CHAPTER VI

MATURATION AND REDUCTION. MEIOSIS

"There must be yet another kind of karyokinesis, in which the primary equatorial loops are not split longitudinally, but are separated without division into two groups."

WEISMANN. [1]

We have now to examine the far-reaching vistas of inquiry opened by Van Beneden's fundamental discovery that the gamete-nuclei, and hence the two parents from which they are respectively derived, contribute each a haploid or single group of chromosomes to the fertilized egg. Each act of fertilization doubles the gametic number of chromosomes; yet the number characteristic of the species remains constant from generation to generation. Somewhere in the course of the life-cycle, accordingly, the diploid or so-called "somatic" number must be reduced by one-half to the haploid or gametic. When and how is this accomplished?

The first guess (Van Beneden, Boveri, Rückert, Van Bambeke, Van der Stricht) was that reduction might be effected by some process of degeneration or casting out of half the chromosomes from the nucleus; but subsequent research showed that the process is of very different type.[2] Reduction results from a regrouping of the chromosomes of the diploid group and their segregation into two single or haploid groups corresponding in a general way to those that originally came together in the egg. So far as the chromosomes are concerned this process may be regarded broadly as the reverse of nuclear union or karyogamy. Its fundamental interest for the problems of genetics has made it the object of innumerable cytological researches, and the main facts now seem well established. Its critical study offers, however, many intricate and difficult questions of detail, some of which are still matters of controversy. We shall here consider only the cytological problems of meiosis, deferring to later chapters an account of their relation to the genetic phenomena for the explanation of which they provide the key.

I. GENERAL SURVEY

Reduction or *meiosis* takes place at a particular part of the life-history, known as the *meiotic phase*, the preliminary operations of which some-

[1] *Essays on Heredity*, '87, p. 360.

[2] A review of the earlier history of this question will be found in the work of Maréchal ('07) and more recently of O. Hertwig ('17).

times take place very early in the individual life; for instance, in the eggs of higher vertebrates the process begins about the time of birth or earlier, though not completed until near the time of sexual maturity. In higher plants it takes place in a different generation (sporophyte) from that which

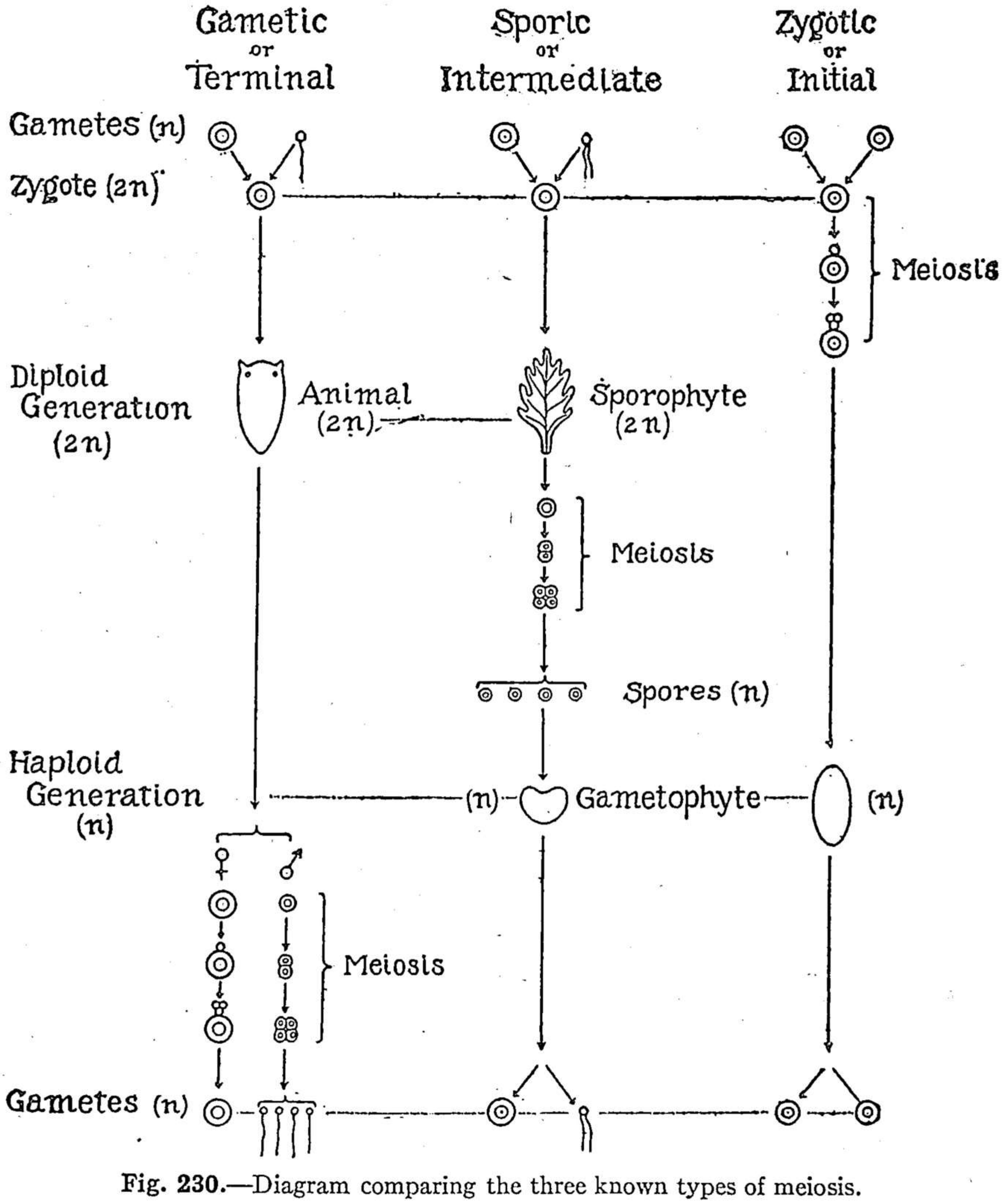

Fig. 230.—Diagram comparing the three known types of meiosis.

produces the gametes. Its climax appears in two peculiar mitoses called the *meiotic* or *maturation-divisions* during which the actual sorting out of the chromosomes into two haploid groups is completed; hence these divisions are often designated as *segregation-divisions*. In general aspect they are of mitotic type; but they are distinguished by certain special peculiarities in the history of the chromosomes, and in some instances also in the character of the achromatic figure. Meiosis seems to be accomplished by

two divisions, neither more nor fewer, throughout nearly the whole of the plant and animal kingdoms. The only seeming exceptions to this are offered by a few cases in which but one division has been identified, or in which the meiotic divisions are closely associated with one or more additional equation-divisions (*e. g.*, in ciliates or in *Fucus*). It is probable, however, that these exceptions are only apparent, and that the meiotic divisions under many disguises everywhere have the same fundamental characteristics.

The period at which meiosis takes place, though constant in the species, differs widely in different groups, in a few cases even within the limits of smaller groups, as in the conjugate algæ (desmids, diatoms), in the red algæ (Rhodophyceæ), and perhaps in the Sporozoa. The known cases fall into three clearly marked groups or types, which may be characterized as (1) *Gametic or Terminal*, (2) *Zygotic or Initial*, and (3) *Sporic or Intermediate Meiosis*. These are shown in diagram by Fig. 230.

(1) *Gametic or Terminal Meiosis* is characteristic of animals generally, including all Metazoa and many Protozoa (Figs. 230, 282). It occurs in a few lower plants (Thallophyta), the best known examples being found per-

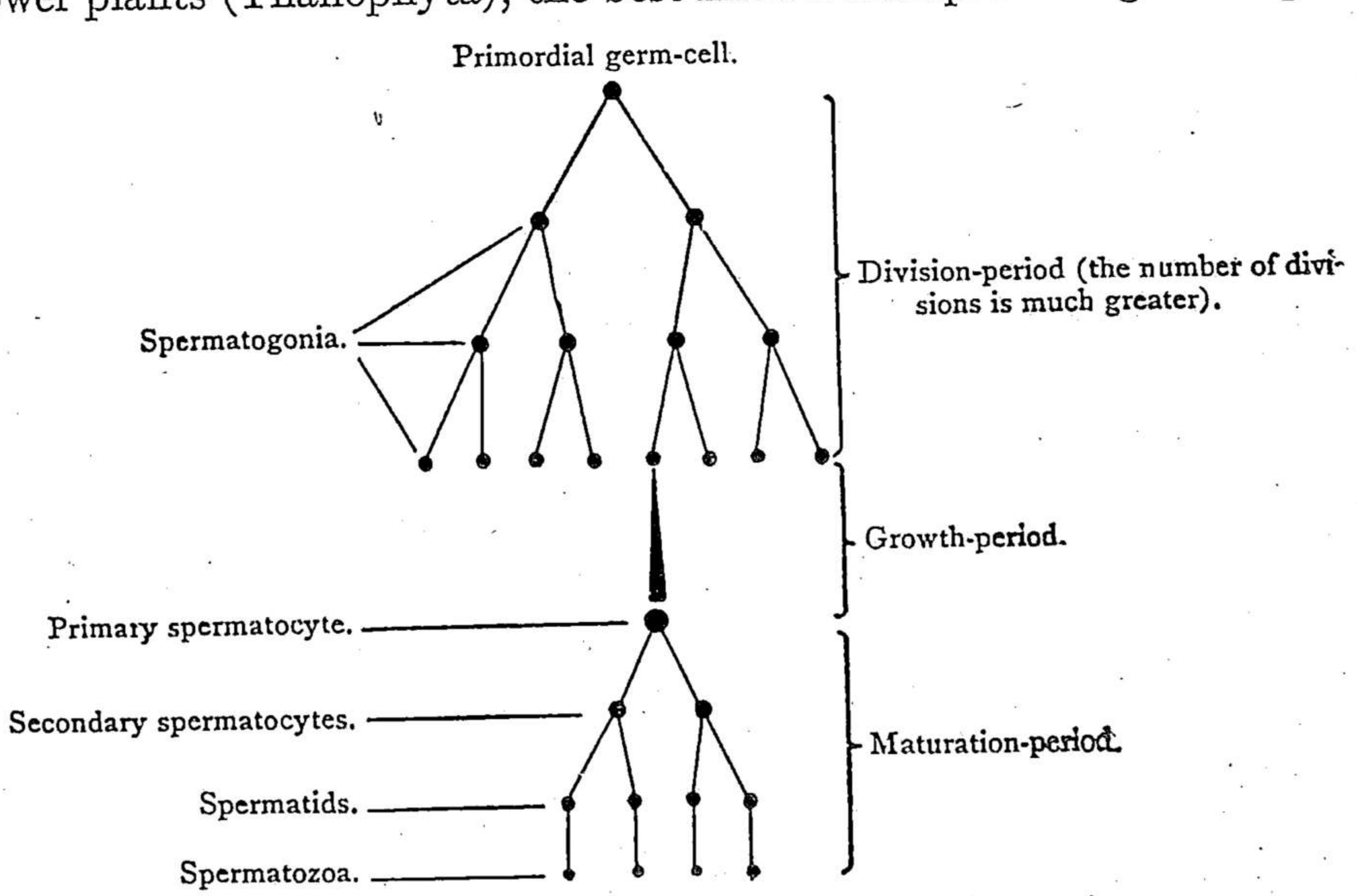

Fig. 231.—Diagram showing the genesis of the sperm (BOVERI).

haps in the Fucaceæ (*Fucus*) and the diatoms. Meiosis of this type takes place during the last two divisions by which the gametes (or their nuclei) are produced. The meiotic divisions here form part of the general process of *oögenesis* in the female and of *spermatogenesis* in the male; and since the gametes result from two successive divisions they are typically formed in

quartets or groups of four.[1] Externally a marked contrast exists between the sexes in respect to these quartets (p. 493), but internally the phenomena are fundamentally alike in both, as was first indicated by Platner in 1889 and brilliantly demonstrated in detail by O. Hertwig in the following year.

(2) *Zygotic or Initial Meiosis* is a rare but interesting form which stands at the opposite extreme from the gametic type (Figs. 230, 297). At present it is known only in a few of the algæ (*Spirogyra*, *Zygnema*, desmids and certain diatoms, *Coleochæte*, *Nemalion* and *Scinaia*), and in certain Sporozoa (*Diplocystis*, *Aggregata*). Here the meiotic divisions occur just after instead of just before the union of the gametes, *i. e.*, they are the initial divisions of the zygote and take place at the beginning of the sexual life-cycle. The products of the zygote (ordinary vegetative cells), therefore, possess nuclei of haploid instead of diploid organization, the latter condition appearing only in the zygote as a transitory result of syngamy. From a theoretical point of view there is some reason to suspect that this condition may be a very primitive one (p. 617).

(3) *Sporic or Intermediate Meiosis* is characteristic of all the higher plants (cormophytes) and also occurs in some of the thallophytes, but is thus far

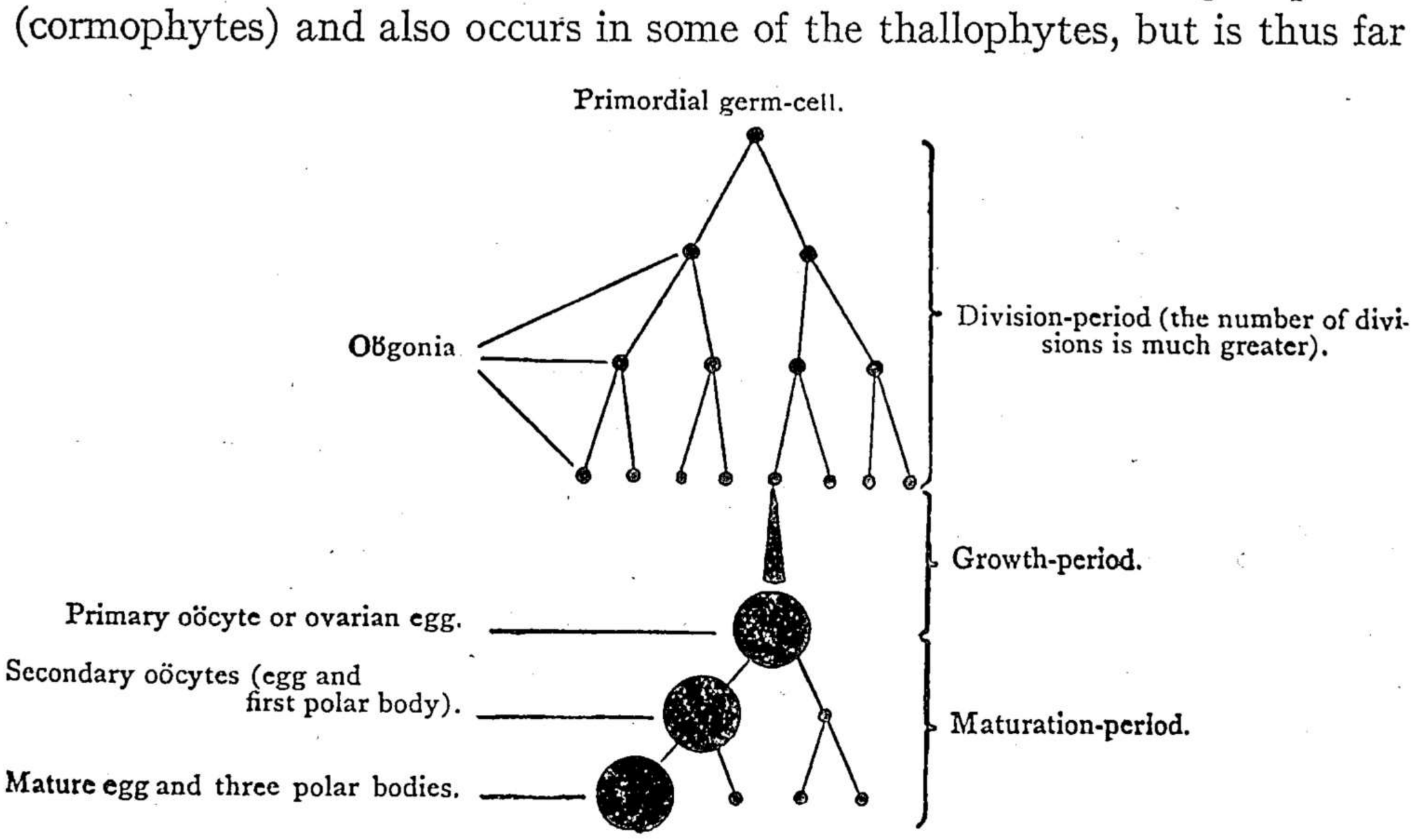

Fig. 232.—Diagram showing the genesis of the egg (BOVERI).

unknown among animals (Fig. 230). The meiotic divisions here take place at some point in the diploid organism intermediate between the zygote and the formation of the gametes, and their products are not gametes but asexual spores (tetraspores, embryo-sacs, pollen-grains, etc.). Here, therefore,

[1] These groups are sometimes called "tetrads," but this term causes confusion with the chromosome-tetrads (p. 505), which may be avoided by use of the word quartet.

the meiotic divisions form part of the general process of *sporogenesis*, and involve an alternation of generations, as follows:[1] The spores (being the products of meiosis) receive the haploid number of chromosomes and develop without fertilization into a haploid, gamete-producing "sexual" generation, known as the *haplont* (in plants the *gametophyte*) which intervenes between meiosis and the gamete-formation. From this organism arise the gametes by ordinary mitosis; and by their union is produced the zygote from which arises a diploid, asexual spore-producing *diplont* (in plants the *sporophyte*), thus completing the life-cycle. This process, typically illustrated by the alternation of the diploid leafy fern-plant and the haploid prothallium, is now generally designated as *antithetic* in contradistinction to *homologous* alternation in which both generations have the same number of chromosomes.[2] In all the higher plants, from bryophytes to seed-plants, and even in some of the algæ (*Cutleria*), the two generations are of markedly different appearance and morphological type. On the other hand, in some of the algæ (*Dictyota*, *Polysiphonia*, etc.), the investigations of Williams, Yamanouchi, Svedelius and others have shown that the haplont and diplont generations are of nearly or quite identical morphological type (p. 627).

Why meiosis should require two divisions is wholly unknown; as far as we can see one division should equally well accomplish the result. A key to the problem is perhaps to be sought in the diploid type of animal parthenogenesis (p. 468), where but a single maturation division takes place and reduction fails to occur.

II. EXTERNAL ASPECTS OF MATURATION

1. In Animals

The origin of the germ-cells, and the general character of the germ-track have already been considered (p. 310). During the growth-period following the final gonial divisions (which like their predecessors are diploid) the auxocytes undergo a marked growth and are designated, in the female as primary *oöcytes*, in the male as primary *spermatocytes*, and in plants generally as primary *sporocytes*, or spore-mother-cells. The auxocytes of the two sexes are at first nearly or quite indistinguishable (p. 329), and both

[1] See also p. 617.

[2] This distinction was first clearly recognized, without knowledge of the cytological relations, on the basis of the vegetative characters by Celakowsky ('74, '77), later by Bower ('91). Homologous alternation was said to take place between sexual and asexual generations of similar morphological type (*e. g.*, in *Vaucheria*), antithetic alternation between generations of essentially different type, as in all cormophytic plants. The distinction first acquired precision when placed upon a cytological basis by the discovery of Dixon ('91), Overton ('93), and Strasburger ('94) that the spore-producing divisions are meiotic, and that the nuclei of the resulting gametophytes are haploid.

alike undergo extensive enlargement during the growth-period. In the female this growth takes place on a far greater scale than in the male, so that the fully grown oöcytes may thus become thousands of times larger than the spermatocytes. In some degree this difference is correlated with the length of the growth-period, which is in general much more prolonged in case of the oöcyte; but this is subject to wide variations in different cases; the growth-period of the oöcyte may last for only a few days (some

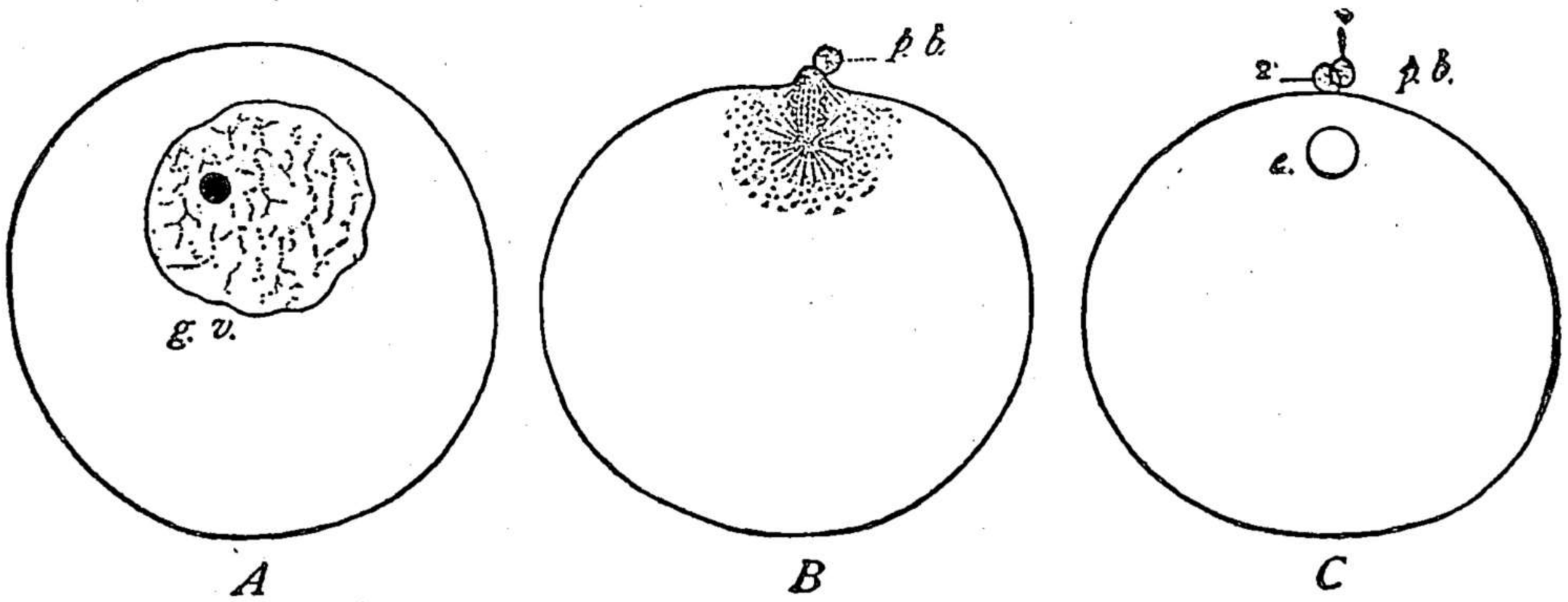

Fig. 233.—Formation of the polocytes before entrance of the sperm, as seen in the living ovarian egg of the sea-urchin, *Toxopneustes* (× 365).

of the Diptera) or may be continued throughout months or even years (mammals). But, obviously, the great size of the oöcyte is not determined by this alone. The prolonged growth-period in the placental mammal, for instance, does not lead to a growth comparable in degree to that occurring in Ornithodelphia or Sauropsida. Fundamentally, the differential factor forms a part of the general mechanism of heredity; and the size of the egg is correlated not alone with the length of the growth-period but also with the conditions of embryonic and larval development, and other unknown factors.

