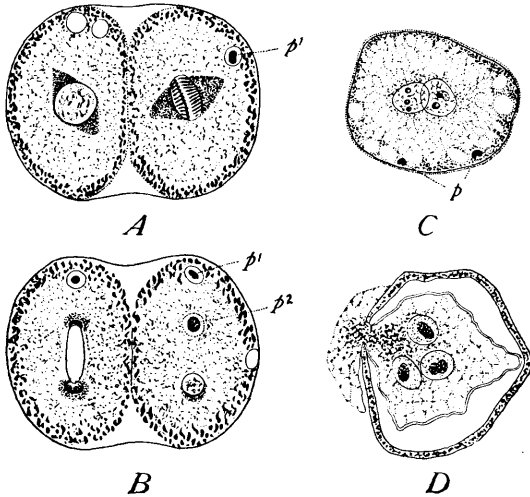


Fig. 139. — Formation of polar bodies and conjugation in *Actinosphaerium*. [R. HERTWIG.]

A. Two gametes ("secondary cysts"), resulting from the division of a "primary cyst"; second maturation-spindle in each; first polar body shown in the right gamete, at p^1 . B. Both polar bodies (p^1, p^2) formed in the right gamete, the second one forming in the left gamete. C. Subsequent fusion of the gametes; nuclei uniting, two polar bodies (probably the second, the first having been absorbed) at p . D. The young *Actinosphaerium* escaping from the cyst-wall; the cleavage-nucleus has divided.

number of chromosomes was not determined. Schaudinn ('96, 2) has observed a like process in *Actinophrys*, each of the gametes' segmenting off a single polar body, after which the germ-nuclei fuse (Fig. 138). It is possible, as R. Hertwig ('98) points out, that in both these forms a second polar body may have been overlooked, owing perhaps to its rapid disintegration. In *Actinosphaerium*, according to R. Hertwig ('98), the nucleus of each gamete divides twice in rapid succession to form two polar bodies (nuclei), which degenerate, after

which the germ-nuclei unite (Fig. 139). Whether a reduction in the number of chromosomes occurs in these cases was not determined.¹