To the same primary cause is traceable the division of labor that has taken place among the cells of the maturation-quartets. In the male, speaking generally, all four of these cells (sperms) are of minute size and are structurally and functionally alike (Fig. 231);[1] and the divisions take place as a rule in the testis. In the female, on the other hand (Figs. 232, 234), but one cell (the ovum) is functional, and it is enormously enlarged at the cost of the others (polar bodies or polocytes) thus becoming a store-house of active protoplasm and of passive food-materials for the use of the developing embryo (p. 256). Here we find ground for the conclusion that the polocytes must be regarded as vestigial gametes, or rudimentary eggs[2]

[1] An important exception to this occurs in the spermatogenesis of rotifers, aphids and phylloxerans, and of bees, ants and other Hymenoptera (p. 797).

[2] This view was first suggested by Mark ('81), and later emphasized by Bütschli ('84).

which have lost the power of development. This conclusion is supported by the fact, reported by Fol ('79) and Platner ('86), that the polocytes may be penetrated by sperms; and by the still more striking fact that by an occasional abnormality of division one or both polocytes may be abnormally large, in extreme cases even as large as the remainder of the egg (Fig. 235). This occurs as a spontaneous abnormality in platodes and gasteropods; [1] and in the former case Francotte has found (in *Prosthecerœus*) that such giant polocytes may actually be fertilized by the sperm and develop into

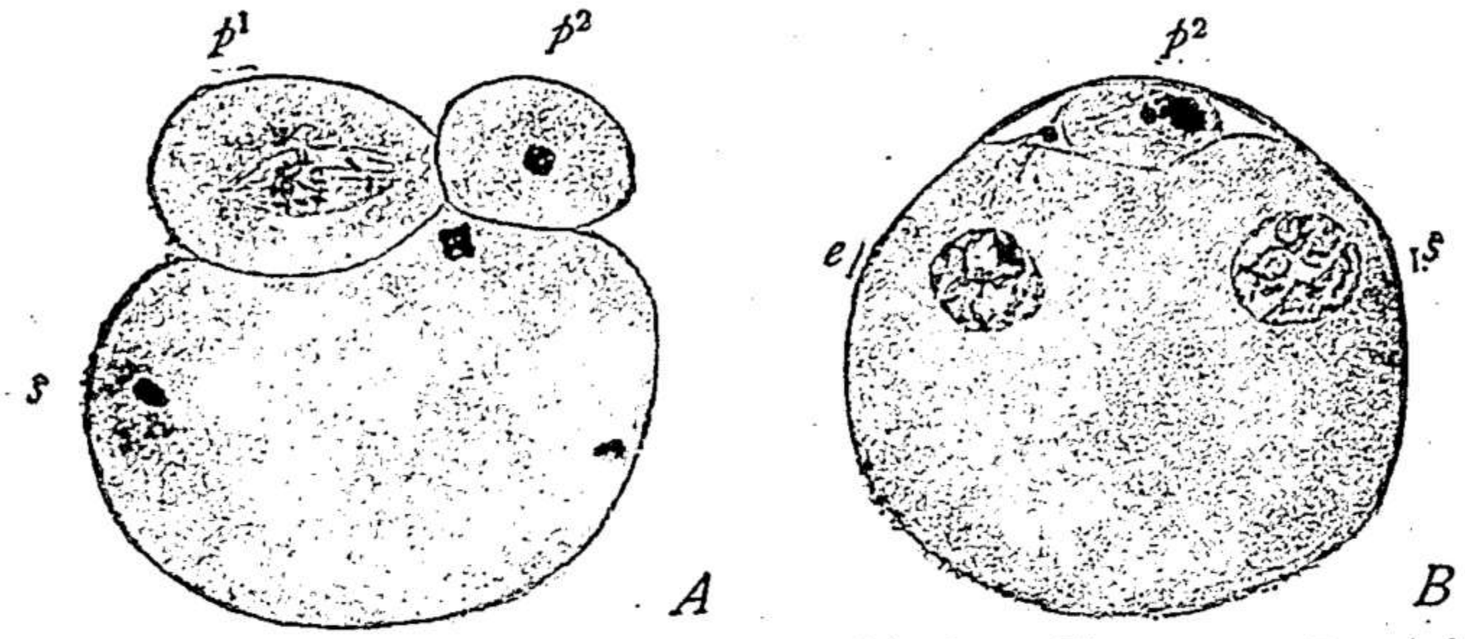

Fig. 234.—Polocytes and fertilization in the mouse (*A*, from KIRKHAM; *B*, original drawing from a preparation by KIRKHAM).

A, earlier stage, both polocytes, the first in division, egg-nucleus and sperm-nucleus (*s*); *B*, later stage, first polocyte not shown.

actively free-swimming dwarf larvæ, two larvæ being thus produced by one egg.[2]

Extrusion of the polocytes from the egg sometimes takes place in the ovary (*e. g.*, in sea-urchins) but commonly is deferred until the egg leaves the ovary or is discharged from the body; not infrequently it does not begin until after the sperm has actually entered the egg, maturation and fertilization being in this case closely associated (p. 398).

In typical cases the first polocyte divides while the second one is being formed (Figs. 183, 199); but frequently this fails (Fig. 198). As a rule the polocytes are extremely minute, and in the case of large, heavily yolk-laden eggs, like those of fishes or reptiles, are thousands of times smaller than the egg. An example of relatively large polocytes is shown in Fig. 198 (*Pterotrachea*), and of very large ones in the mouse (Fig. 234), where according to the measurements of Kirkham the first polocyte may attain to nearly 1/20 the volume of the egg. In some cases, espe-

[1] See Francotte ('97), Lams ('08), and Conklin ('17).

[2] The writer has observed the same in *Leptoplana*. Conklin found that in *Crepidula* giant polocytes (which are readily induced by centrifuging the eggs) never develop. This is no doubt due, as Conklin points out, to the fact that in *Crepidula* the sperm normally enters the egg before formation of the polocytes, so that the latter, like the egg, have passed the "second critical period" (p. 420) and become immune to additional sperms. In the platode, on the other hand, the sperm does not enter until after extrusion of the first polocyte, which like the egg has not yet passed the second critical period.

cially in eggs heavily laden with yolk (insects, crustacea), the polocytes fail to be actually extruded from the egg, their nuclei remaining in the egg-protoplasm near the periphery (Fig. 194). Here we can hardly speak of polar bodies or polocytes but rather of polar nuclei; but as usual two polar divisions typically occur, a group of three polar nuclei thus being formed near the periphery of the egg. In many such cases among the insects the

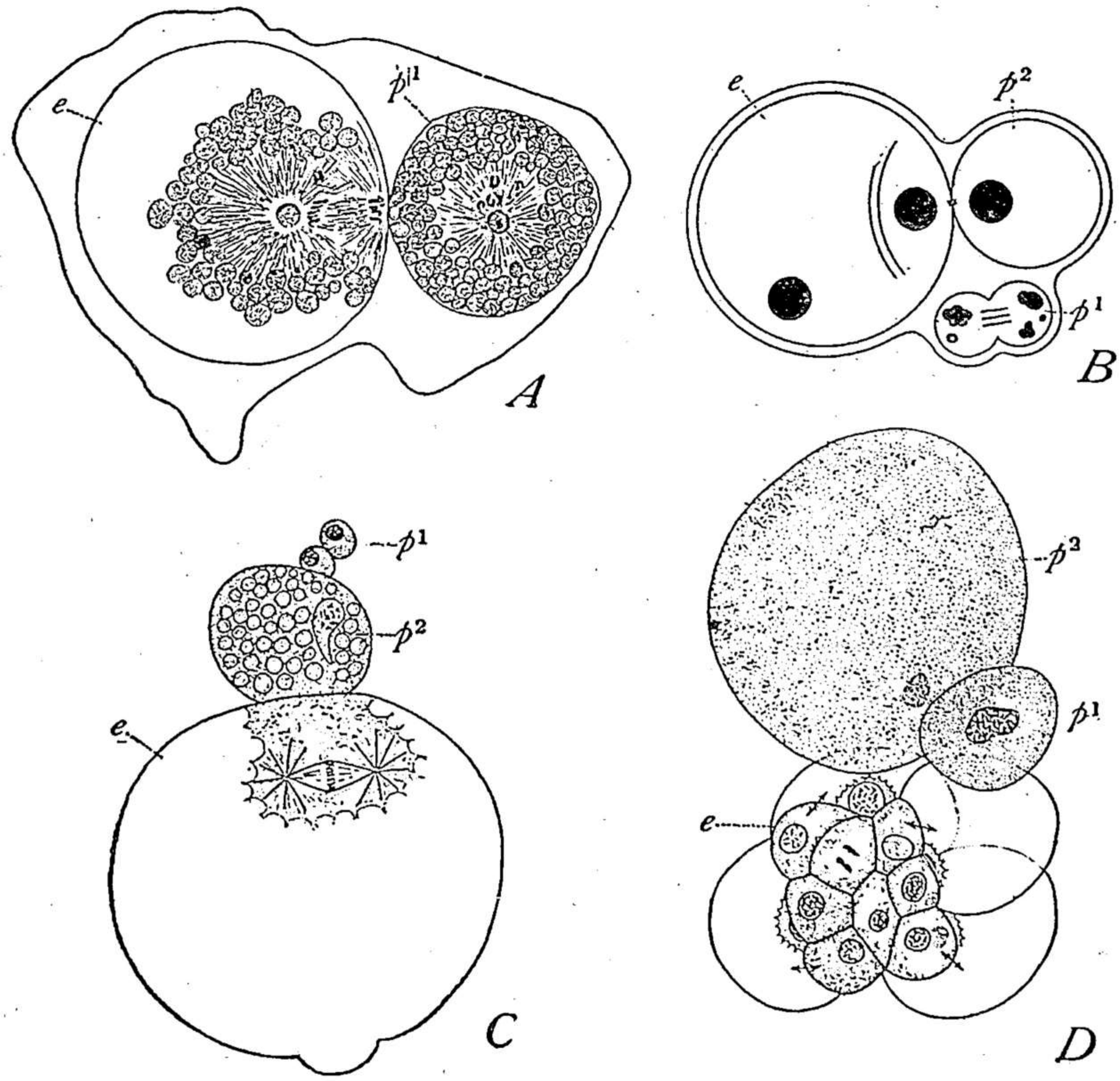

Fig. 235.—Giant polocytes in the eggs of platodes and snails.

A, egg of *Thysanozoön*, with giant first polocyte and second polar spindle (VAN DER STRICHT); *B*, *Arion*, with both polocytes abnormally large, schematic (LAMS); *C*, *D*, *Crepidula*, after centrifuging the egg, showing various degrees of giantism of the polocytes; in *D* the second polocyte is as large as the diminished egg; the latter has segmented normally (CONKLIN).

second polar nucleus fuses with the inner one of the pair arising by division of the first; in other cases all three polar nuclei fuse together. In either case the fusion-nucleus may then progressively divide for a considerable time. An example of this is described by Silvestri ('06–'08) in the parasitic hymenopter *Litomastix*, where this nucleus thus gives rise to a mass of cells that finally almost surrounds the embryo (Fig. 142).[1]

[1] This has superficially the appearance of a gametophore generation analogous to the gametophyte in plants, but the resemblance is of no significance and the cells in question must be triploid instead of haploid.

Most commonly the meiotic divisions take place in rapid succession, often without the formation of a resting nucleus during the interkinesis, or interval between them. In such cases the telophase-chromosomes of the first division pass directly into the equatorial plate of the second (Figs. 238, 239, etc.). More commonly a nucleus is reconstructed during the interkinesis; but in many of these cases the chromosomes do not completely break up, the nucleus attaining only to a "semi-resting" stage in which the chromosomes, or at least a spireme-like condition, can still be recognized (p. 532). At the close of the second division a true "resting-nucleus" is almost always formed, which in the oögenesis is always much smaller than the original oöcyte-nucleus or "germinal vesicle" (Fig. 189, 237).

During the foregoing process the number of chromosomes has been reduced to one-half, *i. e.*, from the diploid to the haploid number. The only exceptions to this occur in the diploid type of parthenogenesis and in the spermatogenesis of haploid animals (pp. 789, 797).

2. In Plants

Externally meiosis in plants offers a more involved aspect owing to the complications introduced by the alternation of generations (p. 492). Among the thallophytes, as later described (p. 627) there are cases in which the haploid and diploid generations are separate plants, closely similar in general appearance and differing little save in respect to the reproductive organs and the number of chromosomes (p. 627). In higher plants a progressive series can be traced in the reduction of the sexual generations (gametophyte) until it becomes a vestigial structure. In the seed-plants it wholly loses its chlorophyll and becomes a minute and as it were parasitic structure within the sporophyte, represented by the products of the embryo-sac (megaspore) or of the pollen-grain (microspore), and in the higher forms loses in greater or less degree its internal cell-walls so as to become syncytial, at least in its earlier stages. The reduction of the male gametophyte goes much further than that of the female, and in the seed-plants it is represented only by the pollen-tube, containing a few nuclei. The climax is reached in the angiosperms, where previous to fertilization the female gametophyte commonly contains but eight nuclei and sometimes but four, including that of the egg, and the male but three, including two generative or sperm-nuclei (Figs. 216, 308).[1] A slight further reduction would lead to the disappearance of the gametophyte or

[1] By some botanists the male gametophyte is regarded as having been reduced to a single antheridium which produces two gametes.

haploid generation as such and thus produce a condition essentially like the gametic reduction seen in animals.[1]

The foregoing series in respect to the evolution of the gametophyte is accompanied by an interesting parallel series in the spore-formation. Like

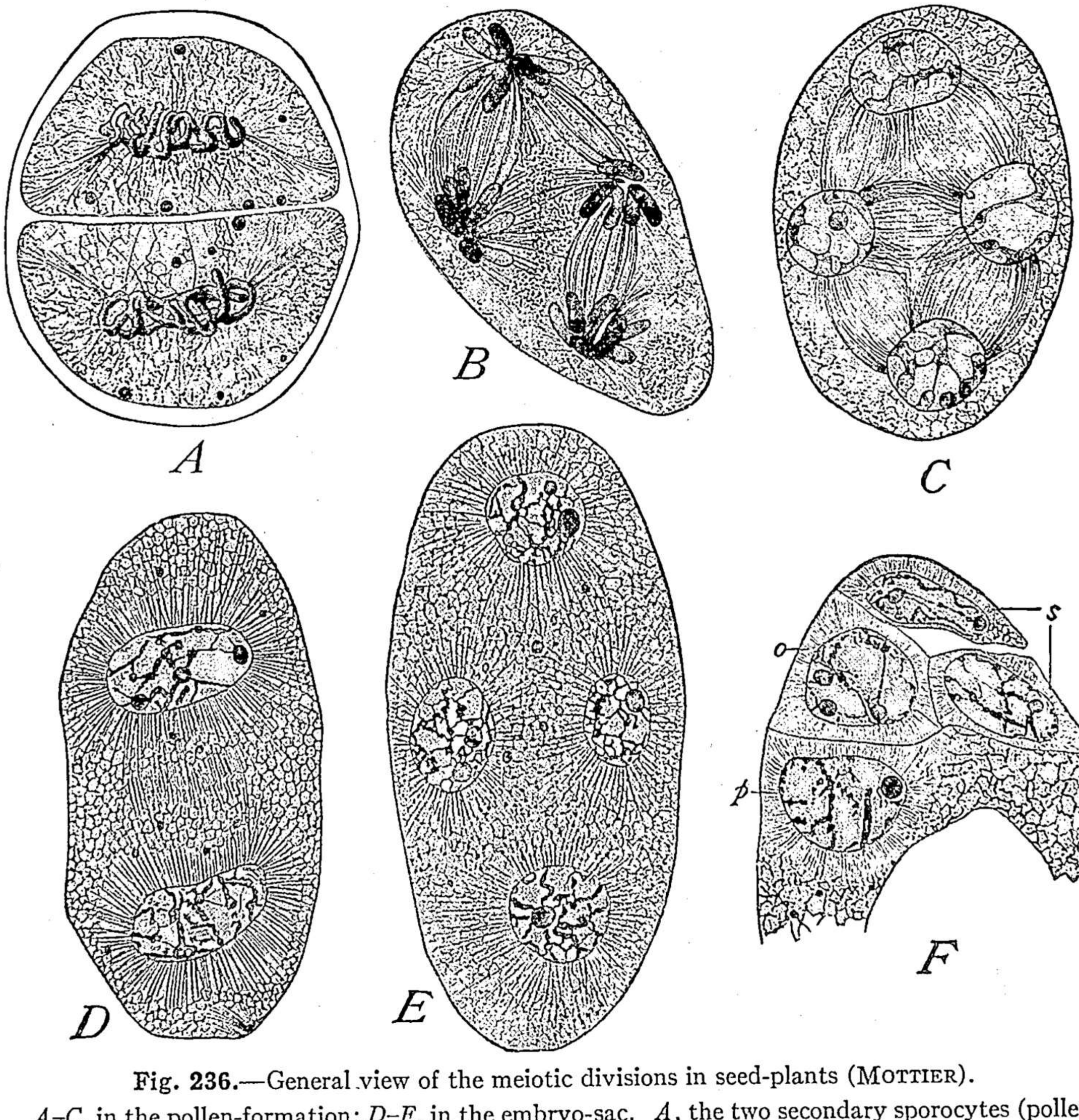

Fig. 236.—General view of the meiotic divisions in seed-plants (MOTTIER).

A–C, in the pollen-formation; *D–F*, in the embryo-sac. *A*, the two secondary sporocytes (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 *o*, ovum; *p*, upper polar cell; *s*, synergidæ.

the gametes the spores are typically formed in quadruple groups or quartets. Lower plants generally (*e. g.*, algæ, bryophytes or ferns) are *isosporic*, *i. e.*, the four members of each quartet show no morphological differences; but even here the work of Blakeslee, the Marchals and others has proved that

[1] This comparison is further developed at p. 621.

in some cases the spores are physiologically already predetermined as male-producing or female-producing (p. 746). In higher plants, beginning in some of the pteridophytes (*Selaginella*, *Isoëtes*, *Marsilia*) isospory gives way to heterospory, in which a sexual predetermination appears in the size of the spores, which are differentiated into larger female-producing megaspores and smaller male-producing microspores.[1] Of this type are all seed-plants, the megaspore being represented by the primary embryo-sac, the microspore by the pollen grain. In the evolution of the heterosporic forms we find, finally, a pretty analogy to the egg with its three polocytes; for here, too, one cell of each quartet becomes larger than the others and it alone becomes a functional spore.[2] Typically the mother-cell (primary megasporocyte) undergoes two meiotic divisions to form a linear series of four cells, of which, as a rule, only the innermost becomes the functional megaspore or embryo-sac. Not uncommonly, however (as in *Lilium* and some other monocotyledonous plants), the quartet-formation is suppressed, the meiotic divisions producing no more than a quartet of nuclei within the primary sporocyte, which is itself directly converted into the embryo-sac (Figs. 236, 308). In this case a third and last division produces eight nuclei (cells) of which one is the egg while the other seven give rise to the synergidæ, polar nuclei and antipodal cells. In this case, too, but one of the four original products of the meiotic divisions normally gives rise to the egg.[3]

III. INTERNAL PHENOMENA OF MEIOSIS

A. Introduction

1. Historical and Theoretical

We need not here consider the earlier and unsuccessful attempts to interpret meiosis (in case of the polocyte-formation in oögenesis) as a factor in sex-production.[4] Of greater interest was the view of Weismann ('87) that only the second meiotic division is concerned in reduction, based on the fact that in diploid parthenogenesis (as in the daphnids or aphids), where no reduction takes place, the second polocyte fails to be formed (p. 468). The first polocyte, Weismann therefore argued, plays no part in reduction, but merely removes from the egg an "histogenetic" plasm, so as finally to transmit only germ-plasm. This hypothesis evidently breaks down in the case of spermatogenesis and is also disproved by more recent cyto-

[1] This presents an interesting analogy to the differentiation of the eggs of certain animals (rotifers, phylloxerans, *Dinophilus*) into larger female-producing and smaller male-producing forms. *Cf.* p. 806.

[2] For a further development of this comparison see p. 620.

[3] See p. 496.

[4] See Minot ('77), Balfour ('80), Van Beneden ('84) and for criticisms Nägeli ('84), Strasburger ('84) and Weismann ('85).

logical observations which show that both meiotic divisions may be concerned in reduction (p. 573). Nevertheless it is quite possible that Weis-

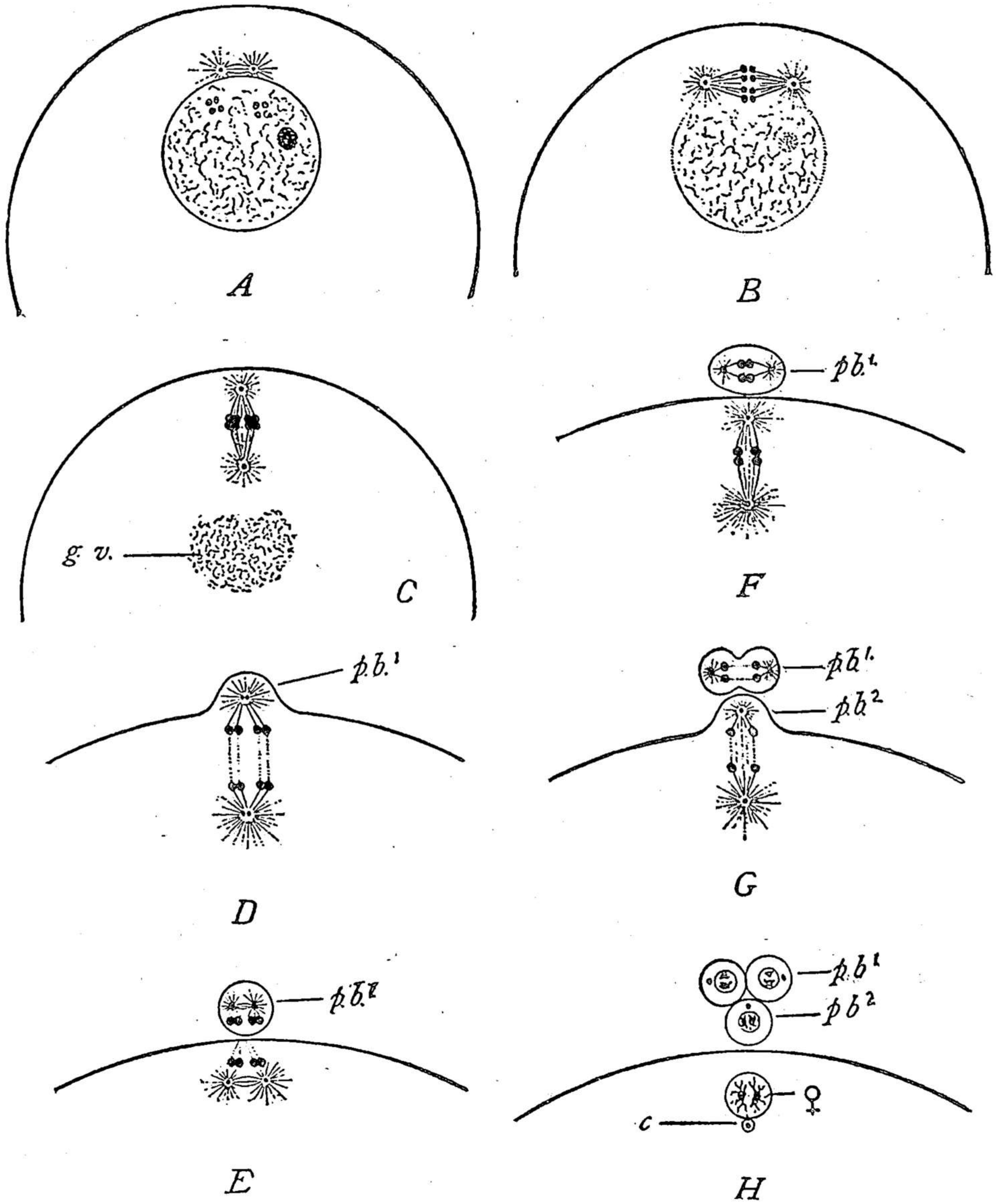

Fig. 237.—Diagrams showing the essential facts in the meiosis of the egg. The diploid number of chromosomes is supposed to be four.