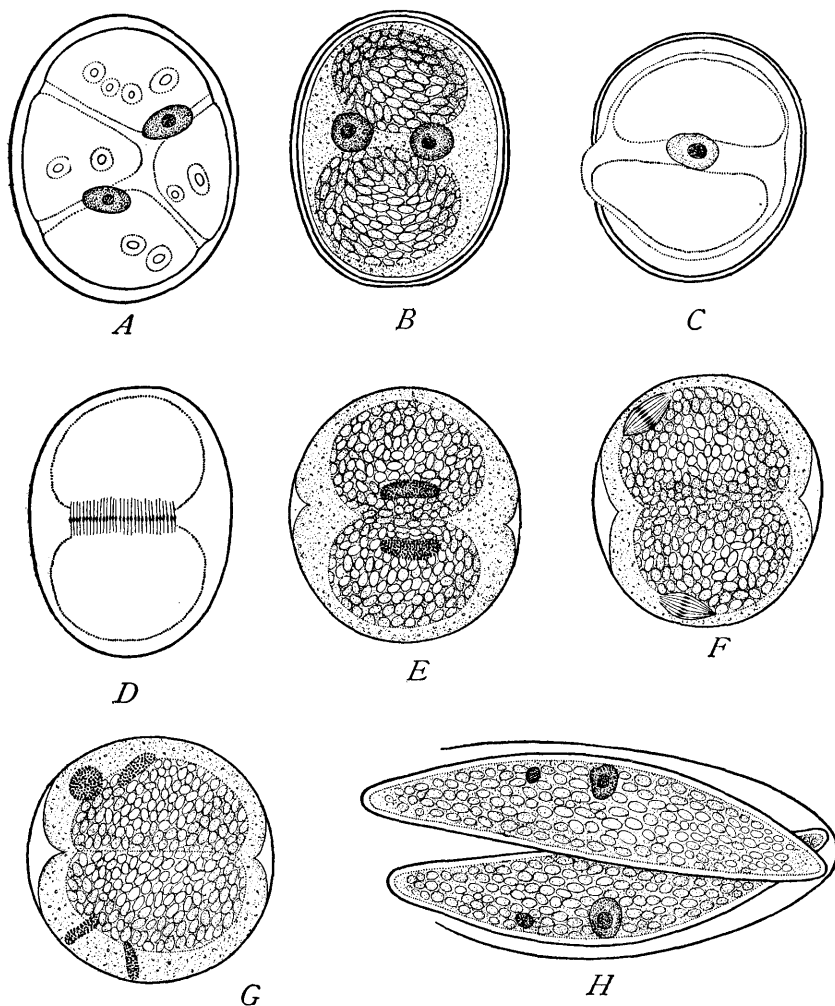


Fig. 140. — Conjugation of *Closterium*. [KLEBAHN.]

A. Soon after union, four chromatophores. B. Chromatophores reduced to two, nuclei distinct. C. Fusion of the nuclei. D. First cleavage of the zygote. E. Resulting 2-cell stage. F. Second cleavage. G. Resulting stage, each cell bi-nucleate. H. Separation of the cells; one of the nuclei in each enlarging to form the permanent nucleus, the other (probably representing a polar body) degenerating.

¹ *Actinosphaerium* forms one of the most extreme known cases of in-breeding; for the gametes are *sister-cells* which immediately reunite after forming the polar bodies. The general facts are as follows: The mother animal, containing very numerous nuclei, becomes encysted, and a very large number of the nuclei degenerate. The body then segments into

Adelea (one of the Coccidiæ) is a very interesting case, for according to Siedlecki ('99) polar bodies or their analogues are formed in both sexes. The gametes are here of very unequal size. Upon their union the smaller male cell divides twice to form apparently equivalent spermatozoids, of which, however, only one enters the ovum, while three degenerate as polar bodies. These two divisions are of different type; the first resembles true mitosis, while the second is of simpler character and is believed by Siedlecki to effect a reduction in the number of chromosomes. In the meantime the nucleus of the macrogamete moves to the surface and there expels a portion of its chromatin, after which union of the nuclei takes place. Interesting facts have been observed in unicellular plants which indicate that the reduction may here occur either before (diatoms) or after (desmids) fusion of the conjugating nuclei. In the former (*Rhopalodina*) Klebahn ('96) finds that each nucleus divides twice, as in many Infusoria, giving rise to two large and two small nuclei. Each of the conjugates then divides, each daughter-cell receiving one large and one small nucleus. The four resulting individuals then conjugate, two and two, the large nuclei fusing while the small (polar bodies) degenerate. The comparison of this case with that of the Infusoria is highly interesting. In the desmids on the other hand (*Closterium* and *Cosmarium*, Fig. 140), according to Klebahn ('92), the nuclei first unite to form a cleavage-nucleus, after which the zygote divides into two. Each of the new nuclei now divides, one of the products persisting as the permanent nucleus, while the other degenerates and disappears. Chmielewski asserts that a similar process occurs in *Spirogyra*. Although the numerical relations of the chromosomes have not been determined in these cases, it appears probable that the elimination of a nucleus in each cell is a process of reduction occurring after fertilization.

G. MATURATION OF PARTHENOGENETIC EGGS

The maturation of eggs that develop without fertilization is a subject of special interest, partly because of its bearing on the general theory of fertilization, partly because it is here, as I believe, that one of the strongest supports is found for the hypothesis of the individuality of chromosomes. In an early article by Minot ('77) on the

a number (five to twelve) of "primary cysts," each containing one of the remaining nuclei. Each primary cyst divides by mitosis to form two gametes ("secondary cysts"), which, after forming the polar bodies, reunite, their nuclei fusing to form a single one. The resulting cell soon creeps out of the cyst-wall and assumes the active life, its nucleus meanwhile multiplying to produce the multinuclear condition characteristic of the adult animal. What is here the physiological motive for the formation of the polar bodies, and how shall it be explained under the Weismann hypothesis?