A, initial phase; two tetrads in the germinal vesicle; *B*, *C*, the first polar spindle; *D*, *E*, formation of the first polocyte; *F*, *G*, the second division; *H*, final result; three polocytes and the egg-nucleus (♀), each containing two single chromosomes (half the diploid number); *c*, the egg-center which now disappears from view.

mann's suggestion contained a nucleus of truth; for we have thus far no other clue to the meaning of "diminution" (p. 323), nor have we as yet

any more satisfactory explanation of why two meiotic divisions should take place instead of one.

Many of the earlier writers either ignored the chromosomes as such or relegated them to a position of comparative unimportance in the discussion of the reduction-problem. Some of them treated the problem as merely or mainly a quantitative one; but this position quickly proved untenable. As will later be shown, however (Chap. XII), modern research has proved the hopeless inadequacy of any analysis that does not reckon with the chromosomes as leading factors in the problem.

The first fruitful attempt to analyze the internal phenomena of reduction was made on purely theoretical grounds by Weismann ('87) in one of those brilliant essays on heredity which contributed in so important a way to the enlargement of our views concerning cytological research. Roux had argued ('83) that the transformation of the nuclear substance into long threads, and their division by longitudinal splitting can only mean that in some sense or other this substance must embody many different "qualities" that assume a linear alignment in the threads. Splitting of the threads thus insures not merely a mass-division of the nucleus as a whole, but beyond this a meristic division of all its constitutional "qualities." Upon this highly fruitful thought Weismann built an elaborate speculative system of pangenesis and development of which the basic assumption was that the nucleus consists of self-propagating units or "biophores" aggregated to form "ids," that are aligned like Roux's "qualities" in linear series in the spireme-threads and undergo division by splitting of the threads. Each "id" was assumed to possess the complete architecture of the germ-plasm, the "ids" differing slightly from each other in a manner corresponding to individual differences within the species. Each chromosome, therefore, represents a linear group of complete but slightly different germ-plasms. We now know that these particular conceptions concerning the "ids" were untenable; for the experimental work of Boveri on multipolar mitosis (p. 916) demonstrated that the whole chromosome group is necessary to the integrity of the germ-plasm even of a single individual. In principle, nevertheless, Weismann was right in urging that a process of reduction must periodically occur to counteract "the excessive accumulation of different kinds of hereditary tendencies or germ-plasms" which otherwise would so soon result from the periodic process of doubling in fertilization.[1] He was also right in the prediction that "there *must* be a form of nuclear division in which the ancestral germ-plasms contained in the nucleus are distributed to the daughter-nuclei in such a way that each of them receives only half the number contained in the original nucleus." Weismann indicated two

[1] *Cf.* Nägeli ('84, p. 224).

Fig. 238.—Formation of the polocytes in *Ascaris megalocephala*, var. *bivalens* (BOVERI).

A, the egg with the sperm 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 polocyte 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.

possible ways in which such a result might be effected, namely, either (1) by a form of division in which the chromosomes do not split length-

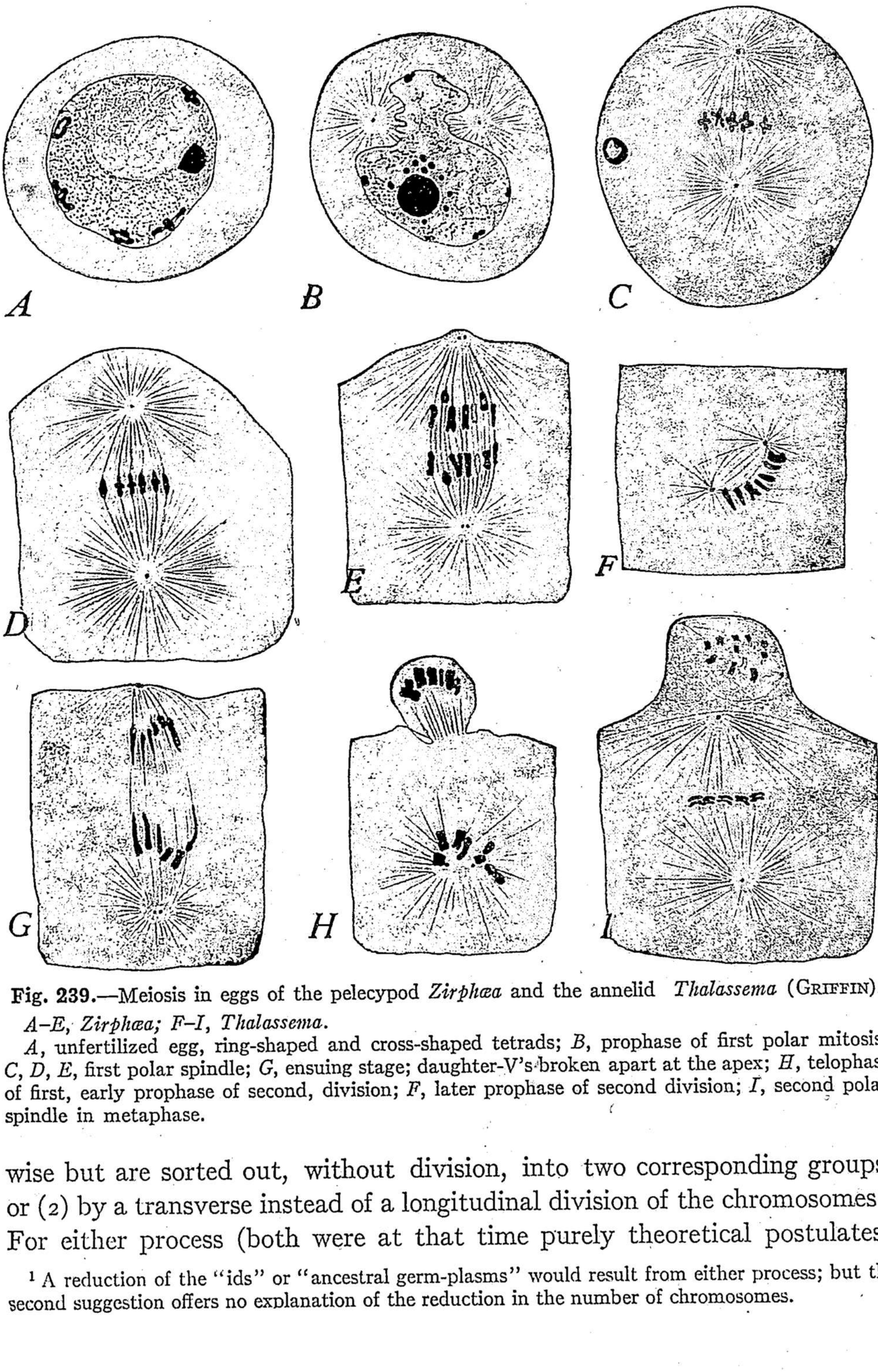

Fig. 239.—Meiosis in eggs of the pelecypod *Zirphæa* and the annelid *Thalassema* (GRIFFIN).

A–E, Zirphæa; F–I, Thalassema.

A, unfertilized egg, ring-shaped and cross-shaped tetrads; *B*, prophase of first polar mitosis; *C*, *D*, *E*, first polar spindle; *G*, ensuing stage; daughter-V's broken apart at the apex; *H*, telophase of first, early prophase of second, division; *F*, later prophase of second division; *I*, second polar spindle in metaphase.

wise but are sorted out, without division, into two corresponding groups, or (2) by a transverse instead of a longitudinal division of the chromosomes.[1] For either process (both were at that time purely theoretical postulates)

[1] A reduction of the "ids" or "ancestral germ-plasms" would result from either process; but the second suggestion offers no explanation of the reduction in the number of chromosomes.

he proposed the term *reduction-division* in contradistinction to the ordinary type or *equation-division*, in which longitudinal division of the whole chromosome takes place. In the case of the female he believed the reduction division to coincide with the second of the two maturation-divisions, and predicted that a corresponding type of division would also be found in the male.

The fulfillment of Weismann's prediction is one of the most interesting results of modern cytological research, though opinion is not yet unanimous in respect to the details of the process. From the start investigation of the problem has been confused by the emphasis that Weismann laid upon the supposed theoretic significance of a transverse division of the chromosomes, thus implying that a longitudinal division is *ipso facto* an equation-division. Some of the leading early investigators, such as O. Hertwig, Boveri and Brauer, found both maturation-divisions to be longitudinal, and were thus led to deny the occurrence of a reduction-division. The fallacy of this was demonstrated as it gradually became clear, especially through the work of Winiwarter ('00) and his successors, that what seems to be a longitudinal split may in reality be the separation of two chromosomes that have been associated side by side; and conversely, that a division that seems to be transverse may be only the final separation of such a pair (*cf.* p. 133). The apparent contrast between longitudinal and transverse division in meiosis thus in large measure loses its significance; and it becomes evident that the problem of the reduction-division cannot be solved by study of the actual meiotic-divisions alone but involves also the whole series of preceding events in the meiotic prophases.

2. Preliminary Outline

It is now widely held that reduction is initiated by a preliminary process or *synapsis* or *syndesis* in the course of which the chromosomes conjugate —or otherwise become closely associated—two by two to form *bivalents* or *gemini* (Figs. 102, 105). The two chromosomes of each pair, called *synaptic mates*, are in general alike in size and form (though there are some exceptions to this). There is the strongest ground for the conclusion that in each case the synaptic mates are respectively of paternal and of maternal descent (Montgomery) and that they are homologous (Montgomery, Sutton, Boveri). Conjugation of the chromosomes does not, however, in itself effect reduction. It is no more than a preliminary coupling or *pseudo-reduction* (Rückert) producing a haploid group of bivalents; and since each of these represents a pair of chromosomes the total number remains unchanged. Actual reduction first occurs in the course of one or the other of the meiotic divisions, when the two synaptic mates are disjoined by the "reduction-division," and pass into different germ-nuclei.

Thus far all is clear. The process just outlined is, however, complicated by the fact that sooner or later after synapsis each of the synaptic mates itself undergoes a "secondary" longitudinal split which represents a future equation-division. The bivalent thus becomes a quadripartite body or

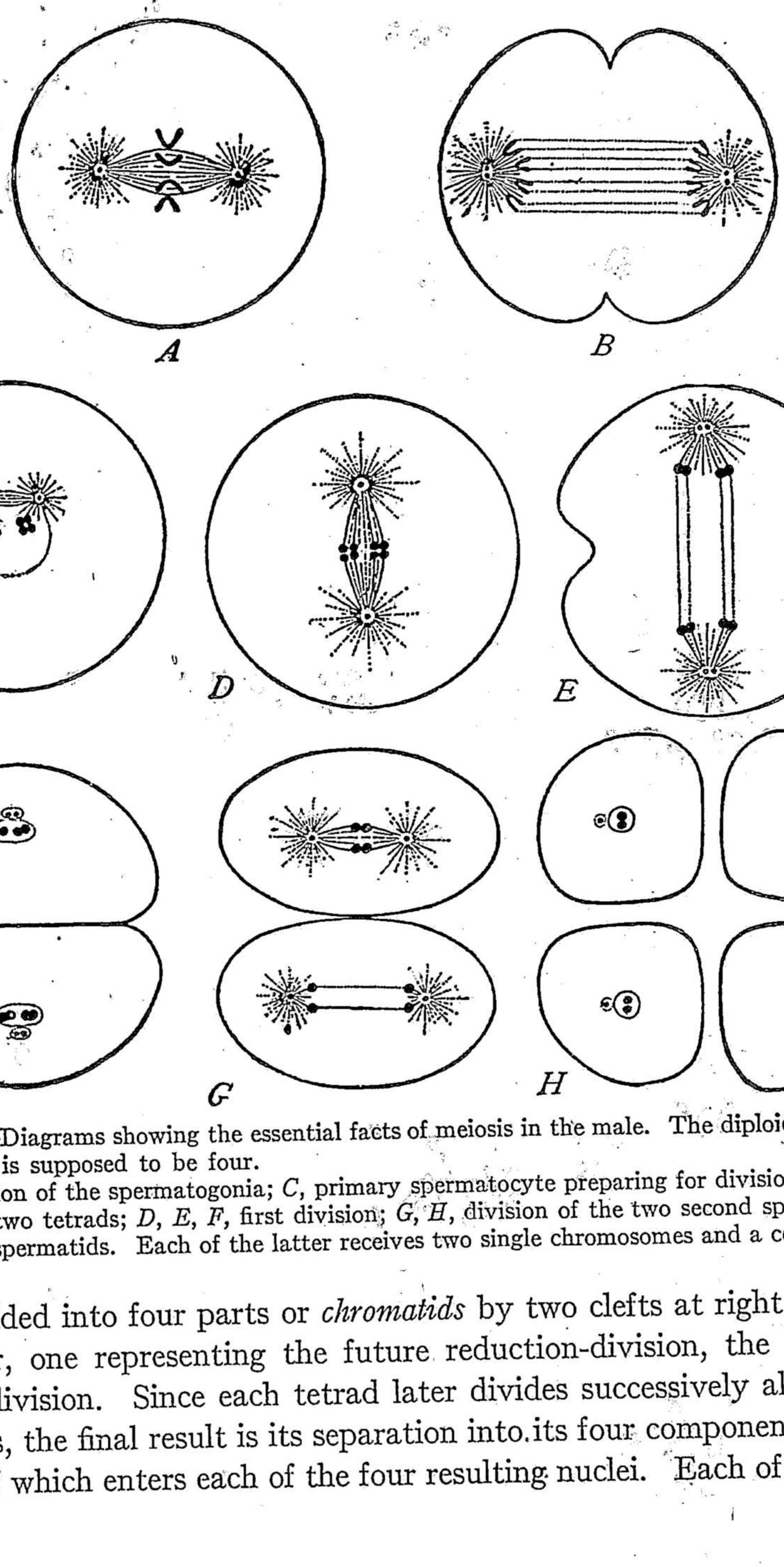

Fig. 240.—Diagrams showing the essential facts of meiosis in the male. The diploid number of chromosomes is supposed to be four.

A, *B*, division of the spermatogonia; *C*, primary spermatocyte preparing for division; the chromatin forms two tetrads; *D*, *E*, *F*, first division; *G*, *H*, division of the two second spermatocytes to form four spermatids. Each of the latter receives two single chromosomes and a centriole.

tetrad, divided into four parts or *chromatids* by two clefts at right angles to each other, one representing the future reduction-division, the other the equation-division. Since each tetrad later divides successively along these two planes, the final result is its separation into its four component chromatids one of which enters each of the four resulting nuclei. Each of the latter

thus receives a haploid group of single or univalent chromosomes (Figs. 237, 238, 240).

This process is readily made clear when schematized as follows: Let us designate the chromosomes of the diploid group by the letters *A*, *B*, *C*, *D*, *a*, *b*, *c*, *d*, etc., capitals representing chromosomes of maternal descent, and small letters those of paternal. Synapsis of the homologous chromosomes produces the bivalents *Aa*, *Bb*, etc., the number of which is of course half the original chromosome-number. By equational splitting of these arise the tetrads $\frac{Aa}{Aa,}\ \frac{Bb}{Bb,}$ etc., or (indicating the plane of apposition or synapsis) $\frac{A}{A}\Big|\frac{a}{a.}$ Division of such a tetrad along the vertical plane gives the two dyads $\frac{A}{A}$ and $\frac{a,}{a,}$ which then separate into the four single chromosomes *A*, *A*, *a*, and *a*, which finally enter four different gametes.

It is evident that if the original synaptic mates retain their identity during this process *each of them actually divides but once during the maturation-process*, namely, along the horizontal plane (second division) in the above diagram. This division, clearly, is an equation-division quite comparable to an ordinary somatic division. The other "division" of the tetrad, on the contrary, involves no actual division but only disjoins the two associated mates—a process which obviously meets all the theoretical demands of Weismann's postulate. This process takes place in every bivalent, and is not affected by variations affecting the order of division, the time at which the equational split makes its appearance, or of the particular mode in which the mates of each pair are connected. We can thus understand how tetrads of the most diverse forms give the same result in the course of the two divisions. This interpretation finds a striking confirmation in the maturation-divisions of organisms having only a haploid group of chromosomes, or of those in which the diploid number of chromosomes is odd; for example in certain types of mutants (p. 874), in the males of many insects (p. 750) or in forms having unpaired supernumerary chromosomes (p. 844).

So far as the actual divisions are concerned, and apart from all questions of hypothetical interpretation, the main facts concerning the structure of the tetrads and their history during the meiotic divisions are now perfectly well established. Existing differences of opinion relate almost solely to their earlier history. In particular the following questions demand critical examination: (1) Is the conception of synapsis and bivalence valid? Do corresponding chromosomes become associated two by two to form double chromosomes or bivalents? (2) If such be the fact, is the reduction-division

also a fact? Do the two conjugants or synaptic mates subsequently disjoin or separate? (3) Do they retain their identity throughout these operations? Each of these questions has long been debated. The reality of the whole conception of synapsis, bivalence and the reduction-division

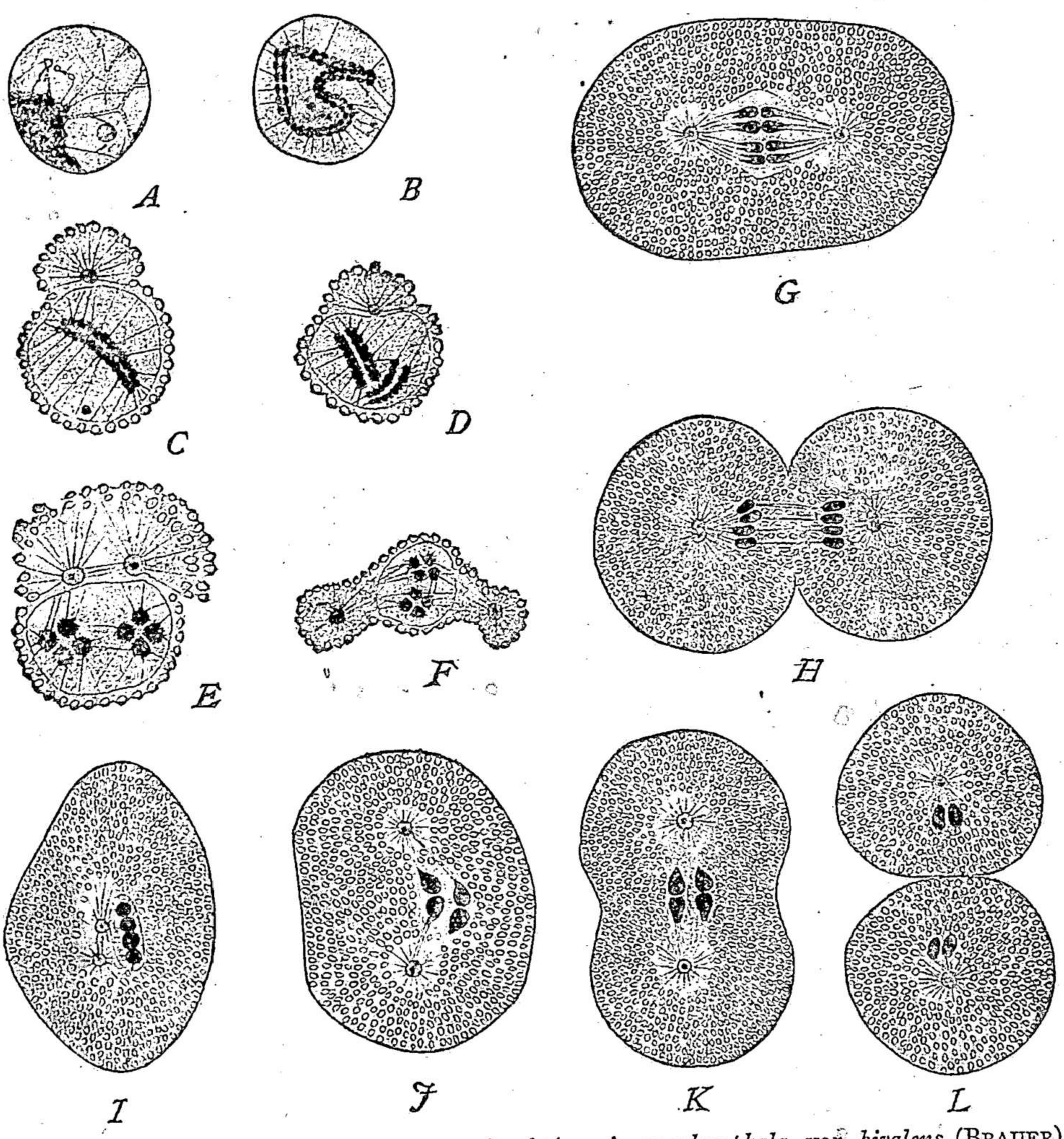

Fig. 241.—Reduction in the spermatogenesis of *Ascaris megalocephala*, var. *bivalens* (BRAUER).

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.

has been in effect denied (Meves, Fick, Della Valle, Champy, Regaud). Other cytologists, while accepting the fact of synapsis, have maintained that conjugation results in a complete fusion of the mates to form new chromosomes or *mixochromosomes* (Winiwarter, Bonnevie). Were this correct, the

conception of the reduction-division, in its original form, would fall to the ground. These negative conclusions, however, far overshot the mark; for both synapsis and disjunction (reduction-division) have now been demon-

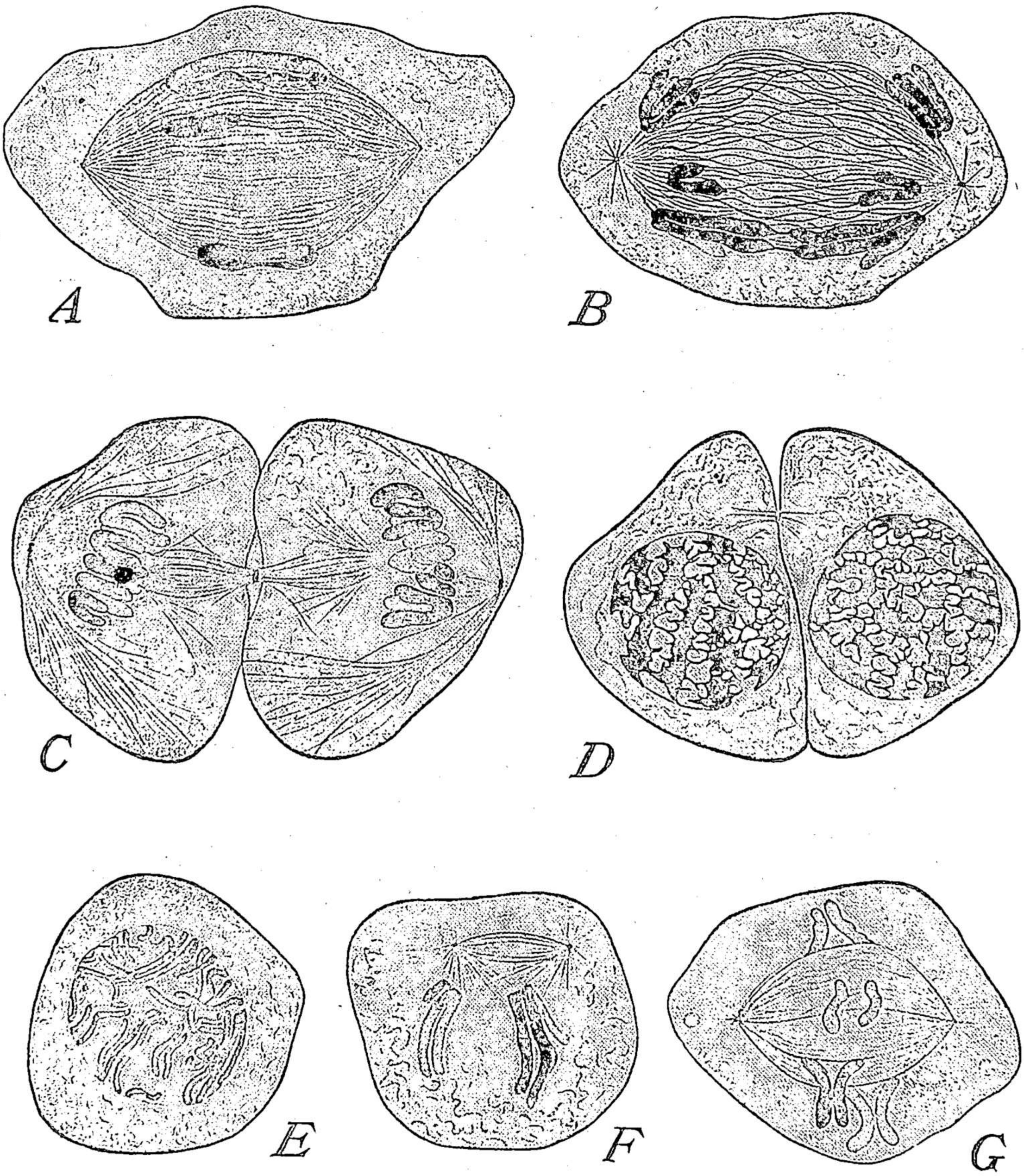

Fig. 242.—Spermatocyte-divisions in *Salamandra* (*E*, from FLEMMING, the others from MEVES). *A*, first (heterotypic) division in metaphase, showing heterotype rings; *B*, anaphase; longitudinal splitting of the daughter-loops; *C*, telophase, *D*, ensuing pause; *E*, early prophase of second division with longitudinally divided segmented spireme; *F*, later prophase; *G*, metaphase of second division.

strated in the case of certain particular chromosomes with a clearness that leaves nothing to be desired. On the other hand, genetic evidence has of late given the strongest grounds to conclude that definite exchanges of

material often take place between the synaptic mates (by "crossing over," p. 942) during the period of their close association in synapsis. To whatever extent this occurs the chromosomes separated by the reduction division are no longer identical with those that conjugated in synapsis. As will later be shown, however, these exchanges do not destroy the homology between the synaptic mates nor the principle of disjunction in meiosis. For the moment, therefore, they may be disregarded.[1] An important question, still to a certain extent in doubt, concerns the mode of synapsis. Evidence has steadily accumulated to show that in a large class of cases synapsis involves a side-by-side union of the synaptic mates (*parasynapsis* or *parasyndesis*) instead of an end-to-end union (*telosynapsis* or *metasyndesis*) as was formerly supposed; but an important group of observers still hold to the latter interpretation, particularly in case of the higher plants (p. 557). It is possible that both modes occur, and even possible that both may coexist in the same species.

3. General Characteristics of the Divisions

The meiotic divisions are distinguished from the ordinary somatic mitoses by certain marked peculiarities of the chromosomes and sometimes also of

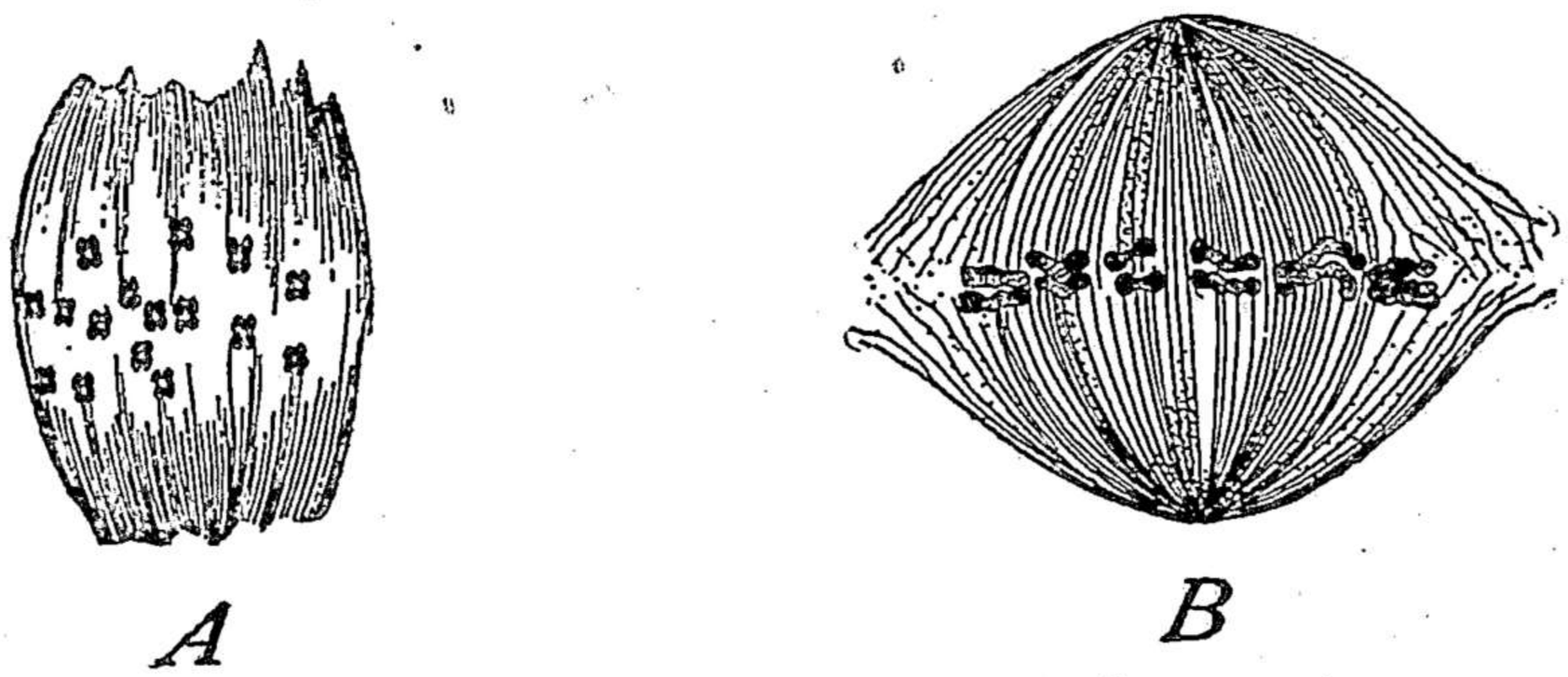

Fig. 243.—Anastral polar spindles.

A, first polar spindle with tetrads, in *Heterocope* (HÄCKER); *B*, second polar spindle in *Triton* (CARNOY and LEBRUN).

the achromatic figure. Among the latter may be mentioned the fact earlier referred to (p. 150) that in the eggs of certain animals the polar mitoses are of the anastral type. In these cases the spindle is typically barrel-shaped, having truncated or rounded ends, and is formed by a direct transformation of the substance of the germinal vesicle (Figs. 238, 243). Such spindles are seen in the oögenesis of *Ascaris* (Van Beneden, Boveri) of copepods (Haecker, Rückert), insects (Henking), tunicates (Crampton, Golski, Conklin), *Amphioxus* (Sobotta), and many vertebrates.[2] The absence of asters is a

[1] *Cf.* p. 572.

[2] See Van Beneden ('87), Boveri ('87, '88), Haeckel ('95a), Rückert ('94), Henking ('92), Sabotta ('97), Conklin ('05a), etc.

noteworthy feature of these spindles because in these same forms the cleavage-figures, somatic divisions, and the spermatogenetic divisions of the male, are characterized by the presence of conspicuous asters and central bodies. Such anastral spindles are somewhat exceptional; and in many forms (platodes, annelids, mollusks) the polar mitoses offer very fine examples of the amphiastral type (Fig. 239, etc.). In higher plants, also, differences often appear between the meiotic and the somatic divisions in respect to the achromatic figure, the former being in general characterized by the multipolar type of spindle-formation, the latter, as a rule, by the formation of polar caps (p. 153). Of the meaning of these differences nothing as yet is known.

For the problems of meiosis the important peculiarities of the meiotic divisions appear in the chromosomes, especially during the prophases and later stages of the first division, and are so marked as to have led to the designation of this division as *heterotypic* (Flemming, '87). In the second or *homeotypic* division the chromosomes approach much more closely in type to those of the somatic divisions.[1]

The most salient peculiarities of the heterotypic division are as follows:

(1) The number of heterotypic chromosomes [2] is seemingly haploid; but when we consider the composition of these chromosomes, it becomes evident that this appearance is deceptive. The actual reduction has not yet occurred; for each heterotypic chromosome represents two gonial chromosomes (synaptic mates) in close association. The total number of originally single chromosomes is therefore still diploid.

(2) In most cases, perhaps in all, each of the synaptic mates thus associated in pairs is now itself longitudinally split. Each bivalent as already explained, has thus become a quadripartite *tetrad*, consisting of four components or *chromatids*. The total number of chromatids is therefore tetraploid or double the diploid number, precisely as is the case in an ordinary somatic metaphase, when each chromosome of the diploid group is longitudinally split. This split is generally regarded as the forerunner of the equation-division. It makes its appearance early in the meiotic process—sometimes soon after synapsis, in some cases possibly even earlier—but often becomes obscured in later stages so that it is sometimes not clearly evident before the heterotypic metaphase, or even the anaphases. The earlier history of these chromosomes indicates, however, that they are probably always

[1] Flemming employed these terms in a purely descriptive sense without regard to the problem of meiosis in the modern sense. Since then the heterotypic division has been so widely identified with the reduction-division that the two terms have come to be used almost as synonyms. As will later appear (p. 572), this usage is inadmissible; and the word heterotypic will here be used, as it was by its author, merely as a convenient descriptive term to designate the first meiotic division.

[2] For the sake of brevity each separate chromatin-mass in this mitosis will be spoken of as a "chromosome," whatever be its actual composition.

quadripartite in internal structure even when this escapes the eye. We shall therefore speak of them indifferently as bivalents or tetrads as may be convenient, the former term indicating their mode of origin, the latter their prospective value and in most cases their visible structure.

(3) The bivalents (or tetrads) are of many different forms, some of which differ widely from those seen in the somatic divisions. They result from

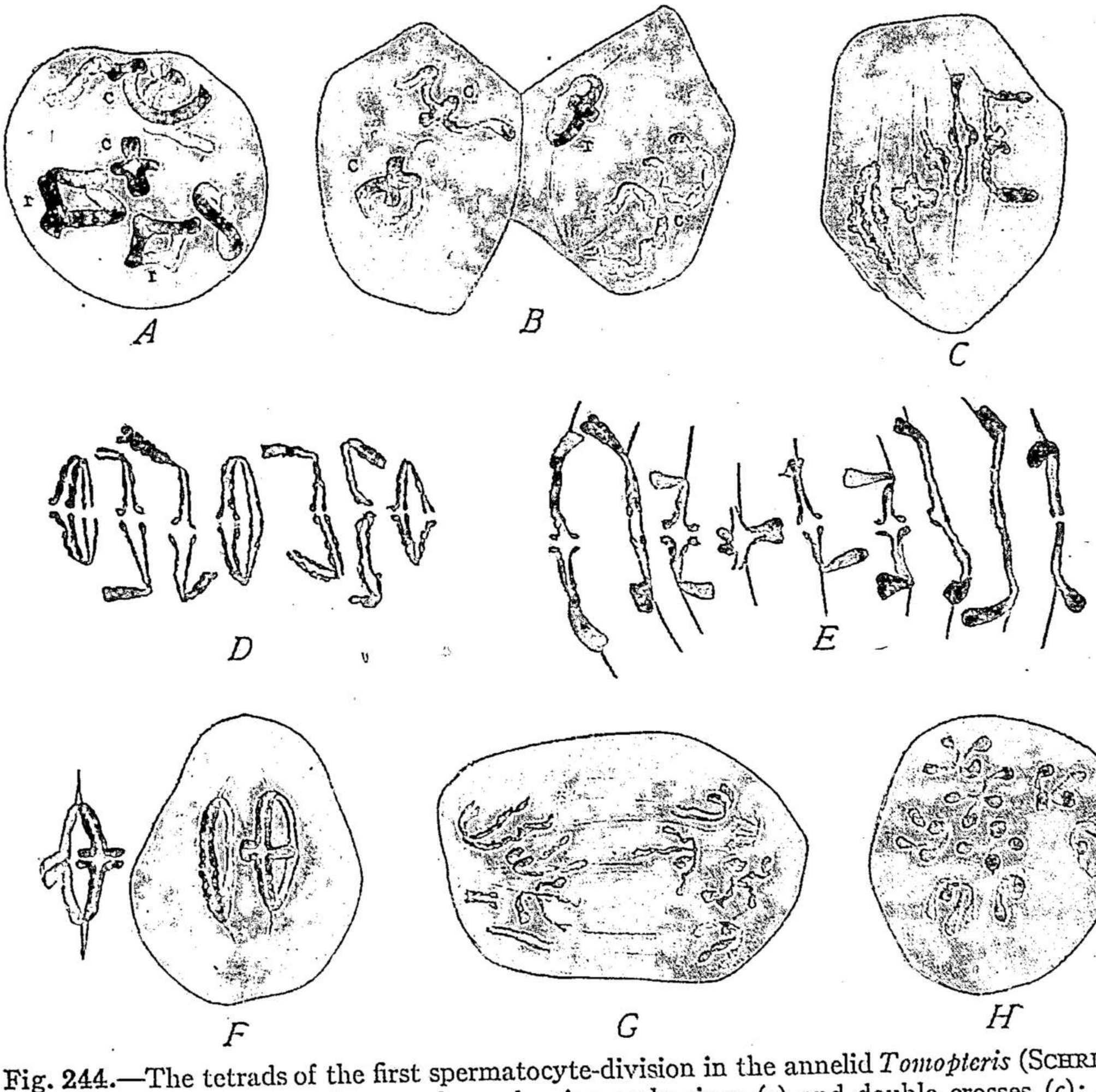

Fig. 244.—The tetrads of the first spermatocyte-division in the annelid *Tomopteris* (SCHREINER). *A*, first spermatocyte prophase-nucleus, showing early rings (*r*) and double crosses (*c*); *B*, two slightly later nuclei; *C*, five of the tetrads of the first spindle, showing ring, double cross, transverse rod-tetrads and *E* figure; *D*, seven of the tetrads from another spindle; *E*, all of the nine tetrads from another spindle, showing various forms of rod-tetrads and double-crosses; *F*, three varieties of the rings at metaphase; *G*, anaphase of first division, showing various forms of anaschistic dyads; *H*, interkinesis, with dyads.

processes that begin early in the prophases (diakinesis) and undergo various modifications as the divisions proceed. The most characteristic of these forms are rings (especially emphasized by Flemming) and cross-shaped figures; but V-shaped and hook-shaped figures and a great variety of others may also appear, differing more or less from species to species and to a certain extent characteristic of particular tetrads (Figs. 242, 244, 255). The analysis of

these various figures has proved a laborious and protracted task but, in the main, order has now been brought out of the former chaos.

B. The Heterotypic Division

Introductory [1]

It is now generally agreed that the heterotypic chromosomes are always derived from more or less elongated spireme-threads that are longitudinally double from an early period (*diplonema*, p. 544), and sooner or later longitudinally quadripartite (Figs. 268, 436, etc.). The primary longitudinal cleft is generally regarded as representing the synaptic plane along which two synaptic mates have conjugated side-by-side, and the secondary cleft as an equational splitting of each of these mates. In the later stages of the growth-period the double (or quadruple) threads condense, shorten, become intensely basophilic, and typically tend to take up a peripheral position near the nuclear membrane. The period thus marked is generally called the *diakinesis* (Haecker), and in a broad sense it corresponds to the later prophases of an ordinary somatic mitosis. It is important to bear in mind that the process of condensation varies widely both in rate and in degree among different species. For instance, in *Tomopteris* (Fig. 244) it never proceeds as far as in *Ascaris* (Fig. 238) or in Hemiptera (Fig. 369), while intermediate conditions are found in the urodeles (Fig. 242) or in many of the seed-plants (Fig. 252). In *Tomopteris*, therefore, the tetrads enter the metaphase group at a stage which in *Ascaris* or the insects only appears at a much earlier period, during the prophases. Cases of the *Tomopteris* type are of great importance for an exact analysis of the mode of division of the tetrads, for in many cases this is impracticable without tracing the whole earlier history of the bivalents. It will be understood, therefore, that the following account of the bivalents takes into account the earlier stages as well as the metaphase.

1. The Heterotypic Chromosomes. Forms and Spindle Attachments

The diversity of form displayed by the heterotypic chromosomes arises early in the diakinesis and becomes more marked as the prophases advance. It is due to two distinct causes. One of these is correlated with corresponding differences in mode of attachment to the spindle-fibers. The studies of many observers have made it clear that these differences are approximately constant and result from corresponding differences present already

[1] This introductory sketch is based on the conditions observed in animals generally, leaving out of account for the moment the process of synapsis by loop-formation advocated especially in the case of higher plants by Farmer and Moore, Mottier and their followers. For an account of this, see p. 557.

in the diploid groups (somatic or gonial).[1] Thus in the case of any particular pair of synaptic mates the attachment as seen in the gonial groups whether terminal, median or intermediate, is found also in the tetrads resulting from their synaptic union, and in the resulting dyads of the second or homeotypic division (Figs. 245, 247, etc.). Remarkable examples of

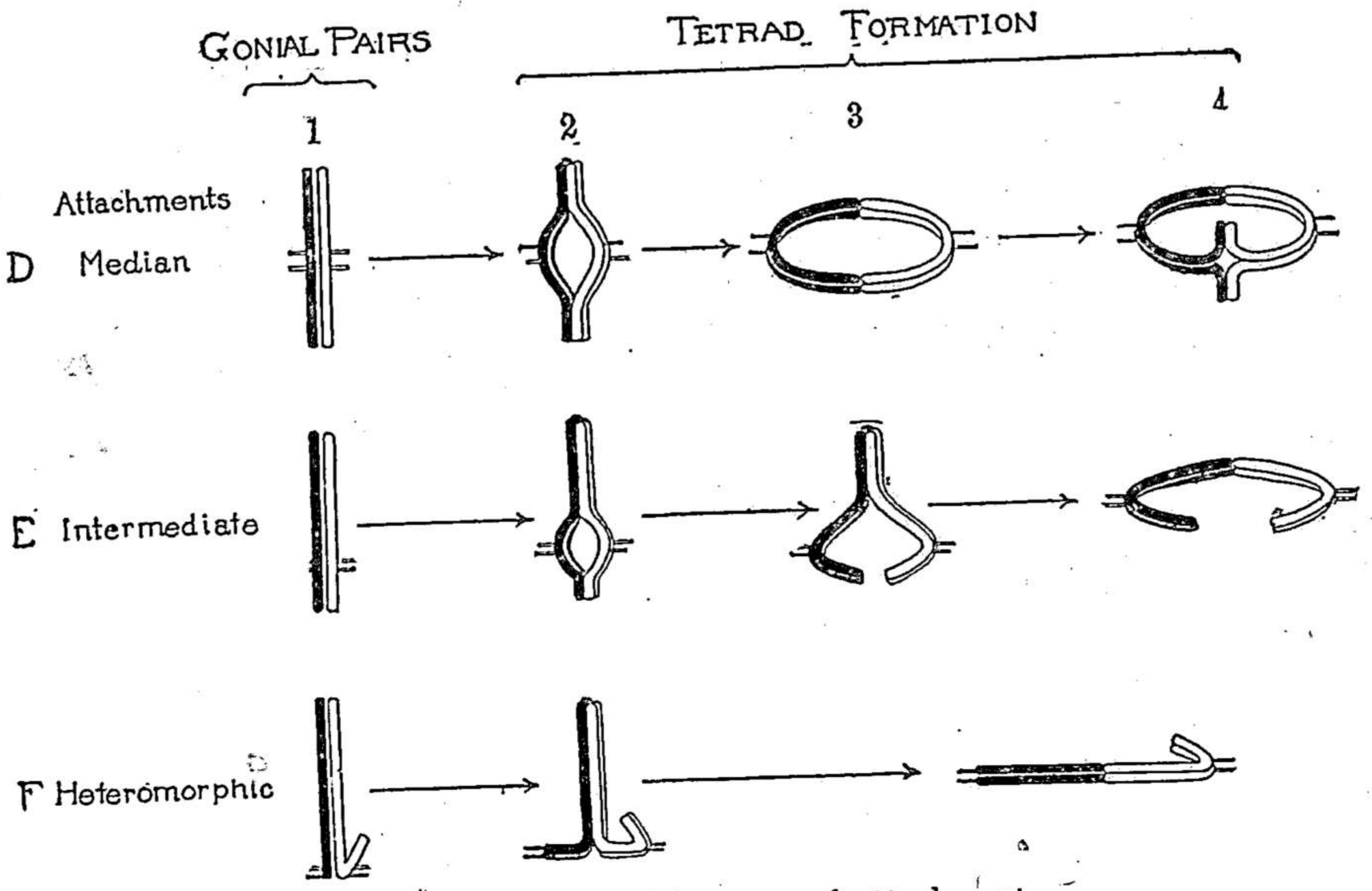

Fig. 245.—Atelomitic types of attachment.

D, median producing atelomitic or tangential ring (*Tomopteris* type); E, intermediate, producing unequal anaschistic Vs or J-shaped figures; F, heteromorphic, with both terminal and non-terminal attachment (*Trimerotropis* type).

this are offered in cases of chromosome-linkage (pp. 779, 879) or in heteromorphic tetrads (p. 571).

It is important to bear in mind the fact that some of the forms thus correlated with the spindle-attachments are assumed long *before the actual spindle-attachments have been established* (for instance in certain types double crosses and rings). We are thus led to recognize a second type of diversity due to various displacements of the tetrad-components (chromatids) with reference to one another, which in extreme cases completely alter their original form of association.[2] Rings, for instance, arise by the separation of the chromatids along the middle-region of one cleft while the ends remain united (Figs. 246, 257), double crosses by a related but different process (Fig. 254). The differences arising from both these causes appear

[1] For a discussion of this point see especially McClung ('14) and other works referred to in the following footnote.

[2] These changes have been studied by numerous observers, prominent among them Flemming ('87), Farmer and Moore ('95), Meves ('96), Janssens ('01, '03, '05, etc.), Sinéty ('01), Allen ('05), Grégoire ('99, '05, '10), the Schreiners ('06, etc.), Mottier ('03, '14, etc.), more recently by Robertson ('08, '16, etc.), Wilson ('12), McClung ('14), Mohr ('14), Wenrich ('16, '17), and others.

not only in the form of the heterotypic chromosomes but also in their apparent modes of division in the second or homeotypic mitosis. The feature common to all alike is the division of the bivalent (or tetrad) into two daughter-chromosomes or dyads, each of which is itself double, or soon becomes so, in preparation for the second division.