theoretical meaning of maturation, the suggestion is made that parthenogenesis may be due to failure on the part of the egg to form the polar bodies, the egg-nucleus thus remaining hermaphrodite, and hence capable of development without fertilization. This suggestion forms the germ of all later theories of parthenogenesis. Bal-four ('80) suggested that the function of forming polar cells has been acquired by the ovum for the express purpose of preventing parthenogenesis, and a nearly similar view was afterward maintained by Van Beneden.¹ These authors assumed accordingly that in parthenogenetic eggs no polar bodies are formed. Weismann ('86) soon discovered, however, that the parthenogenetic eggs of *Polyphemus* (one of the Daphnidæ) produce a *single* polar body. This observation was quickly followed by the still more significant discovery by Blochmann ('88) that *in Aphis the parthenogenetic eggs produce a single polar body, while the fertilized eggs produce two*. Weismann was able to determine the same fact in ostracodes and Rotifera, and was thus led to the view² which later researches have entirely confirmed, that it is the *second* polar body that is of special significance in parthenogenesis. Blochmann observed that in insects the polar bodies were not actually thrown out of the egg, but remained embedded in its substance near the periphery. At the same time Boveri ('87, 1) discovered that in *Ascaris* the second polar body might in exceptional cases remain in the egg and there give rise to a resting-nucleus indistinguishable from the egg-nucleus or sperm-nucleus. He was thus led to the interesting suggestion that parthenogenesis might be due to the retention of the second polar body in the egg and its union with the egg-nucleus. "The second polar body would thus, in a certain sense, assume the rôle of the spermatozoön, and it might not without reason be said: "*Parthenogenesis is the result of fertilization by the second polar body.*"³

This conclusion received a brilliant confirmation through the observations of Brauer ('93) on the parthenogenetic egg of *Artemia*, though it appeared that Boveri arrived at only a part of the truth. Blochmann ('88-'89) had found that in the parthenogenetic eggs of the honey-bee *two* polar bodies are formed, and Platner discovered the same fact in the butterfly *Liparis* ('89)—a fact which seemed to contradict Boveri's hypothesis. Brauer's beautiful researches resolved the contradiction by showing that there are *two types* of *parthenogenesis* which may occur in the same animal. In the one case Boveri's conception is exactly realized, while the other is easily brought into relation with it.

(a) In both modes typical tetrads are formed in the germ-nucleus to the number of eighty-four. In the first and more frequent case

¹ '83, p. 622.

² Essay VI., p. 359.

³ *l.c.*, p. 73.

(Fig. 141) but one polar body is formed, which removes eighty-four dyads, leaving eighty-four in the egg. There may be an abortive attempt to form a second polar spindle, but no division results, and the eighty-four dyads give rise to a reticular cleavage-nucleus. From