The various forms assumed by the heterotypic chromosomes are not merely haphazard fluctuations. Within certain limits they are character-

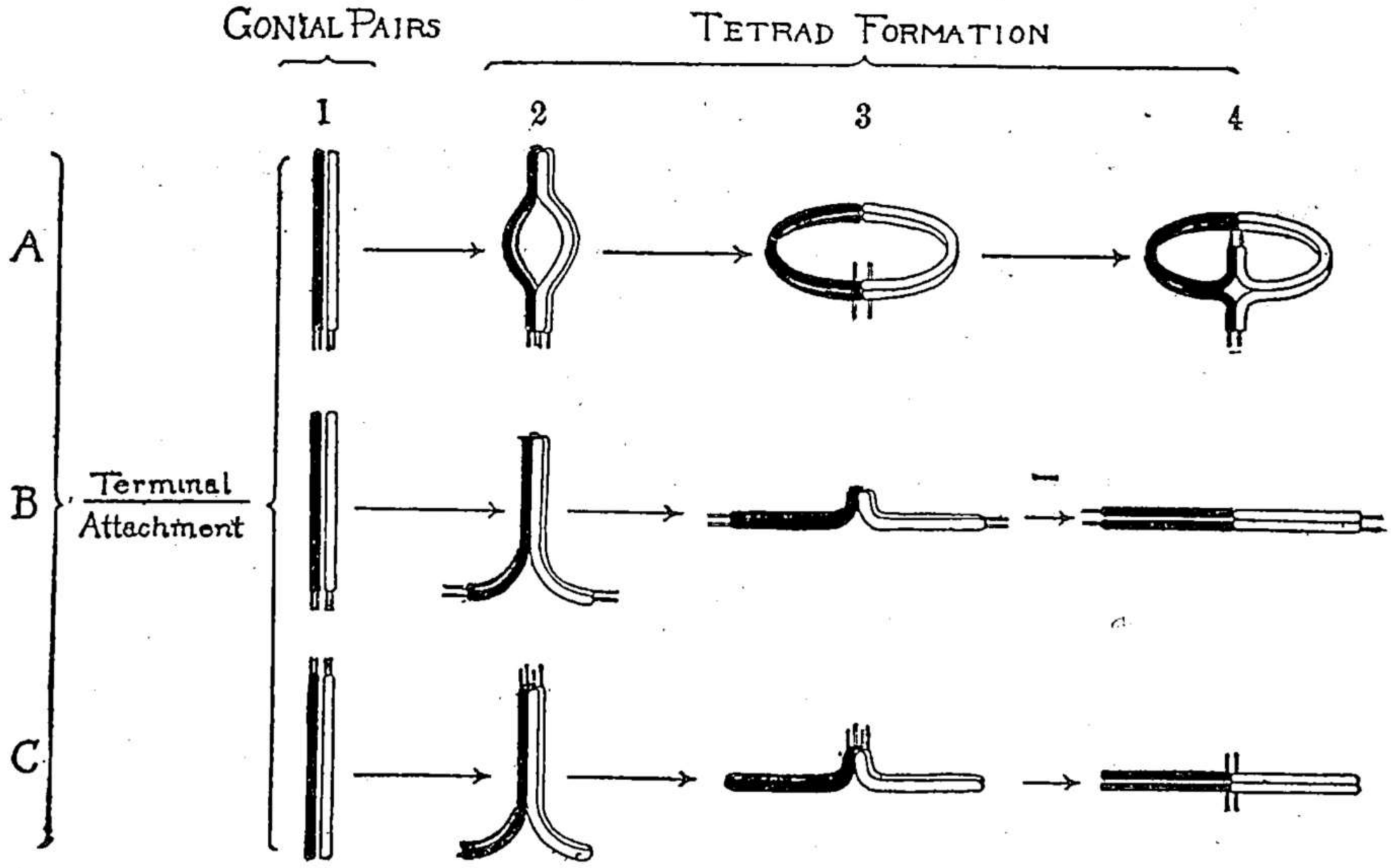

Fig. 246.—Terminal spindle-attachments in meiosis. In each case 1 represents the original gonial pair (synaptic mates) in parasynaptic association.

A, the formation of telomitic or equatorial rings (*Hippiscus* type); B, formation of transverse rod-tetrads with biterminal attachment (diaschistic) readily converted into double cross (Fig. 254); C, transverse rod-tetrad with apparently median attachment (diaschistic, *Mecostethus* type) convertible into diaschistic V by median flexure.

istic of particular bivalents as urged by Baumgartner ('04), Moore and Arnold ('05) and many later observers. Numerous cases have been observed in which certain individual bivalents are at once recognizable both by their size and form (p. 834). On the other hand, it has been clearly shown, by studies especially on insects (Orthoptera, Hemiptera) that a considerable range of variation often exists in the external form of particular tetrads. Robertson, McClung and others have shown that sometimes the number of rings may vary materially in different cells of the same individual. Rings and V's are, however, closely related forms, as is proved by their mode of formation; and all the facts point to the conclusion that each bivalent conforms to its general type, *provided its whole history be taken into account*. Many examples of this will hereafter be given in connection with various related topics such as the spindle-attachments (p. 516), random assortment (p. 931) and the individuality of the chromosome (p. 828).

In comparing the various forms of tetrads as seen in the late diakinesis or metaphase it is convenient to recognize two types that *seem* to differ widely in respect to the relation of the two cleavage-planes along which they are destined to divide. These may be designated as A and B. In A (*Ascaris*, vertebrates generally, many higher plants) both divisions are plainly longitudinal with reference to the spireme-thread (diplotene) from which the tetrad arises (Fig. 249); while in B (common among insects) but one division

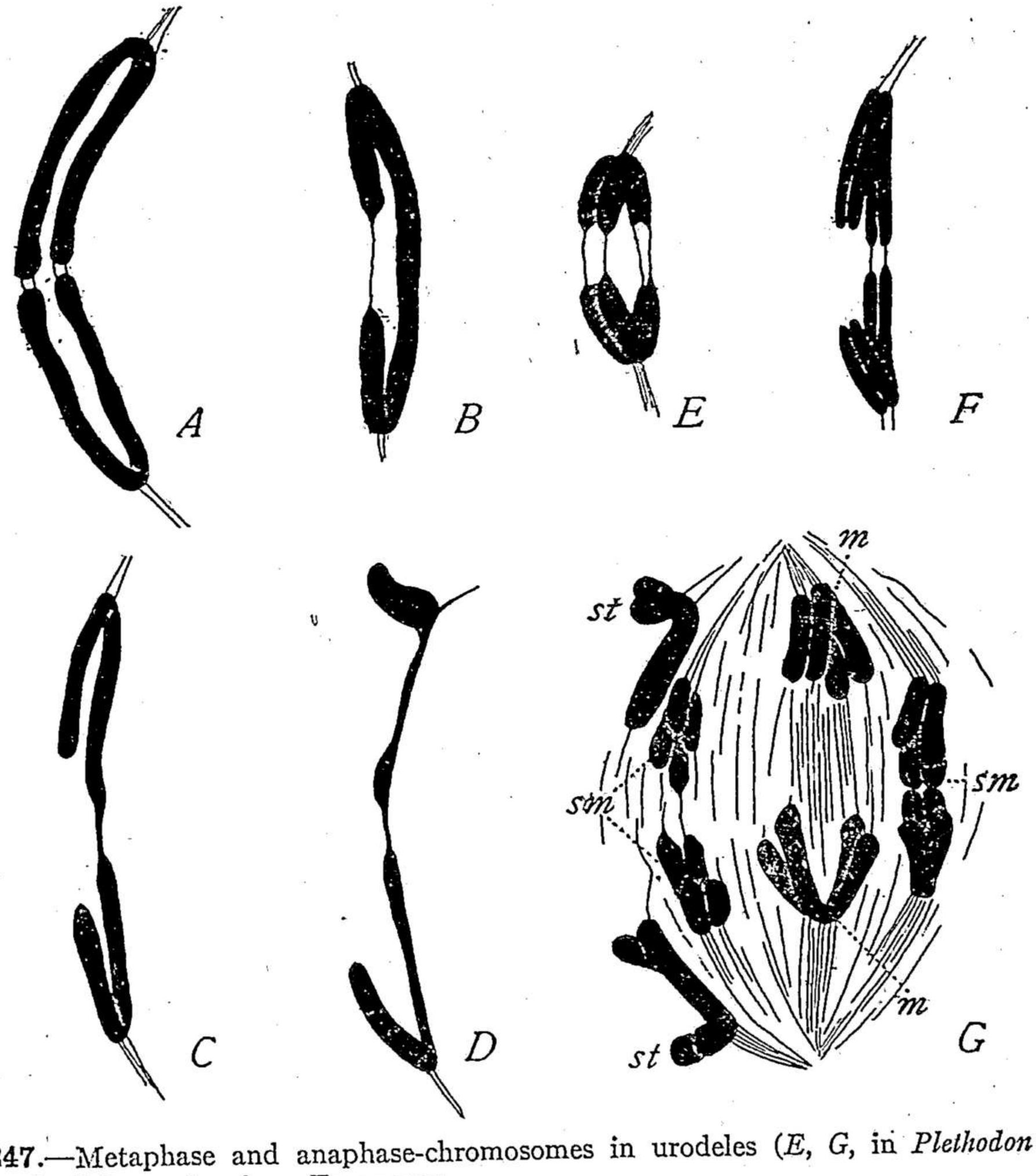

Fig. 247.—Metaphase and anaphase-chromosomes in urodeles (*E*, *G*, in *Plethodon* original), the others in *Salamandra*, from FLEMMING.

A, ring with median attachment; *B*, *C*, sub-median attachments; *D*, nearly sub-terminal attachment; *E*, ring, median attachment with secondary (equational) split; *F*, similar form, sub-median attachment; *G*, anaphase-figures, non-terminal attachments, giving anaschistic V's and J's (*s*, *t*, sub-terminal; *s*, *m*, sub-median; *m*, median).

is longitudinal and the other apparently transverse (Fig. 251). This difference, now known to be of quite secondary importance, was overemphasized by earlier writers because of the emphasis laid by Weismann on transverse division as a possible mode of reduction (p. 502). By Korschelt and Heider ('03) the two types were distinguished as *eumitotic* (A) and *pseudo-*

mitotic (B); by Farmer and Moore ('05) more appropriately as *anaschistic* (A) and *diaschistic* (B). The former terms are obsolete. Those of Farmer and Moore have never come into general use but nevertheless have a certain utility for descriptive purposes. They must not, however, be taken to imply any important distinction; for it is now certain that in a large class of cases the so-called transverse or cross-suture of the tetrad in type B *only marks the final separation-point of chromatids that originally lay side-by-side.* In this respect such tetrads are precisely analogous to the later stages of somatic rod-shaped chromosomes having terminal attachments (p. 133). Whether this is true of all tetrads of this type is still an open question. With this distinction in view we may briefly review some of the more important forms of tetrads, and their modes of division.

2. Course of the Division

a. Rod-tetrads. These forms, widely distributed among both plants and animals, have the form of rods or threads, always longitudinally double, the two longitudinal halves sometimes more or less separate, sometimes united at one or both ends to form loops or elongate compressed rings, in either case sometimes more or less twisted about each other (a remnant of the strepsinema, Fig. 250). They may be of either type A (anaschistic) or B (diaschistic) showing, in the first case two longitudinal clefts, in the second one longitudinal cleft and one transverse suture at the middle point. These two cases may conveniently be distinguished as "longitudinal" and "transverse" rod-tetrads.

(a^1). *Anaschistic or Longitudinal Rod-tetrads.* Tetrads of this type are widely distributed in both animals and plants and may be treated as the fundamental form from which most others may readily be derived. The classical example of such tetrads is offered by *Ascaris megalocephala*, made known by the pioneer works of Van Beneden ('84), Boveri ('88), O. Hertwig ('91) and Brauer ('93), in which the tetrads at first consist of four parallel threads or rods (Figs. 238, 241) which later condense to form very compact quadripartite bodies [1] in which the original long axis cannot be distinguished. More important for our analysis are the forms, often seen in *Tomopteris* higher plants, and in the urodeles and some other animals, which retain their elongate form at the time they pass upon the spindle. In these cases the secondary split is often obscure, so that the bivalent appears longitudinally double; the two halves are often separate throughout, but may be united at

[1] Various futile attempts were formerly made to treat tetrads of this type as pathological formations, as artifacts, as optical illusions, as exaggerated cases of conditions that exist also in the somatic chromosomes, etc.; but all this belongs to a bygone period.

one or both ends and sometimes twisted more or less about each other (Figs. 248, 250).

The history of these bivalents, which is of the most instructive nature, very clearly illustrates the diversity of form resulting from different modes of attachment to the spindle. Like those of the somatic chromosomes (p. 130), these attachments may be either median, intermediate or terminal, and in each case separation of the two halves always begins at the point of attachment, proceeding thence along the chromosome. This process leads

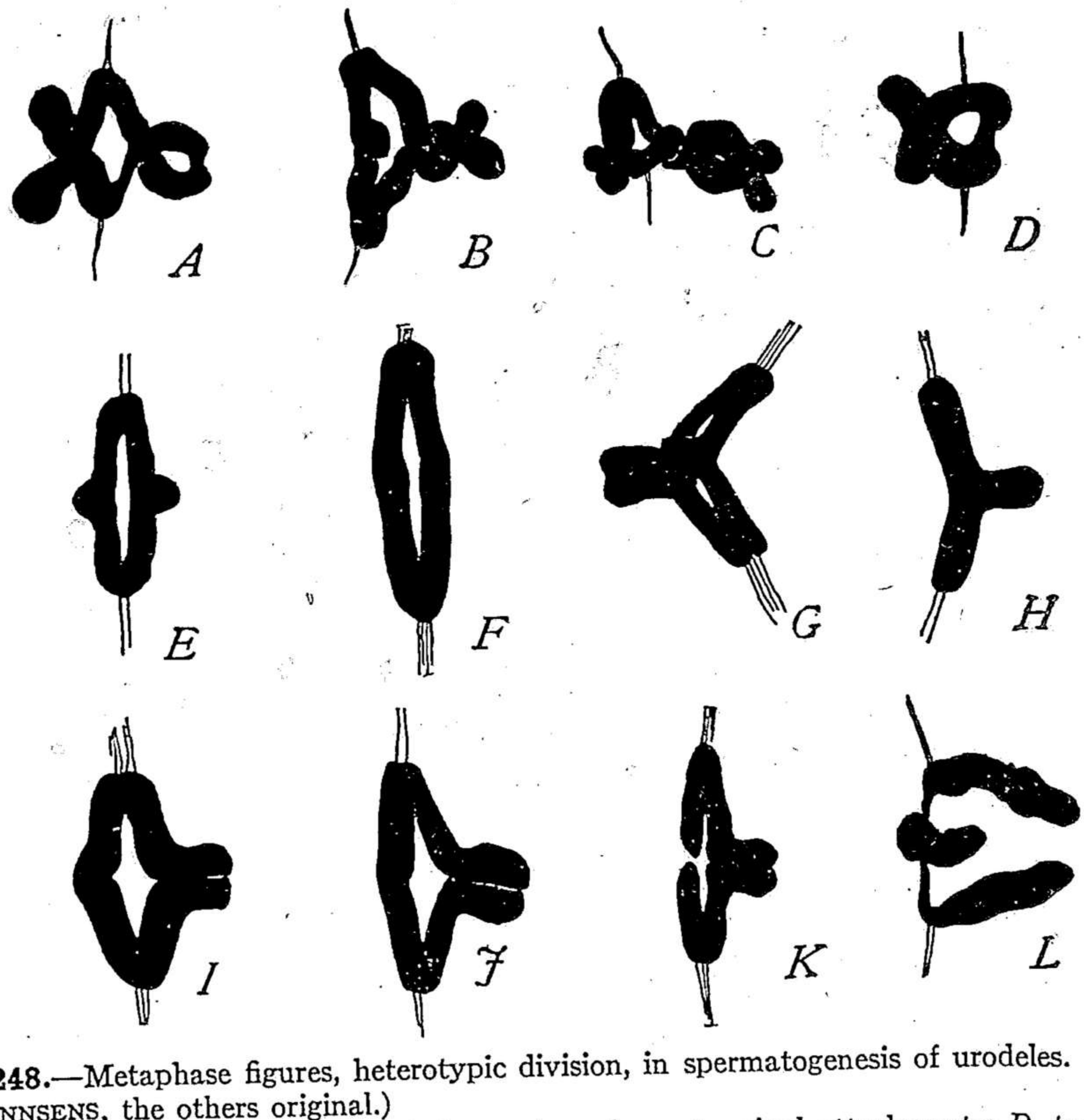

Fig. 248.—Metaphase figures, heterotypic division, in spermatogenesis of urodeles. (*A–D*, *L*, from JANNSENS, the others original.)

A–D, in *Triton*, twisted figures with free ends and non-terminal attachments; *D*, twisted loop, with two ends free; *E*, *F*, *Plethodon*, ring-figures; *G*, *H*, modification of ring-figure, giving cross-shaped figure with median attachment, in *G* seen obliquely, in *H* from one side; *I–K*, *Amphiuma*, ring-figures with sub-median attachments; *L*, *Triton*, *E-figure* resulting from forms like the preceding.

during the late metaphase and early anaphases to characteristic forms analogous to those seen in the somatic divisions modified in the heterotypic division only by the secondary split that is present in each half or makes its appearance as the division proceeds, as follows:

Median Attachment. In this case (as in the somatic divisions) the separating halves have the form of V's or U's connected by their ends to

form ◊-shaped or ring-shaped figures (Figs. 249, 251). These tetrads readily become converted into V-shaped forms by flexure at the point of attachment (Figs. 250, 253); and they differ from atelomitic ring-shaped forms only in that in the latter the separation of the two halves occurs already in the diakinesis (p. 547). Since their history during the anaphases is essentially the same in all these cases they need not at this point be separately described. As the apices draw apart in the initial anaphases the tetrads are drawn out into ◊-shaped or elongate ring-shaped figures which commonly show a transverse suture at the points where the two halves are connected; and often develop on one or both sides a prominent

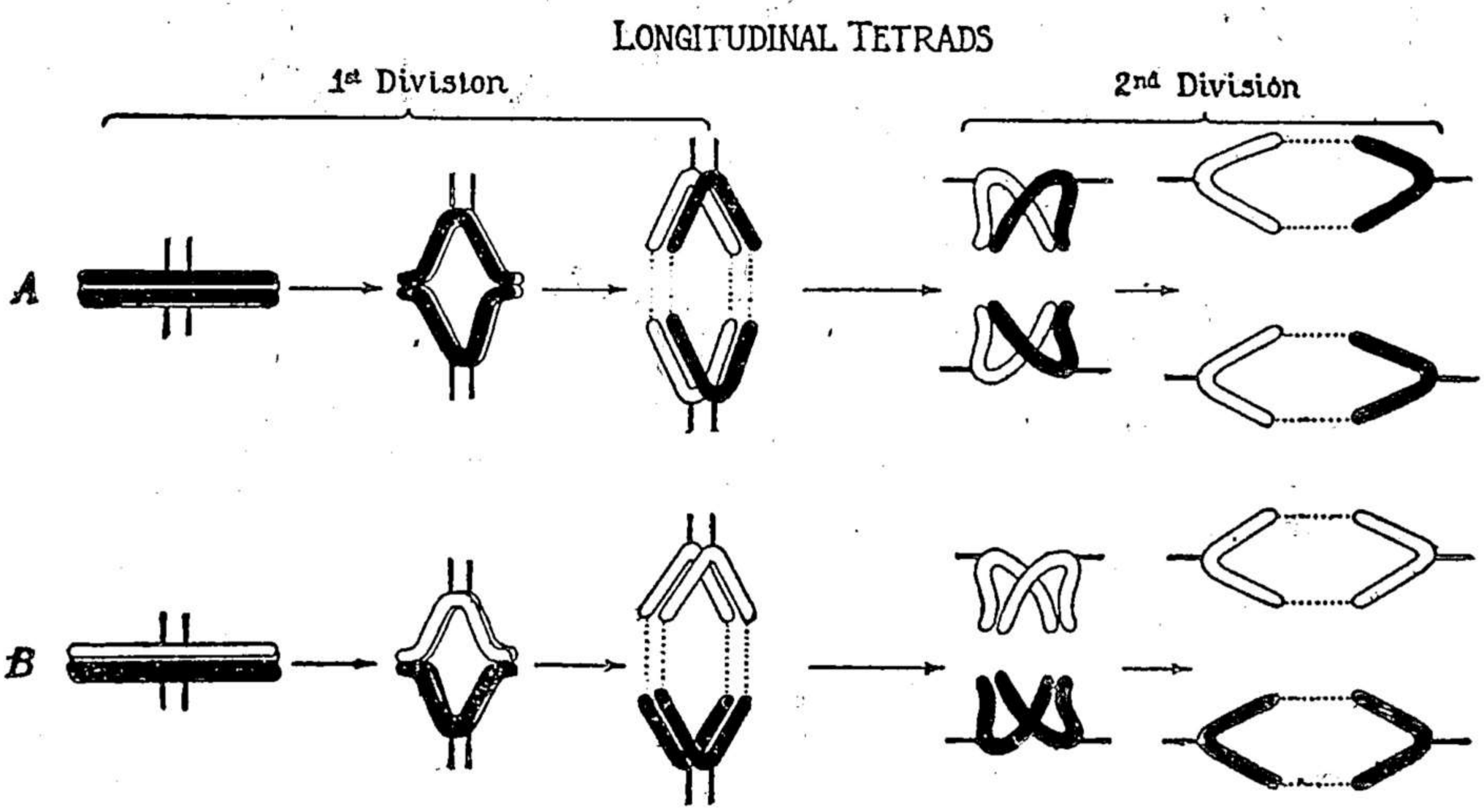

Fig. 249.—Diagrams of longitudinal or anaschistic rod-tetrads. The attachment is in both cases median (giving longitudinally cleft V's in the first anaphases and simple V's in the second). The *A* series shows post-reduction; *B*, pre-reduction. Compare Fig. 247.

projection longitudinally double and sometimes twisted; this represents the peripheral portions of the limbs of the two V's still closely associated, and often swollen to form knobs at the ends. These projections or "lugs" often stand out at a considerable angle both from the central portion (ring) and from the spindle, so as to give in profile view somewhat the aspect of a bird with outstretched wings (Figs. 256, 248). As the division proceeds the two V-shaped (or U-shaped) halves progressively draw apart and finally separate to form two daughter-V's with their apices turned towards the poles *and always, sooner or later, longitudinally cleft*, owing to the development in each of the secondary split (Figs. 252, 256).

With many minor variations rings of this type are of common occurrence in most of the main groups of plants and animals. When fully formed they are often not to be distinguished from early anaphase rings produced by

V-shaped bivalents, or from the atelomitic ring-tetrads, later to be described, which are formed during the early diakinesis (p. 527).

Intermediate Attachment (sub-terminal or sub-median). In this case the daughter-chromosomes, as they separate, have the form of unequal V's or of J's or hooks, in each case longitudinally double (Figs. 247, 245, 252). In this case, too, rings are often temporarily formed as the two halves separate (Figs. 252), the opening being nearer one end of the tetrad, and the ring usually first breaks at this point to form J-shaped sister-chromosomes. Not infrequently as the two halves separate the united ends at the opposite side, standing out at a considerable angle (as above mentioned) give the tetrad as seen in side view the appearance of an E-shaped figure, the upper and lower limbs formed by the two separating halves and the central horizontal bar by the two ends still united (Figs. 244, 248).