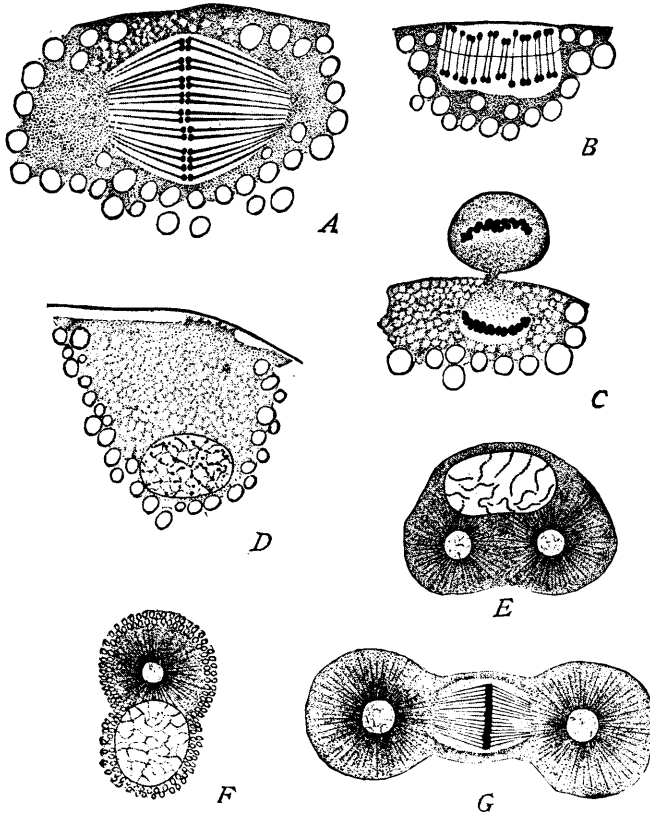


Fig. 141. — First type of maturation in the parthenogenetic egg of *Artemia*. [BRAUER.]

A. The first polar spindle; the equatorial plate contains 84 tetrads. *B. C.* Formation of the first polar body; 84 dyads remain in the egg, and these give rise to the egg-nucleus, shown in *D.* *F.* Appearance of the egg-centrosome and aster. *E. G.* Division of the aster and formation of the cleavage-figure; the equatorial plate consists of 84 apparently single but in reality bivalent chromosomes.

this arise eighty-four thread-like chromosomes, and *the same number appears in later cleavage-stages.*

(*b*) It is the second and rarer mode that realizes Boveri's conception (Fig. 142). Both polar bodies are formed, the first removing eighty-four dyads and leaving the same number in the egg. In the formation of the second, the eighty-four dyads are halved to form

two daughter-groups, each containing eighty-four single chromosomes. Both these groups remain in the egg, and each gives rise to a single reticular nucleus, as described by Boveri in *Ascaris*. These two nuclei place themselves side by side in the cleavage-figure, and give rise each to eighty-four chromosomes, precisely like two germ-nuclei in ordinary fertilization. The one hundred and sixty-eight chromosomes split

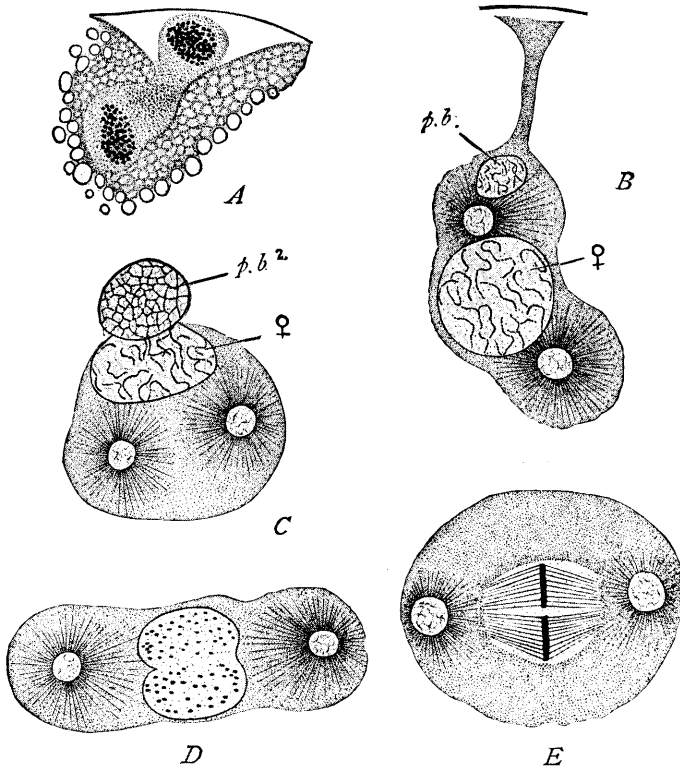


Fig. 142. — Second type of maturation in the parthenogenetic egg of *Artemia*. [BRAUER.]

A. Formation of second polar body. B. Return of the second polar nucleus ($p. b.^2$) into the egg; development of the egg-amphiaster. C. Union of the egg-nucleus (♀) with the second polar nucleus ($p. b.^2$). D. Cleavage-nucleus and amphiaster. E. First cleavage-figure with equatorial plate containing 168 chromosomes in two groups of 84 each.

lengthwise, and are distributed in the usual manner, and reappear in the same number in later stages. In other words, the second polar body here plays the part of a sperm-nucleus precisely as maintained by Boveri.