Terminal Attachment. In this case the process offers a widely different aspect, commonly seen in certain higher plants (*Lilium*, etc.) and frequently in animals. Here again, as in the somatic mitoses, the two halves, each individually split, draw apart apong the spindle from their point of attachment towards the poles (*cf.* Figs. 246, 252), until they lie end-to-end

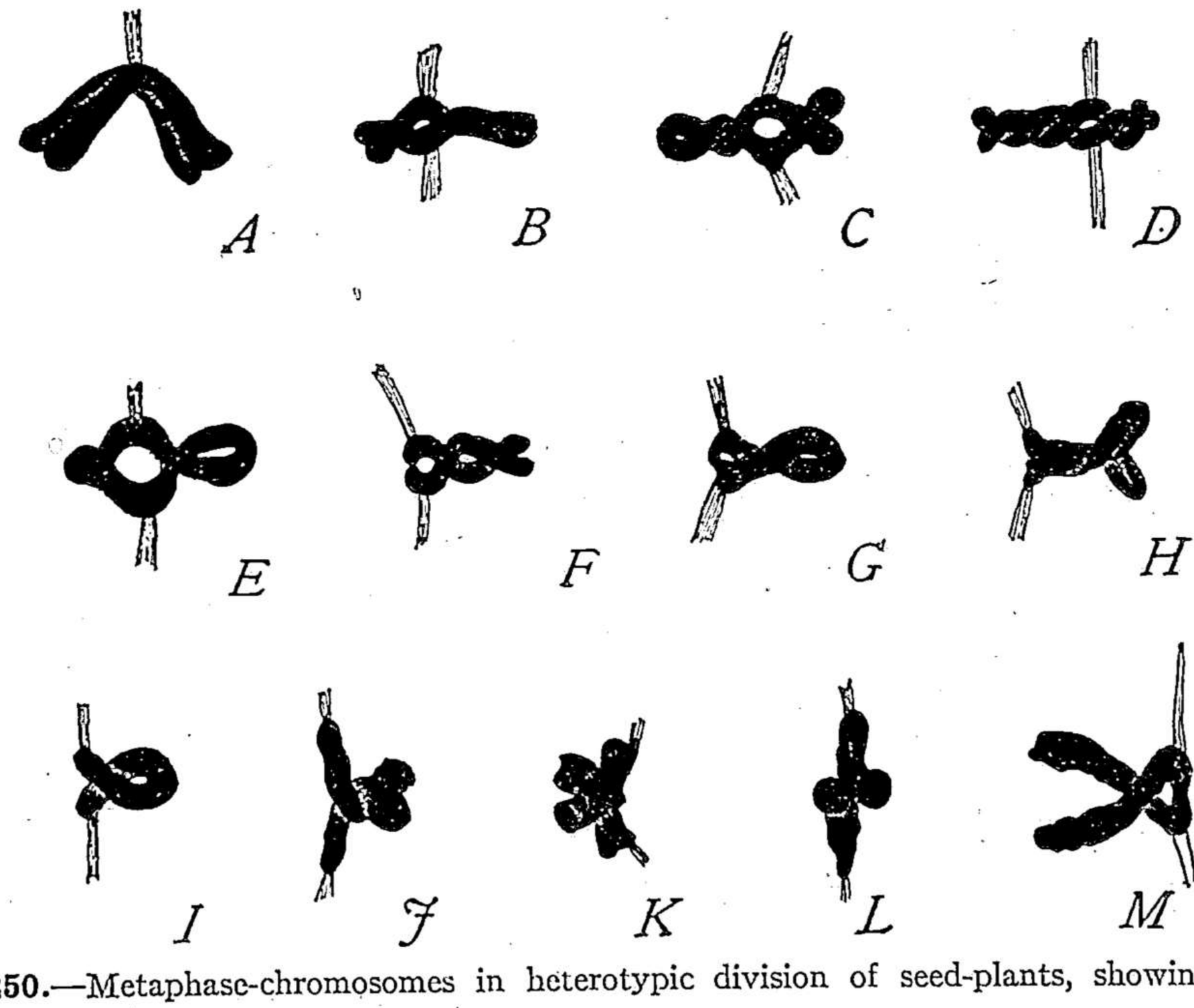

Fig. 250.—Metaphase-chromosomes in heterotypic division of seed-plants, showing various attachments.

(*A*, *D*, *F*, *I*, from GRÉGOIRE; *B*, *E*, *C*, *G*, *H*, from MOTTIER; *J–L*, ALLEN; *M*, STRASBURGER).

A, median attachment (*Trillium*); *B–E*, sub-median, bivalents more or less twisted (*Lilium*); *F–H*, terminal attachments bivalents twisted (*Lilium*); *I–K*, terminal crossed attachment; *L*, later stage of same, *en face*; *M*, sub-terminal crossed attachment.

and finally break apart at the equator by an *apparently* transverse division. In the anaphase the resulting dyads sometimes retain the form of straight rods, longitudinally split, but very commonly their longitudinal halves diverge more or less widely at their free equatorial ends, remaining united only at their attached (polar) ends. The anaphase rod is thus converted into a simple V attached by its apex (Fig. 252, G, H). Such V's do not split lengthwise, like those which result from a median attachment; *the whole chromosome is already split*, and the two halves (diverging limbs of the V) are destined to separate at the apex of the V. This again illustrates how widely tetrads may seem to differ in mode of division merely because of a difference of spindle-attachment; for precisely the same original type of tetrad (the anaschistic rod-type) gives in one case (median attachment) anaphase V's that are anaschistic or longitudinally dividing, and in the other (terminal attachment) anaphase V's which superficially regarded *seem* to be diaschistic or transversely dividing. Fundamentally, the two cases are identical, the tetrads undergoing in both two longitudinal divisions and differing only in the minor details of their distribution.[1]

This is conspicuously shown in cases of terminal attachment in higher plants (*Lilium*, etc.) in which the rod-tetrad clearly shows in certain cases both longitudinal clefts at the metaphase or even earlier.[2] Both clefts may open already in the metaphase before the dyads have separated, the equatorial cleft from the spindle outwards, the axial cleft from the free end inwards (Fig. 252, B, C). The result of this process (as in case of median attachment is a <> shaped figure or ring, very similar in general appearance to those resulting from a median attachment but having a quite different history in the anaphase, the daughter V's in the former case apparently dividing cross-wise at the apex (diaschistic), in the latter case splitting lengthwise (anaschistic).

Crossed Insertion. This mode of terminal attachment, described by Grégoire, Mottier, Allen, Strasburger and others in plants and by Sinéty, Montgomery, Davis and others in animals, is still a matter of dispute. According to the usual account, the two halves of the rod in this case cross one another in the metaphase in such a manner that each is connected with the opposite spindle-pole instead of that on its own side (Figs. 248, 250). The two rods may be free at both ends or united at one end to form a loop (Fig. 250); and in the latter case may be so widely separated as to form a nearly closed ring (Fig. 248, D). In all these cases attachment is at the free ends; and as the halves separate, accordingly, they slide past one an-

[1] The elucidation of this fact is due especially to the work of Grégoire ('99, etc.) and Strasburger ('95, '00, '04, etc.), on higher plants. Grégoire's conclusions on this point have been confirmed by many later observers.

[2] Strasburger ('95), Mottier ('98), Guignard ('98), Grégoire ('99), etc.

other so that each half passes to the pole opposite to that towards which it originally lay.

Assuming the correctness of this account, it seems clear that the crossed insertion is essentially the result of an earlier twisting of the two halves about one another, *i. e.*, is a last remnant of the strepsinema (Fig. 273). It is doubtful whether this account is valid for all cases. In the Orthoptera, for example, McClung ('14) has shown that some supposed cases of this type are due to a misinterpretation of the equatorial rings (described below) as seen in slightly oblique side view. Such an error does not, however, seem possible in the case of crossed rods with both ends completely separated,

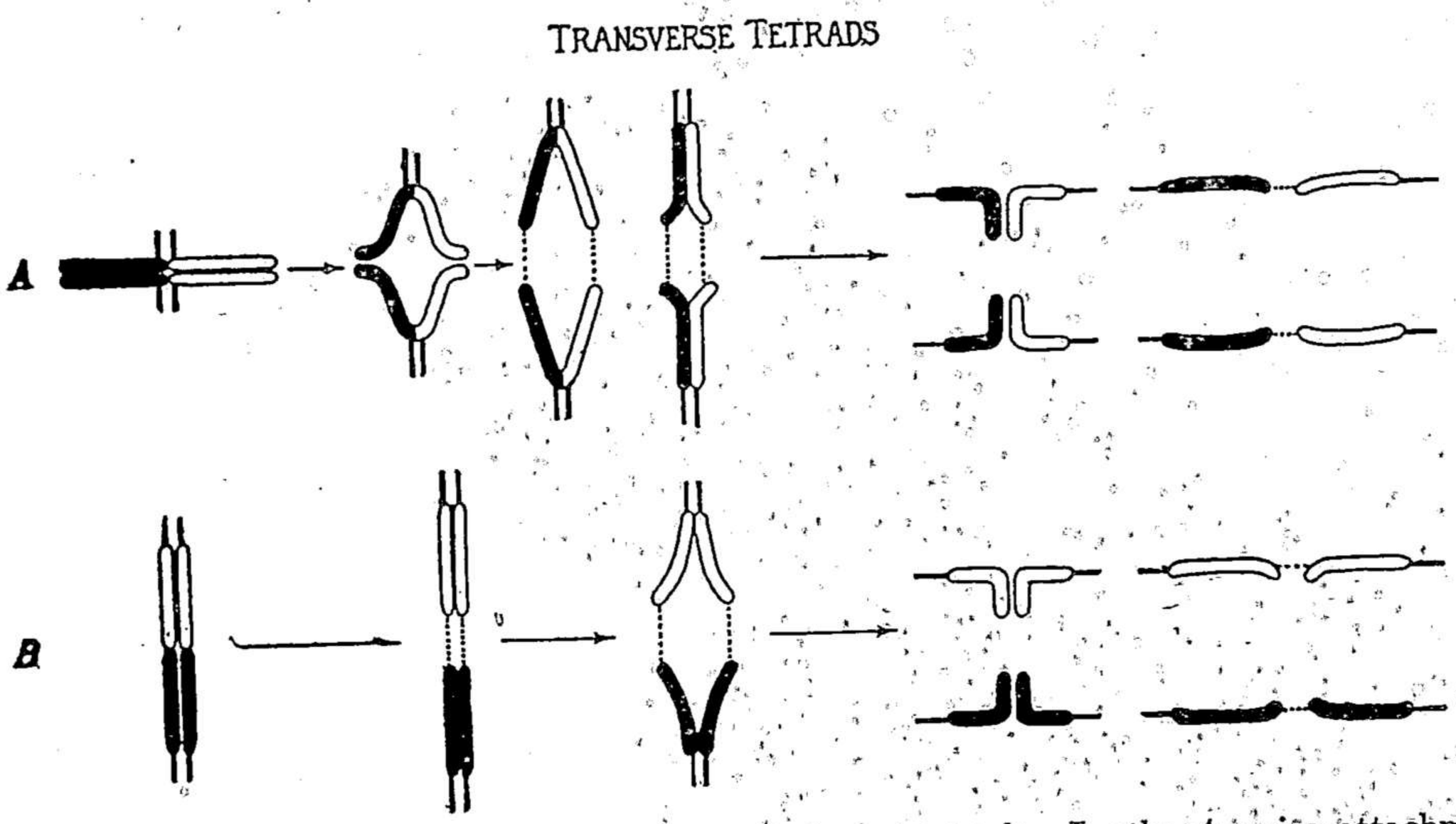

Fig. 251.—Diagram of the transverse or diaschistic rod-tetrads. In the *A* series attachment is median if the tetrad be considered as whole (terminal with respect to the component chromatids) giving simple anaphase-V's and post-reduction; in *B* it is biterminal with pre-reduction, giving anaschistic anaphase-rods or diaschistic simple V's.

such as are described for instance by Strasburger, Mottier, Allen or Grégoire in the higher plants.

(a^2). *Diaschistic or Transverse Rod-tetrads.* Rod-tetrads of this type are of common occurrence in insects and some other animals but are less well known in plants. These tetrads almost invariably divide first across the median cross-suture, and since they are often constricted at this point are commonly referred to as "dumb-bell shaped"; they may, however, show forms transitional to the double crosses described below.

Tetrads of this type most commonly lie parallel to the spindle-axis with the median suture or constriction in the equatorial plane, the spindle-attachments being bi-terminal, *i. e.*, at both ends of the rod (Figs. 251, 367, 369) They then divide crosswise at the middle-point, separating into two longitudinally split rods which pass together to the poles, often in close

association and without opening out to form simple V's, thus contrasting markedly with the longitudinal tetrads described under a^1. Such tetrads formerly seemed to support Weismann's conception of reduction by cross-division (p. 502). This was subsequently proved to be fallacious by the demonstration that such tetrads arise, in many cases at least, by the open-

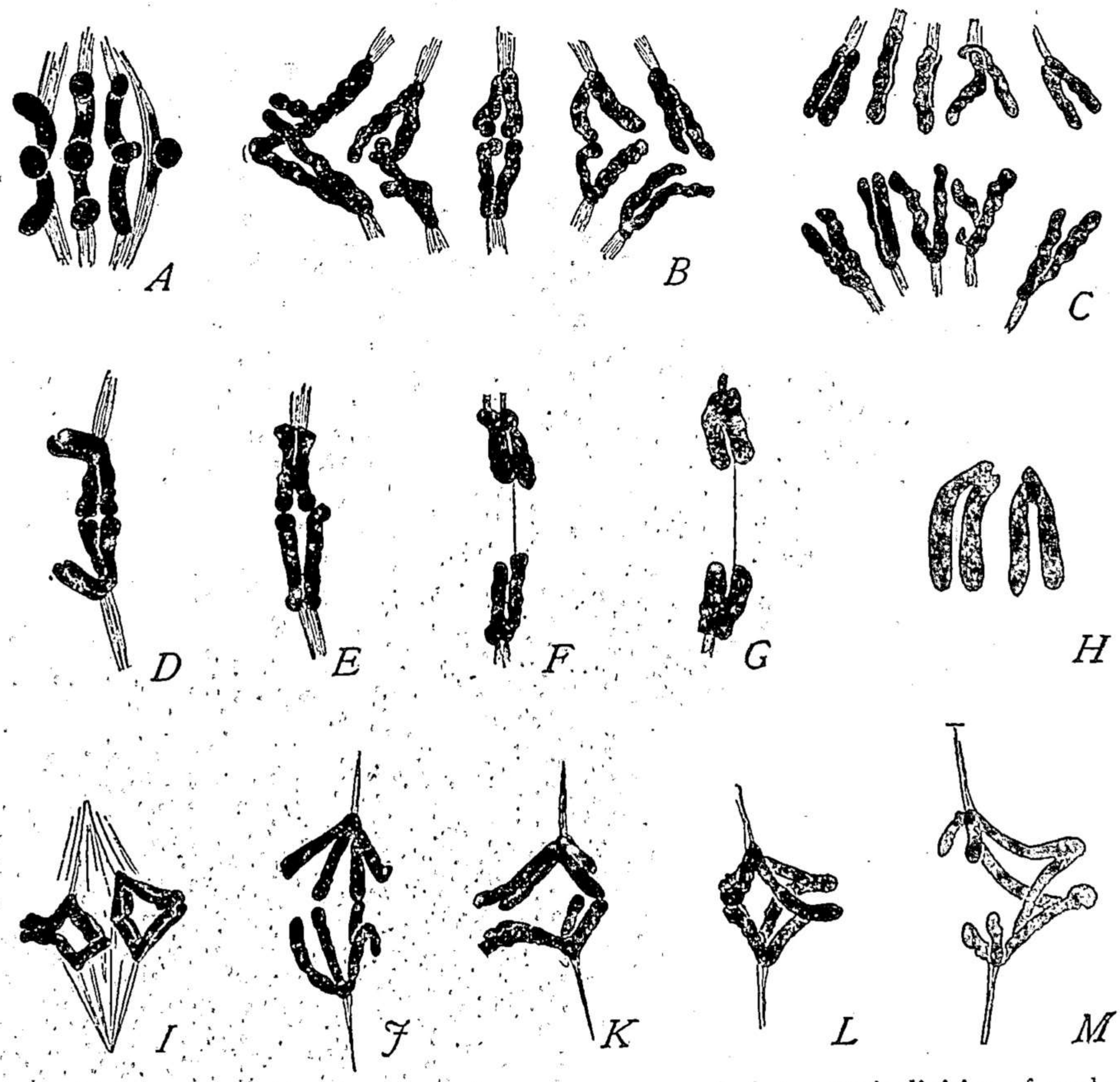

Fig. 252.—Metaphase- and early anaphase-chromosomes in heterotypic division of seed-plants. (*A–E*, from MOTTIER; *F*, *G*, ALLEN; *H*, GRÉGOIRE; *I–M*, STRASBURGER.)

A, metaphase-figures, terminal or sub-terminal attachments (*Podophyllum*); *B*, early anaphase, terminal attachments giving diaschistic V's (*Lilium*); *C*, later stage of same; *D*, *E*, sub-median and sub-terminal attachments (*Podophyllum*); *F*, *G*, anaphase figures, diaschistic V's, terminal attachment (*Lilium*); *H*, similar figure in *Trillium; I*, metaphase-figures, sub-median attachment (*Allium*); *J–K* (*Lilium*), late metaphase, showing "secondary" split; *J*, median attachment; *K*, *L*, sub-median, *M*, sub-terminal.

ing apart from one end of two tetrad-halves that originally lay side-by-side until they are connected only at the opposite end (Figs. 244, 254). Such tetrads are exactly comparable to the final metaphase-form of anaschistic rod-tetrads with terminal attachment. They differ only in the fact that, in the former, the opening-out process takes place already in the diakinesis before the spindle has been formed (p. 547).

The two types of tetrads next to be considered are readily derivable from

rod-tetrads and are actually such during their earlier stages in a large number of cases. The simpler of the two includes:

b. V-shaped Tetrads. This form appears to be less frequent than the foregoing one, though common in certain groups, such as the Orthoptera. It differs from the rod-tetrad only in being fixed at the middle point, where the V is ultimately attached to the spindle. We may distinguish two types of such tetrads, derived respectively from the anaschistic and the dias-

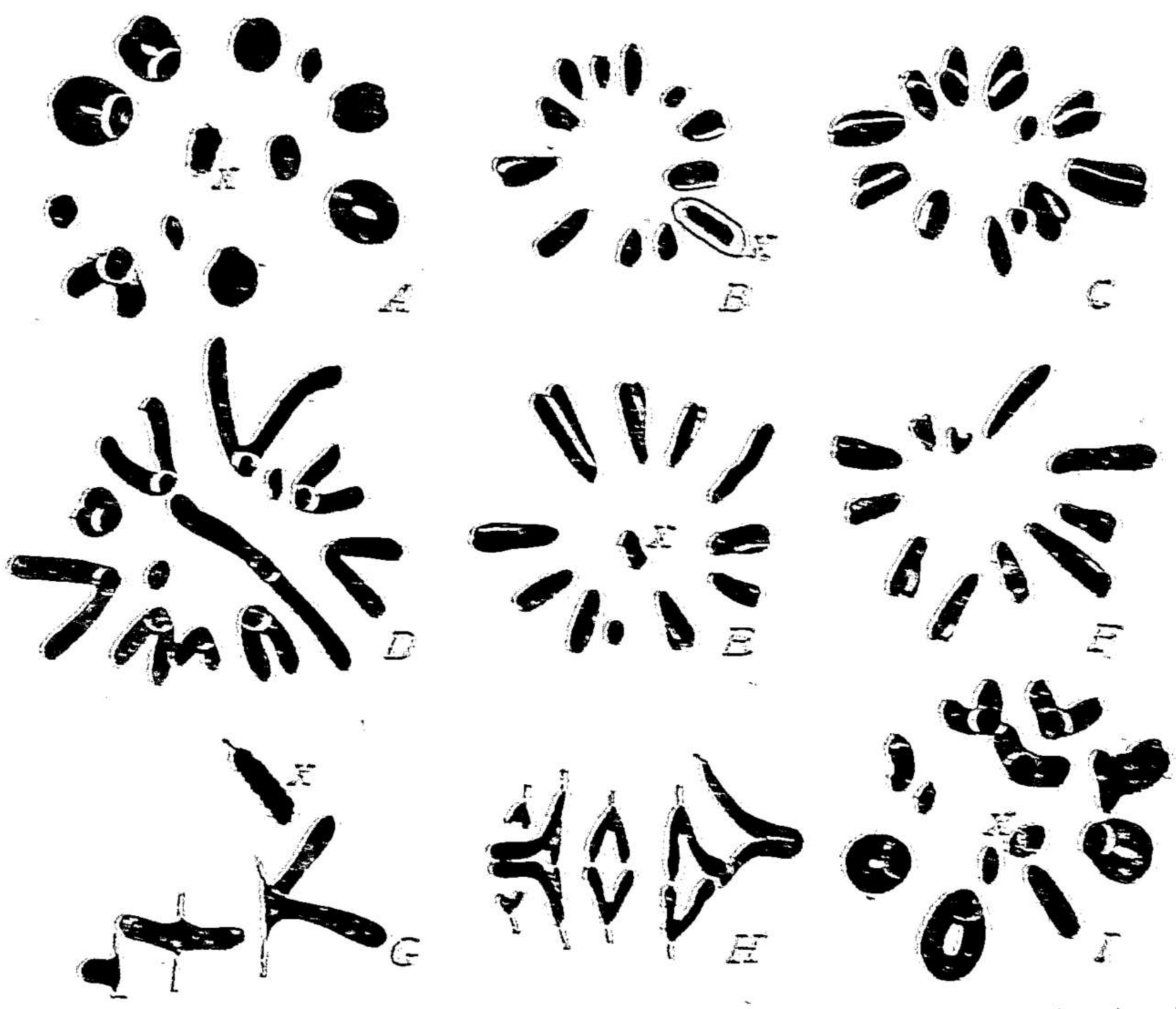

Fig. 138.—Maturation-chromosomes in the spermatogenesis of Orthoptera showing in polar view equatorial rings and other forms (*A*, *I*), rod-shaped anaschistic tetrads with terminal attachment (I) and diaschistic V's and rod with median attachment (D) (McClung).

A, polar view, first spermatocyte-metaphase, 24 + 1 + sex; *B*, second spermatocyte, 12 chromosomes *X*-dass; *C*, same, 11 chromosomes, no *X*-dass. *D*, *E*, *F*, corresponding stages in *Xiphidium*; *G*, *H*, side-views of same, first division; *I*, polar view, first spermatocyte metaphase, *Dapticlophus*.

chistic rod-tetrads. In general, anaschistic V's can hardly be distinguished from anaschistic rods with median attachment; and they have the same later history, the anaphase-dyads having the form of V's longitudinally split (Fig. 247). Diaschistic V's are common among Orthoptera, where they have been studied in various grasshoppers by McClung and his followers.[1] Such V's are essentially diaschistic rod-tetrads, flexed at the middle-point and attached to the spindle at that point (Fig. 246). This is shown with especial clearness in the genus *Macrotettix* (Fig. 253), where they are

[1] See Sutton (01), McClung ('14), Finney ('08), Robertson ('16), Wenrich ('16).

more extended than in most other forms and sometimes almost straight (McClung, '14).