In all individuals arising from eggs of the first type, therefore, the somatic number of chromosomes is eighty-four; in all those arising from eggs of the second type, it is one hundred and sixty-eight. This

difference is clearly due to the fact that in the latter case the chromosomes are single or univalent, while in the former they are bivalent (actually arising from dyads or double chromosomes). The remarkable feature, on which too much emphasis cannot be laid, is that the numerical difference should persist despite the fact that the mass, and, as far as we can see, the quality, of the chromatin is the same in both cases. In this fact we must recognize a strong support, not only of Häcker's and Vom Rath's conception of bivalent chromosomes, but also of the more general hypothesis of the individuality of chromosomes (Chapter VI.).

1. Accessory Cells of the Testis

It is necessary to touch here on the nature of the so-called "Sertoli-cells," or supporting cells of the testis in mammals, partly because of the theoretical significance attached to them by Minot, partly because of their relations to the question of amitosis in the testis. In the seminiferous tubules of the mammalian testis, the parent-cells of the spermatozoa develop from the periphery inwards toward the lumen, where the spermatozoa are finally formed and set free. At the periphery is a layer of cells next the basement-membrane, having flat, oval nuclei. Within this, the cells are arranged in columns alternating more or less regularly with long, clear cells, containing large nuclei. The latter are the *Sertoli-cells*, or supporting cells: they extend nearly through from the basement-membrane to the lumen, and to their inner ends the young spermatozoa are attached by their heads, and there complete their growth. The spermatozoa are developed from cells which lie in columns between the Sertoli-cells, and which undoubtedly represent spermatogonia, spermatocytes, and spermatids, though their precise relationship is, to some extent, in doubt. The innermost of these cells, next the lumen, are spermatids, which, after their formation, are found attached to the Sertoli-cells, and are there converted into spermatozoa without further division. The deeper cells from which they arise are spermatocytes, and the spermatogonia lie deeper still, being probably represented by the large, rounded cells.

Two entirely different interpretations of the Sertoli-cells were advanced as long ago as 1871, and both views still have their adherents. Von Ebner ('71) at first regarded the Sertoli-cell as the parent-cell of the group of spermatozoa attached to it, and the same view was afterward especially advocated by Biondi ('85) and by Minot ('92), the latter of whom regarded the nucleus of the Sertoli-cell as the physiological analogue of the polar bodies, *i.e.* as containing the female nuclear substance ('92, p. 77). According to the opposing view, first suggested by Merkel ('71), the Sertoli-cell is not the parent-cell, but a nurse-cell, the spermatozoa developing from the columns of rounded cells, and becoming *secondarily* attached to the Sertoli-cell, which serves merely as a support and a means of conveying nourishment to the growing spermatozoa. This view was advocated by Brown ('85), and especially by Benda ('87). In the following year ('88), von Ebner himself abandoned his early hypothesis and strongly advocated Benda's views, adding the very significant result that *four spermatids arise from each spermatocyte*, precisely as was afterward shown to be the case in *Ascaris*, etc. The very careful and thorough work of Benda and von Ebner, confirmed by that of Lenhossék ('98, 2), leaves no doubt that mammalian spermatogenesis conforms, in its main outlines, with that of *Ascaris*, the salamander, and other forms, and that Biondi's account is untenable. Minot's theoretical interpretation of the Sertoli-cell, as the physiological equivalent of the polar bodies, therefore collapses.