V's of the diaschistic type divide along their longitudinal split in the first division, giving daughter-V's like the original tetrad but not longitudinally split. In the second division the two limbs of these V's break apart at the apex. From the foregoing it will be seen that simple anaphase V's, dividing diaschistically at the apex, may be produced in two wholly different ways, namely (1), as a result of the terminal attachment of longitudinal or anaschistic rod-tetrads (Fig. 252, B, C) or (2), as just described by the median attachment of diaschistic rod-tetrads commonly flexed at the point of attachment to form V's (Fig. 253). This illustrates once more the purely provisional and secondary nature of the distinction between

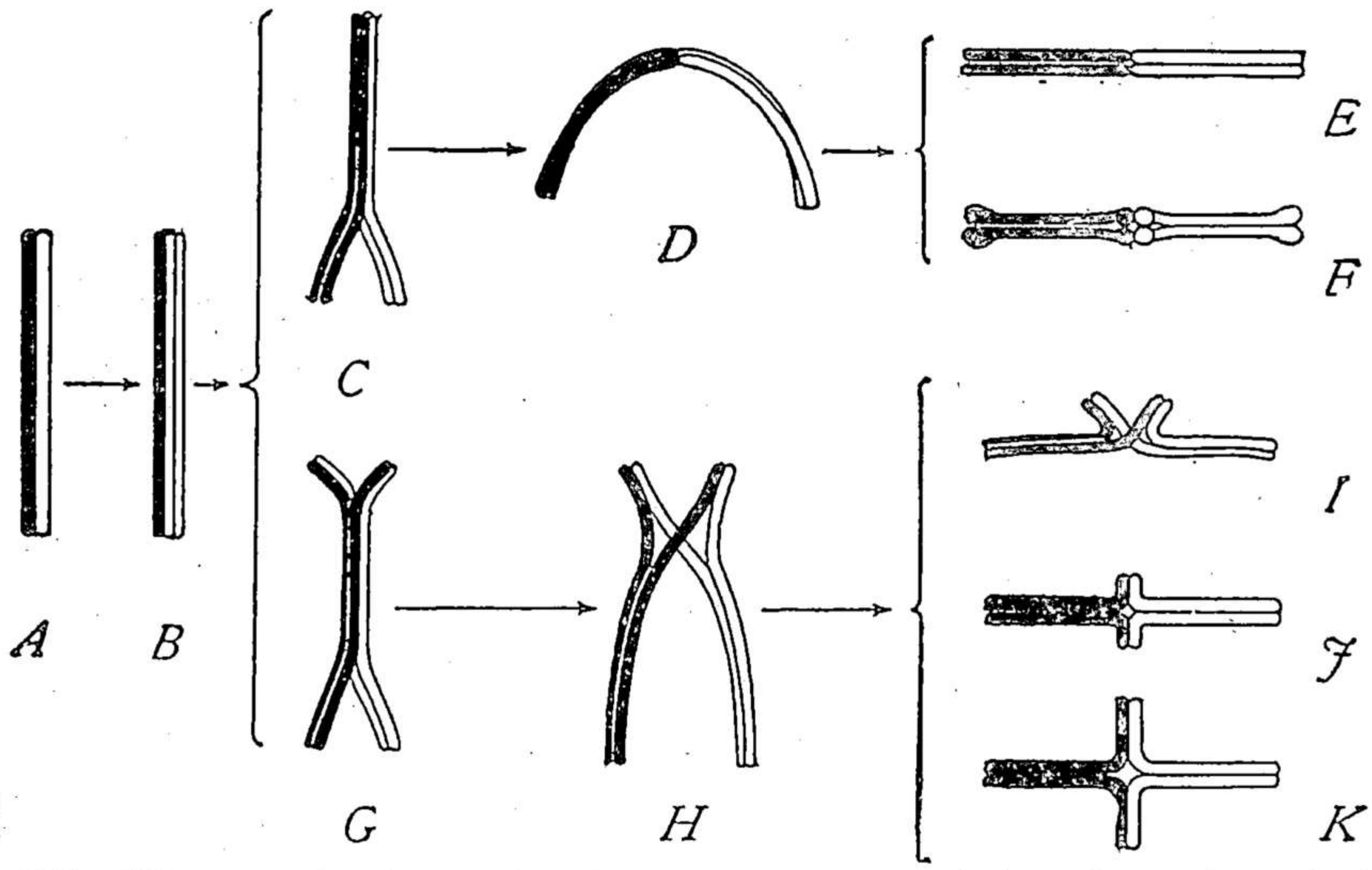

Fig. 254.—Diagrams showing origin of transverse or diaschistic rod-tetrads, and of double crosses. The synaptic mates in black and white.

A, diplotene thread; *B*, longitudinally quadripartite stage, common to both forms of tetrads; *C*, *D*, opening apart of the rod from lower end along the reduction-plane, leading to *E*, *F*, tetrad rods of slightly differing type; *G*, *H*, opening apart along the reduction-plane from lower end and the equation-plane from upper end; *I*, result of further divergence at lower end side-view; *J*, *K*, resulting double crosses in face view after complete straightening out.

the anaschistic and diaschistic modes of division; and it also indicates a prolific source of confusion in the earlier literature of the subject.

c. Double Crosses. By still another modification of the rod-tetrads arise the so-called double crosses, which are among the most interesting and, in animals, the most widespread forms of tetrads. They are perhaps most frequent among the insects and annelids.[1] These tetrads have the form of a rectangular cross, each of the four arms being longitudinally cleft (Figs. 254, 259). As the figures show, four chromatids lie in

[1] See Paulmier ('99), Sutton ('02), Montgomery ('01, '06), Janssens ('01), Schreiner ('06), Wilson 05, '06, '12), Mohr ('14).

one plane, each bent at a right angle and symmetrically grouped about a common center. Each arm of the cross is thus formed by the close approximation of corresponding portions of two chromatids, the cleft between them passing straight through the arm. At the center often appears a considerable open space with which the clefts are continuous. Peripherally the latter may extend completely through to the ends of the arms, but often seem not to do so.

In their fullest development the four arms are equal, but more frequently we may distinguish two longer "axial" arms and two shorter "lateral" ones (Figs. 254, 268). In this respect all gradations occur from equal-armed crosses down to those in which the lateral arms are only just distinguishable (Fig. 244). A step further and these arms would disappear, the double cross becoming a transverse or diaschistic rod-tetrad. The cross might therefore be conceived as arising from a transverse rod-tetrad by drawing apart the two lateral halves of the latter from the region of the cross-suture on each side to form the lateral arms. Such, however, is not its usual mode of formation, the double cross, like the transverse rod-tetrad, arising from a longitudinal rod-tetrad in which the four chromatids originally are straight, lying parallel and side by side (Figs. 244, 268).

The later history of these tetrads in the heterotypic division is practically identical with that of the transverse rod-tetrads. They form a biterminal attachment to the spindle, usually with the axial arms parallel to the spindle-axis and the lateral ones lying in the equatorial plane. In the first division they split in two through the lateral arms and draw apart in the form of double rods or simple V's that subsequently break apart at the apex. If the lateral arms be very short, or disappear entirely it becomes obvious that the first division corresponds to the diaschistic or cross-division of the rod-tetrad (Fig. 259).

d. Ring-tetrads. These are among the most interesting forms of tetrads because of the emphasis laid upon them by Flemming in his first characterization of the heterotypic division, and also because of the numerous elaborate studies of their transformations that have since been made. As we have seen, figures more or less clearly ring-shaped are often temporarily offered by other forms of tetrads (rods, V's) as they draw apart in the late metaphase and early anaphase, especially after median or sub-median spindle-attachments. The rings now to be considered differ only in degree from these, but show the phenomena in more spectacular fashion because of their much earlier origin in the early prophase or diakinesis at a time when the chromosomes are in more extended form, and have no visible connection with the spindle (Figs. 244, 268). Such rings are seen to partic-

ular advantage in insects (Orthoptera, Hemiptera), annelids (*Tomopteris*, *Allolobophora*) and lower vertebrates (Amphibia), where they have been the object of investigation by many observers.[1]

With some possible exceptions these rings are actual tetrads, being longi-

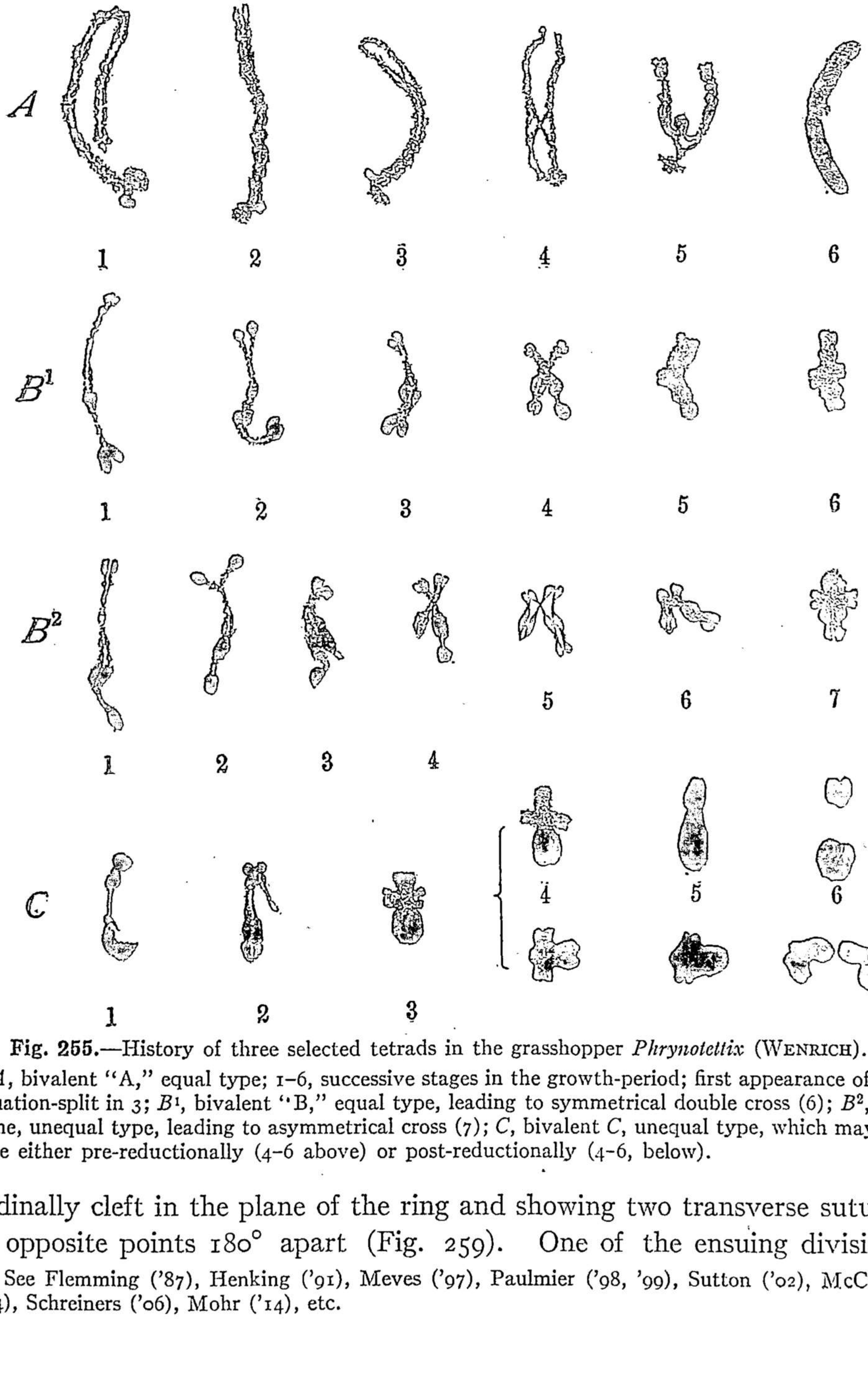

Fig. 255.—History of three selected tetrads in the grasshopper *Phrynotettix* (WENRICH).

A, bivalent "A," equal type; 1–6, successive stages in the growth-period; first appearance of the equation-split in 3; B^1, bivalent "B," equal type, leading to symmetrical double cross (6); B^2, the same, unequal type, leading to asymmetrical cross (7); *C*, bivalent *C*, unequal type, which may divide either pre-reductionally (4–6 above) or post-reductionally (4–6, below).

tudinally cleft in the plane of the ring and showing two transverse sutures at opposite points 180° apart (Fig. 259). One of the ensuing divisions

[1] See Flemming ('87), Henking ('91), Meves ('97), Paulmier ('98, '99), Sutton ('02), McClung ('14), Schreiners ('06), Mohr ('14), etc.

thus divides the ring lengthwise, the other transversely through the two cross-sutures into two half-rings. They may therefore be characterized as diaschistic. They differ widely in degree of condensation at the time they enter the metaphase. In *Tomopteris* (Fig. 244) they remain still widely open so that their history is easily followed, and the same is true in some of the urodeles. Frequently, however, they condense to such an extent that the ring-shape is obscured or even lost, *e. g.*, in the grasshoppers (Fig. 253). In the Hemiptera such rings, though often perfectly clear in the prophases, are no longer distinguishable as such in the metaphases, having condensed to a compact tetrad-shape. It will conduce to clearness if the ring be described as composed (as it probably actually is) of two synaptic mates (A and a) united at both ends but widely separate elsewhere; in other words, the ring-

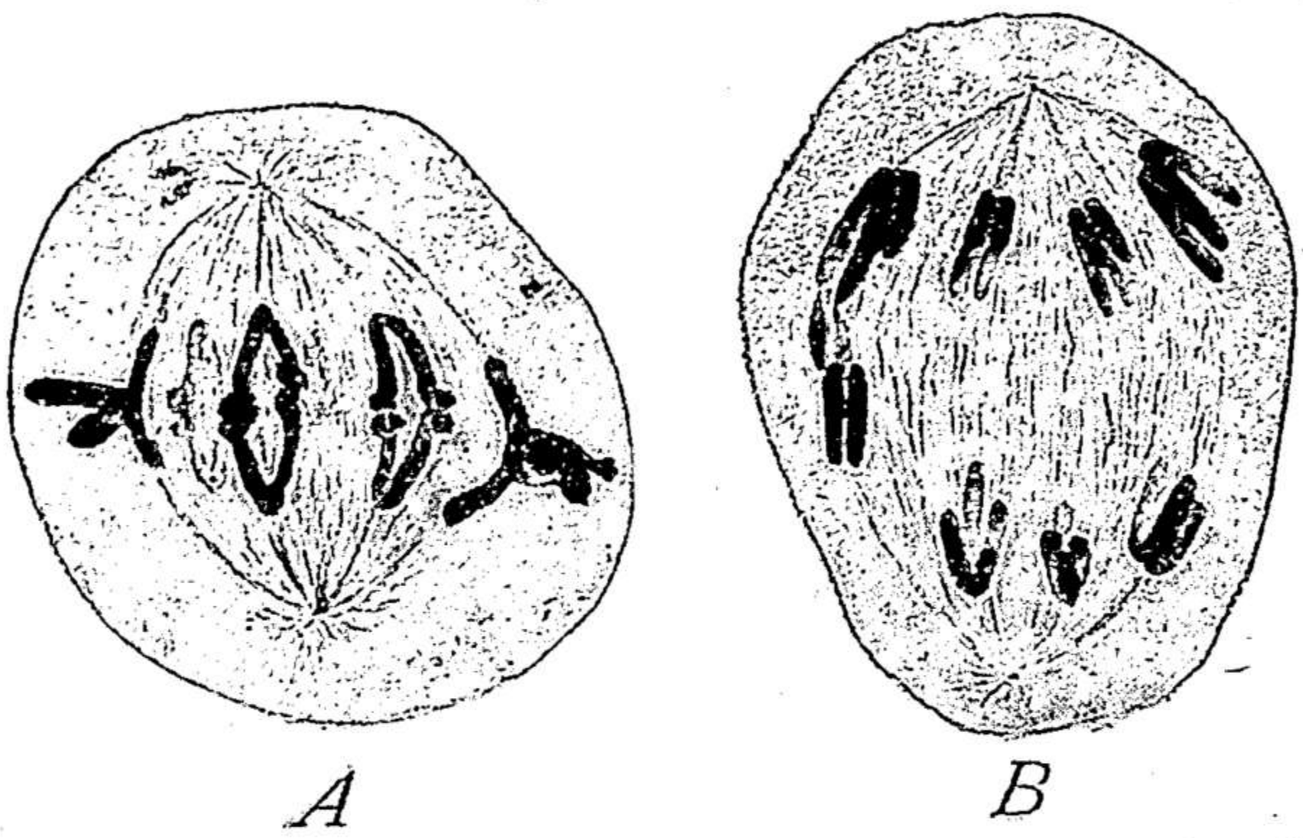

Fig. 256.—Heterotypic division in the urodele *Amphiuma* (McGregor).

A, metaphase, with ring-figures (median attachments) shown in profile at either side; *B*, anaphase-figure with anaschistic V's.

opening is surrounded by the two mates, their ends meeting at the cross-sutures, 180° apart, and both longitudinally split.

In the simpler types of rings the longitudinal split is often obscure. Such rings, first described by Flemming in the salamander are of wide distribution in both plants and animals. They are often compressed or asymmetrical (Figs. 247, 248) and may be more or less twisted at the time they pass upon the spindle. In the metaphase or early anaphase they are hardly to be distinguished from the rod-shaped or V-shaped tetrads of groups *a* and *b*. More commonly the ring shows a lateral prominence or "lug" at one or both cross-sutures, often drawn out into arm-like processes (Figs. 244, 257), longitudinally split, each half being continuous with a corresponding half of the ring. The arms are thus seen to result from the fact that the two synaptic mates have still not fully opened apart but remain in contact for a certain distance from their ends (Figs. 244, 259).[1] In many of these cases

[1] Some observers (*e. g.*, Janssens, '01, '05) have described the lateral arms as twisted, a remnant of an earlier twisted condition of the whole tetrad.

as shown in the figures the lateral arms are converted into cross-shaped figures, by a drawing apart of the two halves of the longitudinally split ring on each side of the cross-suture and at right angles to the plane of the ring. Instead of a single arm at this point (as in the preceding case) we now have two arms extending in opposite directions at right angles to the ring, and forming a cross-shaped figure comparable with the four double cross-tetrads. Such figures may appear at both of the cross-sutures or only at one (Fig. 244). In the latter case the close relationship between rings of this type and the double crosses of group *c* is evident, particularly when (as occasionally happens) the ring is incomplete on the side opposite the cross (Fig. 244, B). We may indeed think of the ring as a double cross with one short and one long pair of arms, the latter being bent around until their free ends have joined. This was in fact the original conception of the origin of such rings as conceived by Paulmier, Sutton and other earlier observers; but such is not their actual origin (p. 548).

A remarkable further development of this type, discovered by McClung ('02) and confirmed by Granata ('10) and later observers (Robertson, Wen-

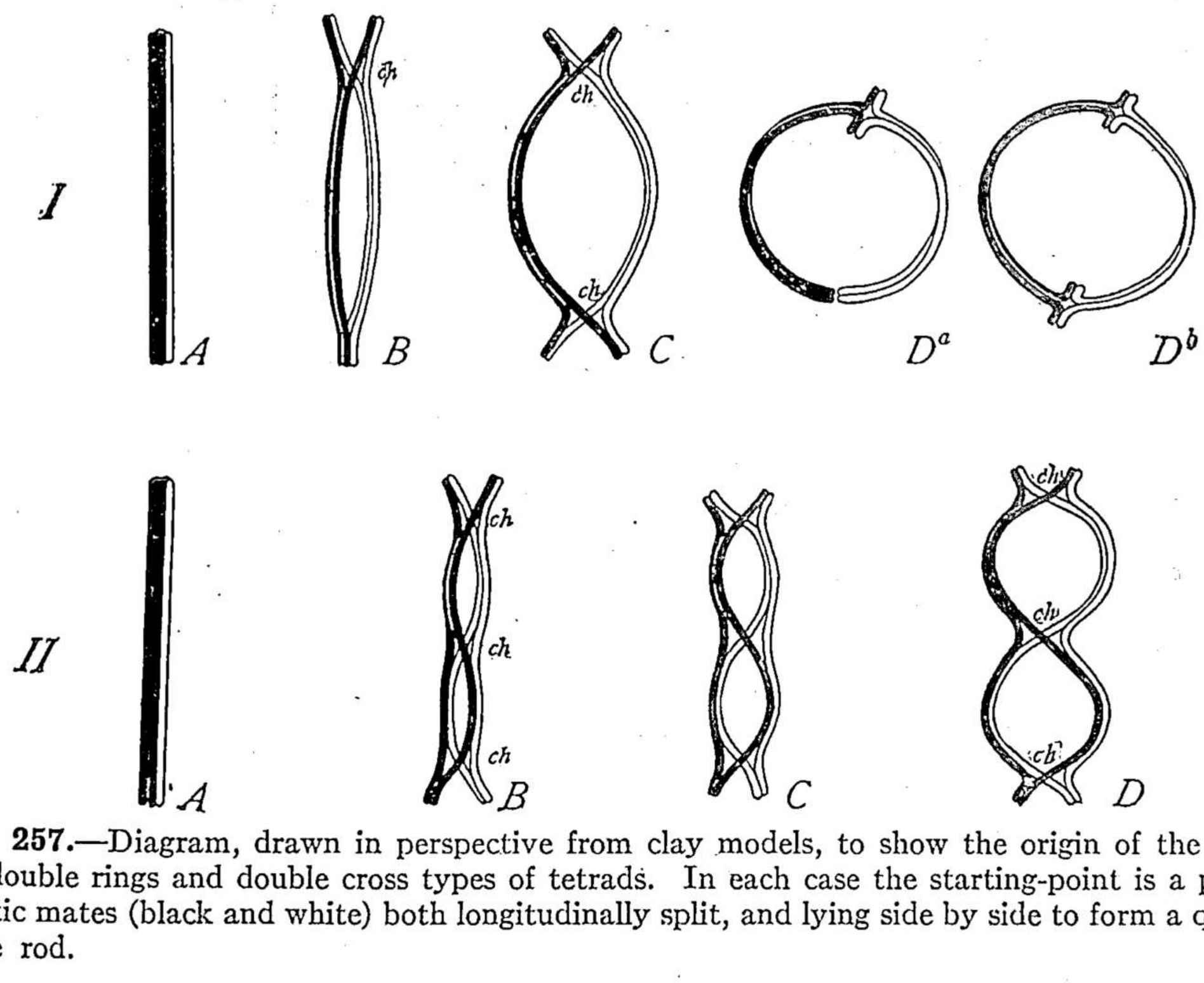

Fig. 257.—Diagram, drawn in perspective from clay models, to show the origin of the single ring, double rings and double cross types of tetrads. In each case the starting-point is a pair of synaptic mates (black and white) both longitudinally split, and lying side by side to form a quadripartite rod.

rich) is offered by double or even triple rings, in connected series. This results from a still greater elongation of the lateral arms of the cross which curve towards each other until they form a second ring at right angles to the first (Figs. 257, 258); and if this occurs on both sides of the primary ring a third ring may arise, the two or three (possibly a larger number) forming a

connected series. The rings in these cases are successively at right angles to each other and the double (or triple) ring involves an "exchange of partners" (Sutton, McClung), the longitudinal halves of each secondary half-ring consisting of one from each of the original half-rings, as will be made plain from Figs. 453, 454.[1]

Behavior in the Heterotype Division. During the heterotypic division the rings are of two types which result respectively from non-terminal (usually median) and terminal attachment (applying these terms to the component chromatids of the tetrad). With non-terminal or atelomitic attachment (typically seen in *Tomopteris*, Figs. 244, 259) the ring lies vertically, or tangential to the spindle with the spindle-fibers attached to each half ring midway between the two cross-sutures, or at some intermediate point. Such