2. Amitosis in the Early Sex-cells

Whether the progenitors of the germ-cells ever divide amitotically is a question of high theoretical interest. Numerous observers have described amitotic division in testis-cells, and a few also in those of the ovary. The recent observations of Meves ('91), Vom Rath ('93), and others leave no doubt whatever that such divisions occur in the testis of many animals. Vom Rath maintains, after an extended investigation, that all cells so dividing do not belong in the cycle of development of the germ-cells ('93, p. 164); that amitosis occurs only in the supporting or nutritive cells (Sertoli-cells, etc.), or in such as are destined to degenerate, like the "residual bodies" of Van Beneden. Meves has, however, produced strong evidence ('94) that in the salamander the spermatogonia may, in the autumn, divide by amitosis, and in the ensuing spring may again resume the process of mitotic division, and give rise to functional spermatozoa. On the strength of these observations Flemming ('93) himself now admits the possibility that amitosis may form part of a normal cycle of development.¹

H. SUMMARY AND CONCLUSION

The one fact of maturation that stands out with perfect clearness and certainty amid all the controversies surrounding it is a *reduction of the number of chromosomes in the ultimate germ-cells to one-half the number characteristic of the somatic cells*. It is equally clear that this reduction is a preparation of the germ-cells for their subsequent union, and a means by which the number of chromosomes is held constant in the species. With a few exceptions the first indication of the numerical reduction appears through the segmentation of the spiremethread, or the resolution of the nuclear reticulum, into a number of masses *one-half that of the somatic chromosomes*. In nearly all higher animals this process first takes place two cell-generations before the formation of the definitive germ-cells, and the process of reduction is completed by two rapidly succeeding "maturation-divisions," giving rise to four cells, all of which become functional in the male, while in the female only one becomes the egg, while the other three — the polar bodies or their analogues — are cast aside. During these two divisions each of the original chromatin-masses gives rise to four chromosomes, of which each of the four daughter-cells receives one; hence, each of the latter receives one-half the somatic number of chromosomes. In the higher plants, however, the two maturation-divisions are followed by a number of others, in which the reduced number of chromosomes persists, a process most strikingly shown in the pteridophytes, where a separate sexual generation (prothallium) thus arises, all the cells of which show the reduced number.

Two general types of maturation may be distinguished according to the manner in which the primary chromatin-masses divide. In one,

¹ For more recent literature on this subject see Meves, *Zelltheilung*, in Merkel and Bonnet's *Ergebnisse*, VIII., 1898.

typically represented by *Ascaris* and the arthropods, each of these masses divides into four to form a tetrad, thus preparing at once for two rapidly succeeding divisions, which are not separated by a reconstruction of the daughter-nuclei during an intervening resting period. In the other, examples of which are given by the flowering plants and the spermatogenesis of the Amphibia, no true tetrads are formed, the primary chromatin-masses dividing separately for each of the maturation-divisions, which are separated by a period in which the nuclei regress toward the resting state, though often not completely returning to the reticular condition. These two types differ, however, only in degree, and with few exceptions they agree in the fact that during the prophases of the first division the chromatin-bodies assume the form of rings, the mitosis thus being of the heterotypical form, and each ring having the prospective value of four chromosomes.

Thus far the phenomena present no difficulty, and they give us a clear view of the process by which the numerical reduction of the *chromosomes* is effected. The confusion of the subject arises, on the one hand, from its complication with theories regarding the individuality of the chromosomes and the functions of chromatin in inheritance, on the other through conflicting results of observation on the mode of tetrad-formation and the character of the maturation-divisions. Regarding the latter question nearly all observers are now agreed that one of these divisions, usually the first, is a longitudinal or equatorial-division, essentially like that occurring in ordinary mitosis. The main question turns upon the other division, which has been shown in some cases to be transverse and not longitudinal, and thus separates what were originally different regions of the spireme-thread or nuclear substance. The evidence in favour of such a division seems at present well-nigh demonstrative in the case of insects and copepods, and hardly less convincing in the turbellarians, annelids, and mollusks. On the other hand, both divisions are regarded as longitudinal by most of those who have investigated the phenomena in *Ascaris* and in the vertebrates, and by some of the most competent investigators of the flowering plants.

The evidence as it stands is so evenly balanced that the subject is hardly yet ripe for discussion. The principle for which Weismann contended in his theory of reducing division has received strong support in fact; yet should it be finally established that numerical reduction may be effected either with or without transverse division, as now seems probable, not only will that theory have to be abandoned or wholly remodelled, but we shall have to seek a new basis for the interpretation of mitosis in general. Weismann's theory is no doubt of a highly artificial character; but this should not close our eyes to the great interest of the problem that it attempted to solve.

The existing contradiction of results has led to the opinion, expressed by a number of recent writers, that the difference between longitudinal or transverse division is of minor importance, and that the entire question of reduction is a barren one. This opinion fails to reckon with the facts on which rests the hypothesis of the individuality of chromosomes (Chap. VI.); but these facts cannot be left out of account. We must find a common basis of interpretation for them and for the phenomena of reduction; yet how shall we reconcile them with reduction by longitudinal division only? I cannot, therefore, share the opinion that we are dealing with a barren problem. The peculiarities of the maturation-mitoses are obviously correlated in some way with the numerical reduction, and the fact that they differ in so many ways from the characters of ordinary mitosis gives ground to hope that their exhaustive study will throw further light not only on the reduction-problem itself but also on mitosis in general and on still wider problems relating to the individuality of the chromosomes and the morphological organization of the nucleus. It is indeed very probable that Weismann's theory is but a rude attempt to attack the problem, and one that may prove to have been futile. The problem itself cannot be ignored, nor can it be dissociated from the series of kindred problems of which it forms a part.

LITERATURE. V¹

- Van Beneden, E.** — Recherches sur la maturation de l'œuf, la fécondation et la division cellulaire: *Arch. Biol.*, IV. 1883.
- Boveri, Th.** — Zellenstudien, I., III. *Jena*, 1887-90. See also "Befruchtung" (List IV.).
- Brauer, A.** — Zur Kenntniss der Spermatogenese von *Ascaris megaloccephala*: *Arch. mik. Anat.*, XLII. 1893.
- Id.** — Zur Kenntniss der Reifung der parthenogenetisch sich entwickelnden Eies von *Artemia Salina*: *Arch. mik. Anat.*, XLIII. 1894.
- Guignard, L.** — Le développement du pollen et la réduction chromatique dans le *Naias*: *Arch. Anat. Mic.*, II. 1899. (Full literature on reduction in plants.)
- Griffin, B. B.** — See Literature, IV.
- Häcker, V.** — Die Vorstadien der Eireifung (General Review): *Arch. mik. Anat.*, XLV. 2. 1895.
- Id.** — Über weitere Übereinstimmungen zwischen den Fertpflanzungsvorgängen der Thiere und Pflanzen: *Biol. Centralb.*, XVII. 1897.
- Id.** — Über vorbereitende Theilungsvorgänge bei Thieren und Pflanzen: *Verh. deutsch. Zool. Ges.*, VIII. 1898.
- Id.** — Die Reifungserscheinungen: *Merkel und Bonnet's Ergebnisse*, VIII. 1898.
- Hertwig, O.** — Vergleich der Ei- und Samenbildung bei Nematoden. Eine Grundlage für celluläre Streitfragen: *Arch. mik. Anat.*, XXXVI. 1890.
- Mark, E. L.** — (See List IV.)
- Peter, K.** — Die Bedeutung der Nährzellen im Hoden: *Arch. mik. Anat.*, LIII. 1898.

¹ See also Literature, IV., p. 231.

- Platner, G.** — Über die Bedeutung der Richtungkörperchen: *Biol. Centralb.*, VIII. 1889.
- Vom Rath, O.** — Zur Kenntniss der Spermatogenese von *Gryllotalpa vulgaris*: *Arch. mik. Anat.*, XL. 1892.
- Id.** — Neue Beiträge zur Frage der Chromatinreduktion in der Samen- und Eireife: *Arch. mik. Anat.*, XLVI. 1895.
- Rückert, J.** — Die Chromatinreduktion der Chromosomenzahl im Entwicklungsgang der Organismen: *Ergebn. d. Anat. u. Entwickl.*, III. 1893 (1894).
- Strasburger, E.** — Über periodische Reduktion der Chromosomenzahl im Entwicklungsgang der Organismen: *Biol. Centralb.*, XIV. 1894.
- Id.** — Reduktionstheilung, Spindelbildung, etc.: *Jena, Fischer*, 1900.