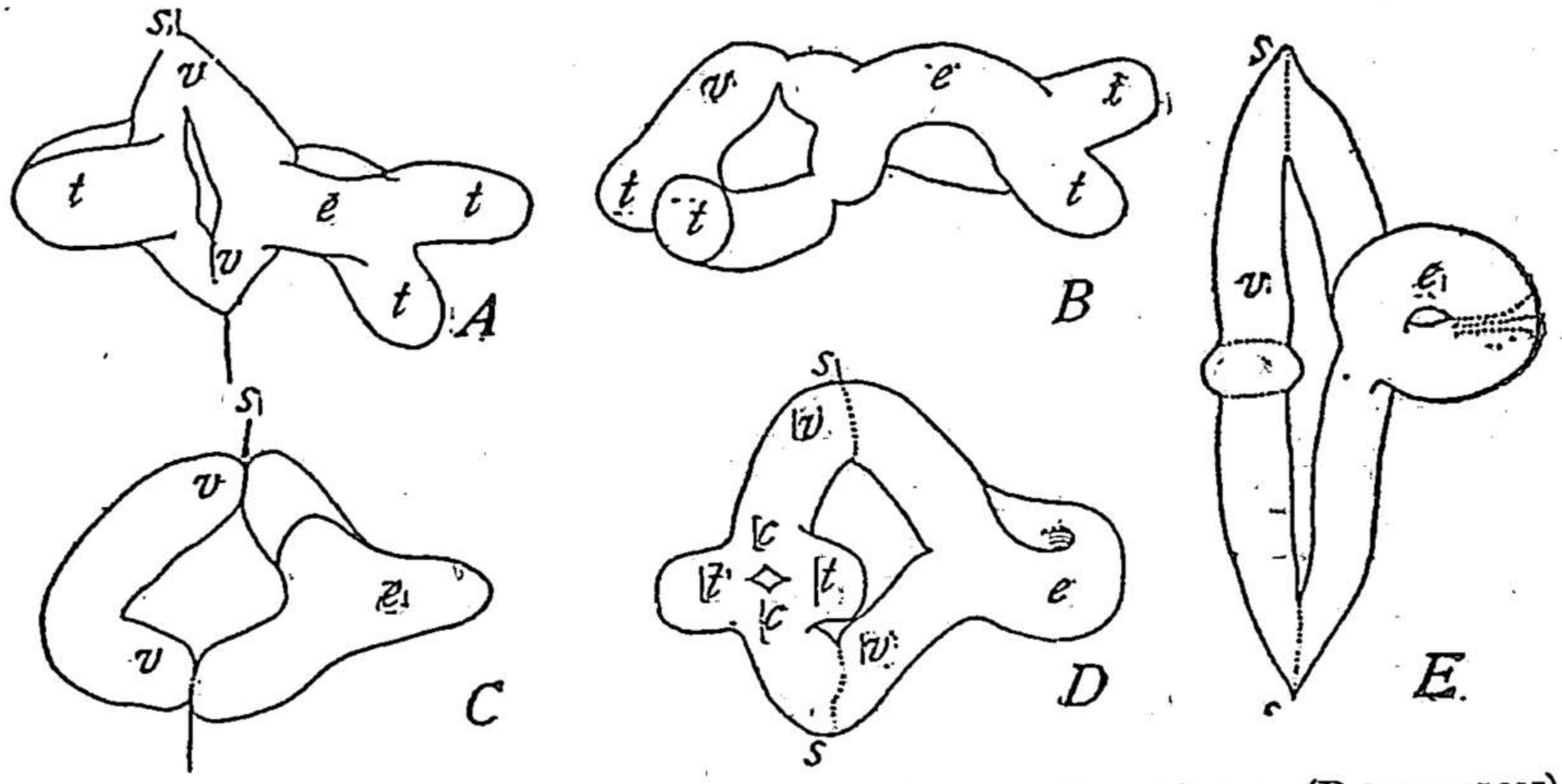

Fig. 258.—Double ring tetrads in the grasshopper *Chorthippus* (ROBERTSON).

All are shown in side-view, attached to the spindle-fibers at the points *s*, *s* (atelomitic attachments). The drawing out of the attached (tangential) ring has begun in *A*, *C* and *D*, and is more advanced in *E*. All of these cases, except *A*, show a cross-suture at the point of attachment, indicating the probably compound nature of these rings.

In each case *e* marks the horizontal or equatorial ring (seen from the side, or obliquely), *v*, the vertical or tangential ring (seen *en face*), *t* the terminal arms. In *D*, the double-cross figure formed by these arms is seen in oblique view at *c*.

rings have conveniently been characterized by McClung ('14) as *axial* or atelomitic. These rings draw out towards the poles and are cut in two crosswise through the cross-sutures, and also through the lateral arms when present. They are thus divided into two half-rings, each longitudinally split (anaschistic), which in the anaphases assume the form of split V's, quite as in the case of longitudinal rod-tetrads (Fig. 259).

The telomitic ring, with terminal attachment, lies in a position at right angles to the atelomitic, *i. e.*, in the equatorial plane, so that its opening is only seen in polar view (hence *equatorial* in contradistinction to *axial* or

[1] These curious facts, of much interest for the chiasmatype theory, are more fully considered at p. 959.

tangential), as shown in Figs. 253, 259. Such rings first divide along the longitudinal cleft, the lateral arms or lugs drawing out towards the poles at the expense of the ring, the latter decreasing as the former increase (Fig. 259). The daughter-chromosomes have the form of single V's or (by close approximation of the two limbs) double rods, each limb being formed from one of the quarter-rings. Their later history is essentially the same as that of the double rods or diaschistic V's resulting from the telomitic rod-tetrads or double crosses, or the V's of *Mecostethus* (Fig. 253).

The axial or atelomitic ring is by far the most common, being widely distributed among both invertebrates and vertebrates and not uncommon in plants. Of this type are the rings of urodeles as originally described by Flemming ('87) and his followers (Meves, Carnoy and Lebrun, McGregor, Janssens, etc.), and remarkable examples of it are seen in annelids (*Tomopteris*, *Allolobophora*).[1] The telomitic or equatorial ring, on the other hand, seems to be of relatively limited occurrence, our knowledge of it being almost wholly confined to the orthopteran family of Acrididæ (*Hippiscus*, *Brachystola*, *Chortophaga*, *Syrbula*, etc.)[2] It is interesting that even within the limits of this family rings of both types occur. Most commonly they are of the telomitic type (as in *Hippiscus*, *Brachystola*, *Syrbula*, etc.), but axial or atelomitic rings are found in *Stenobothrus*, *Chorthippus*, *Chloëaltis* and a few other forms. That species so nearly related should differ in respect to the ring-tetrads is of general interest because the two types, though precisely similar in morphological composition, seem to be reversed with respect to the order of division; if, for example, the *Hippiscus* ring (telomitic) be post-reductional, as believed by McClung, the *Stenobothrus* ring is pre-reductional, and *vice versa* (Fig. 259).

The two extreme types are connected by many intermediate forms. Not infrequently, for example, the atelomitic or axial ring has a sub-median instead of a median attachment. In such cases the ring breaks first on one side and thus gives asymmetrical anaphase V's, or more or less E-shaped figures, as already explained in case of the metaphase-rings of rod-shaped tetrads (p. 518). Many such figures no doubt arise from incomplete rings or loops, as was first pointed out by Janssens ('01) in the case of *Triton* (*cf.* Meves, '97, Flemming, '87). Such loops offer many degrees of transition from complete rings to straight double crosses (Fig. 244), and in another direction graduate insensibly into longitudinal rod-tetrads which give rise to metaphase rings and related figures. In the anaphases the daughter-chromosomes are U's, V's or J's, in each case of course longitudinally double.

[1] See especially Henking ('91), Paulmier ('98, '99), McClung ('14, etc.), Sutton ('02), Granata ('10), Davis ('08). Robertson ('08, '16), Foot and Strobell ('10), Wenrich ('16, '17), etc.

[2] See especially McClung, '14.

The ring-tetrads strikingly illustrate the correlation between the gonial chromosomes and those of the meiotic divisions in respect to the spindle-attachments. The axial or atelomitic ring of *Tomopteris* or the urodele is

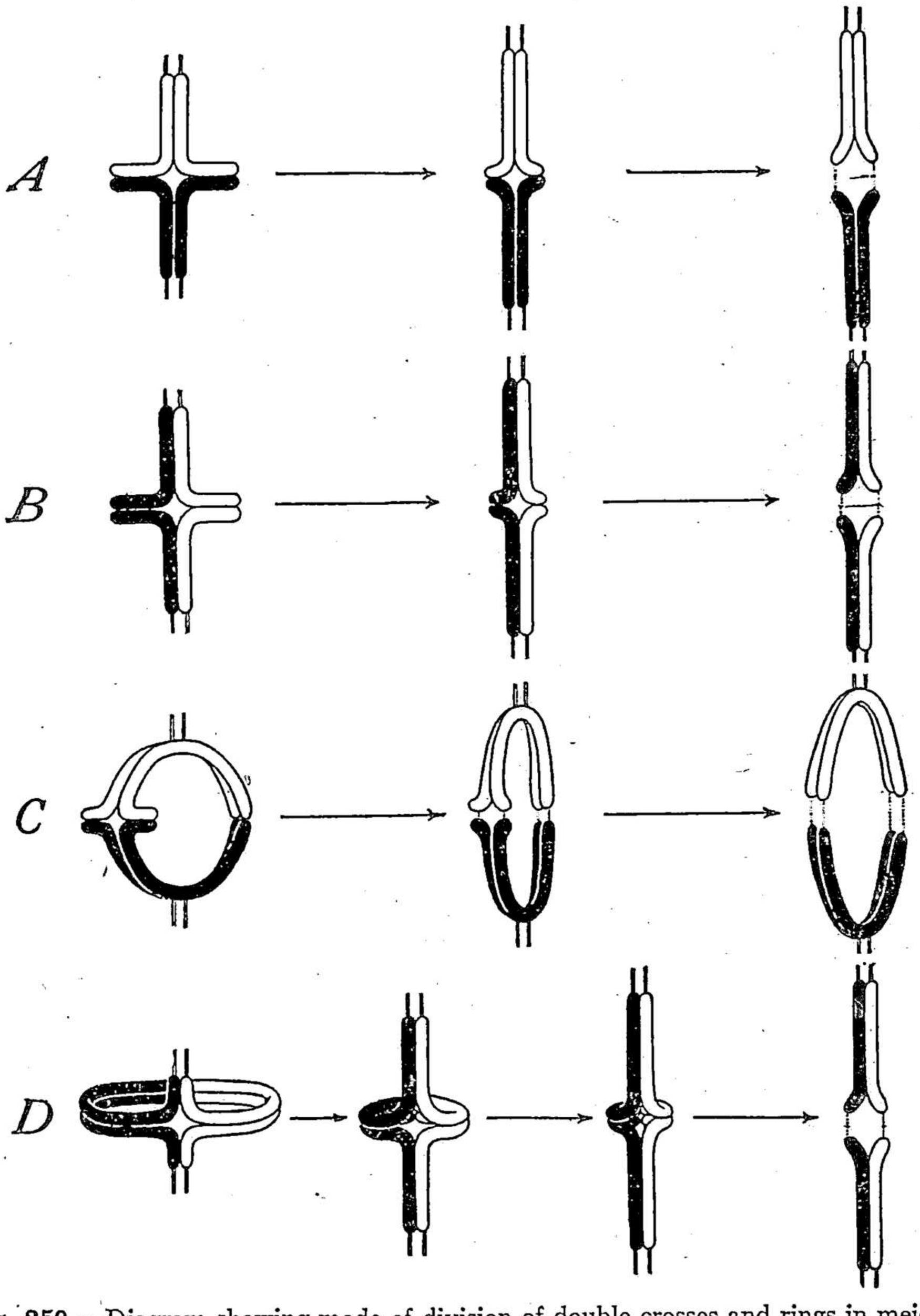

Fig. 259.—Diagram showing mode of division of double crosses and rings in meiosis.

A, double cross with pre-reduction; *B*, the same with post-reduction; *C*, tangential ring with median attachment and pre-reduction (as in *Tomopteris* or urodeles); *D*, equatorial ring with terminal attachment and post-reduction (as in *Hippiscus* type of grasshoppers).

Note that in *A*, *B* and *D* the longitudinal halves of the anaphase-chromosomes often separate more widely from their free ends than is here shown, thus giving diaschistic V's.

obviously correlated with the non-terminal attachments of the gonial chromosome-pair from which it arises. Nearly all the gonial chromosomes in these animals are of V-shaped or similar form, with non-terminal or me-

dian attachments. The union of two such V's side-by-side, followed by their separation in the middle region while the ends remain united obviously produces an atelomitic ring represented by two V's placed base to base, with the attachments at the apices; hence the axial or tangential position of the ring on the spindle (Fig. 259). On the other hand, the telomitic or *Hippiscus* type of ring results from a rod-shaped pair of gonial chromosomes with terminal attachments. When two such chromosomes unite, side-by-side, subsequently opening apart to form a ring, the terminal attachments still persist as such at one of the cross-sutures (or lateral arms) of the ring (Fig. 259). Hence, obviously, the ensuing equatorial position of the ring on the spindle, and its post-reductional division.

That this is the true explanation is demonstrated by the atelomitic or axial rings of *Stenobothrus*, *Chorthippus*, *Chloëaltis*, etc.; for all such cases offer an exception to the rule among the Acrididæ in that certain of the gonial chromosomes are V-shaped, having non-terminal attachments; and it is precisely from these chromosome-pairs, as is proved by their size, that the atelomitic rings arise.[1]

It is the same with the rod-tetrads, or the double crosses. The longitudinal or anaschistic rod-tetrad may have any attachment, its resulting form in the early anaphase varying correspondingly (whether a rod, V, J, E-shaped figure or ring). The typical diaschistic or transverse rod-tetrad and the double crosses both arise from gonial rods with terminal attachments; and since these tetrads arise by the spreading apart of the two from this end while remaining united at the other these forms typically have a biterminal attachment. The diaschistic V-tetrads, so common in Orthoptera, arise in a similar way, but spread apart from the free instead of the attached ends and do not fully open, the V-shape being more or less retained (Fig. 253). Such V's (like the atelomitic rod-retrads of *Mecostethus*) commonly open out in the early anaphase to form axial ring-shaped tetrads (Fig. 253); but differ from the axial rings of *Tomopteris*, etc., in that they are diaschistic, *i. e.*, break across at the middle-point of each half ring during the anaphases (Fig. 259). Prophase-rings of the same type, showing four instead of two cross-sutures, seem to occur also in certain copepods as described by some of the earlier observers (Rückert, Haecker), and are probably open to a similar interpretation.

Such facts emphasize the fact that the tetrads have a quite definite and characteristic organization that is maintained at every state throughout

[1] This is strikingly shown in Mohr's ('16) study of *Locusta viridissima* in which there are (in addition to the X-chromosome) 28 spermatogonial chromosomes, of which 26 are short rods and two large V's (Fig. 394). All of the resulting tetrads arise from double crosses or rod-tetrads excepting one much larger one which is a typical atelomitic ring, the size of which proves it to represent the large V-pair of the spermatogonia. See also especially Robertson ('16).

their history and in which the genetic continuity of the chromosomes remains unbroken throughout.[1] This finds a remarkable confirmation in the heteromorphic tetrads of *Trimerotropis* and *Circotettix* (p. 571) in which certain of the somatic chromosome-pairs differ in mode of attachment of the synaptic mates, one being rod-shaped and terminal, the other hook-shaped and non-terminal (Fig. 439). The crucial proof is given by the fact that the number of non-terminal attachments, though constant in the individual, differs from one individual to another. Close comparison by Carothers has demonstrated that whatever be the number of non-terminal attachments in the gonial groups *the same number reappears in the tetrads of the same individual* (p. 934).

C. The Interkinesis and the Homeotypic Division

The concluding phases of meiosis offer a much simpler problem than the earlier ones. In the anaphases of the heterotypic division, as we have seen, the daughter-chromosomes are typically double, forming dyads each of which is destined to separate into two single chromosomes during the second or homeotypic mitosis. Externally the second division is in this respect closely similar to an ordinary somatic mitosis; its only noticeable peculiarity in many cases, indeed, is the shorter and more compact form of the chromosomes, and even this is sometimes but slightly marked. Nevertheless this division may differ in a very important way from the somatic divisions; for there is now no doubt that at least some of the chromosomes may divide reductionally, as will later be shown.

That the anaphasic duality of the heterotypic division is the forerunner of that which appears in the metaphase-chromosomes of the second division is often readily seen and is practically certain even when not directly demonstrable. The two divisions are separated by a pause or interkinesis usually of short duration, though wide differences in this respect exist between different species. Some of the observed conditions are brought together in Fig. 260 so arranged as to show a progressive series. At one extreme are cases in which no vesicular nucleus or "resting stage" is formed, the dyads persisting as such and passing directly upon the second spindle with only slight change of form and without the formation of a vesicular nucleus. This condition is common in the polar divisions in the animal egg generally, typical cases being given by such forms as *Ascaris* (Fig. 238), the insects, mollusks and annelids (Figs. 194, 239). The same condition is also often seen in the spermatocyte-divisions, *e. g.*, in *Ascaris* (Fig. 241) and in many insects (Fig. 369); and in some of these cases the dyads not only retain their identity as such but also their characteristic anaphasic grouping only slightly

[1] Modified only by the exchanges of material in crossing-over (p. 950).

changed as they enter the second metaphase (Fig. 260, D). All such cases are probably conditioned by a very short pause between the two divisions.

With a longer interkinesis the dyads become inclosed by a nuclear membrane and become less regular in outline, but may still visibly retain their identity and double structure in many forms. In such cases the two halves of the dyads often become partially separated, flexed or displaced so as to produce characteristic X-shaped, V-shaped or other figures. This condition seems to be rare in plants (Fig. 260, E), but is common in animals (annelids,

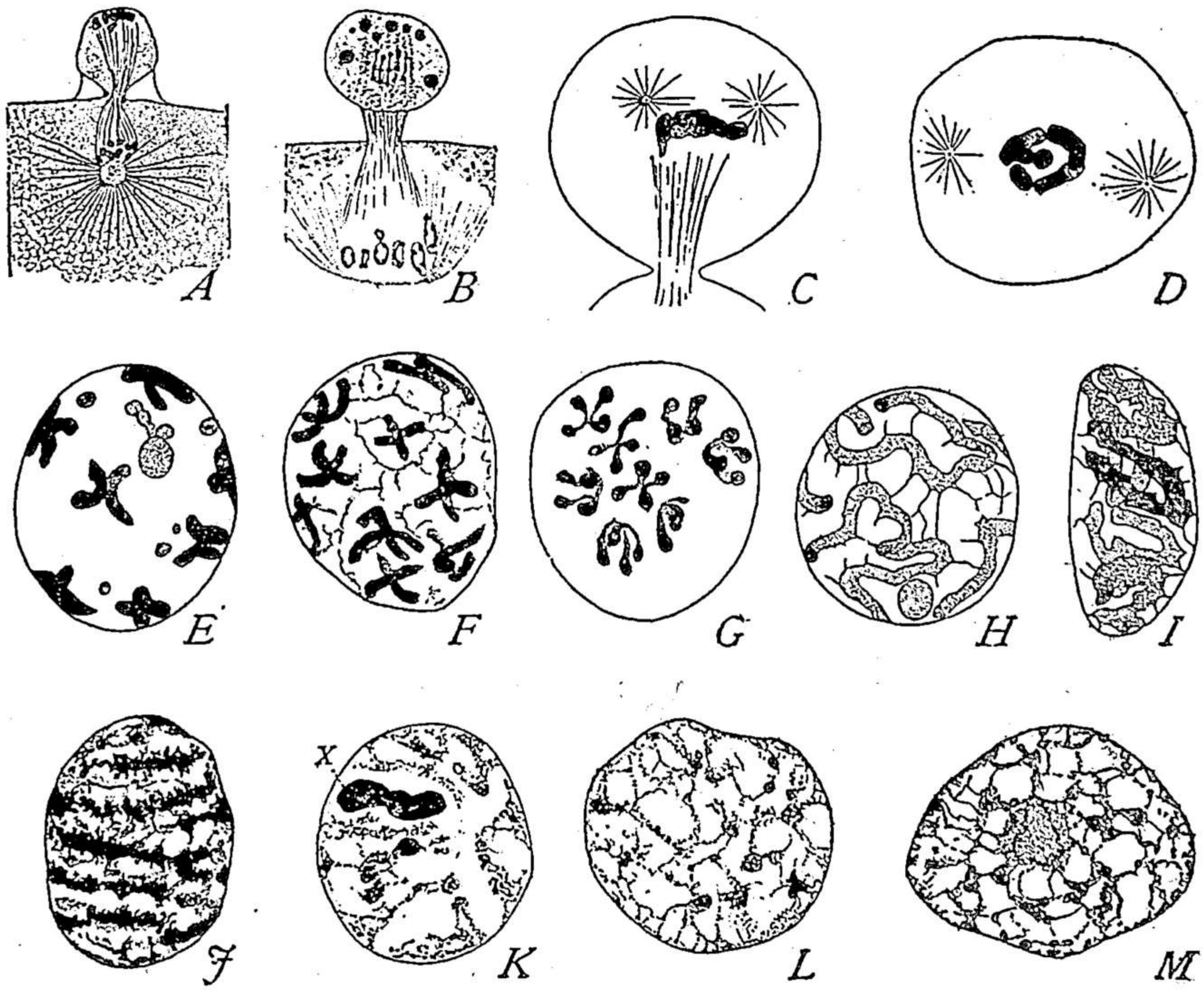

Fig. 260.—Nuclei during the interkinesis, from various plants and animals.

A, oögenesis in the gastropod *Crepidula* (CONKLIN); *B*, in the annelid *Rhynchelmis* (VEJDOVSKÝ) *C*, telophase and *D*, interkinesis in the hemipter *Oncopeltus* (WILSON); *E*, sporogenesis in *Œnothera* (DAVIS); *F*, spermatogenesis in the salamander *Desmognathus* (KINGSBURY); *G*, spermatogenesis, in the annelid *Tomopteris* (the SCHREINERS); *H*, sporogenesis, *Podophyllum*, not yet at full rest (MOTTIER); *I*, *Trillium* (ATKINSON); *J*, spermatogenesis in the salamander *Amphiuma* (MCGREGOR); *K*, *L*, spermatogenesis in the grasshopper *Phrynotettix* (WENRICH); at *X*, the X = chromosome; *M*, sporogenesis in *Galtonia* (DIGBY).

insects, some vertebrates); examples are shown in Fig. 260, F, G.[1] In such cases likewise it is easy to prove that the dyads pass directly upon the second spindle, and are separated into their two components. With a longer interkinesis the dyads undergo more extensive changes, during which the anaphasic duality is often obscured or lost to view. This condition

[1] See Kingsbury ('02), Vejdovský and Mrazek ('03), the Schreiners ('06), Bonnevie ('08), Morse ('09), Kornhauser ('15), etc.

appears, for example, in *Salamandra* (Meves, '98), *Amphiuma* (McGregor, '99), *Lilium* (Strasburger, '00, Mottier, '03) or *Paris* (Grégoire, '05), etc. In such cases the nucleus commonly shows a spireme-like structure (Fig. 260, H–J), but in some forms it may advance almost as far as the "resting" or reticular condition (Fig. 260, K, L, M). Such cases offer the same problem as the somatic nuclei generally. Since, however, these cases are connected by all possible intergradations with those in which the chromatids as such are never lost to view, the conclusion seems fully justified that the two original

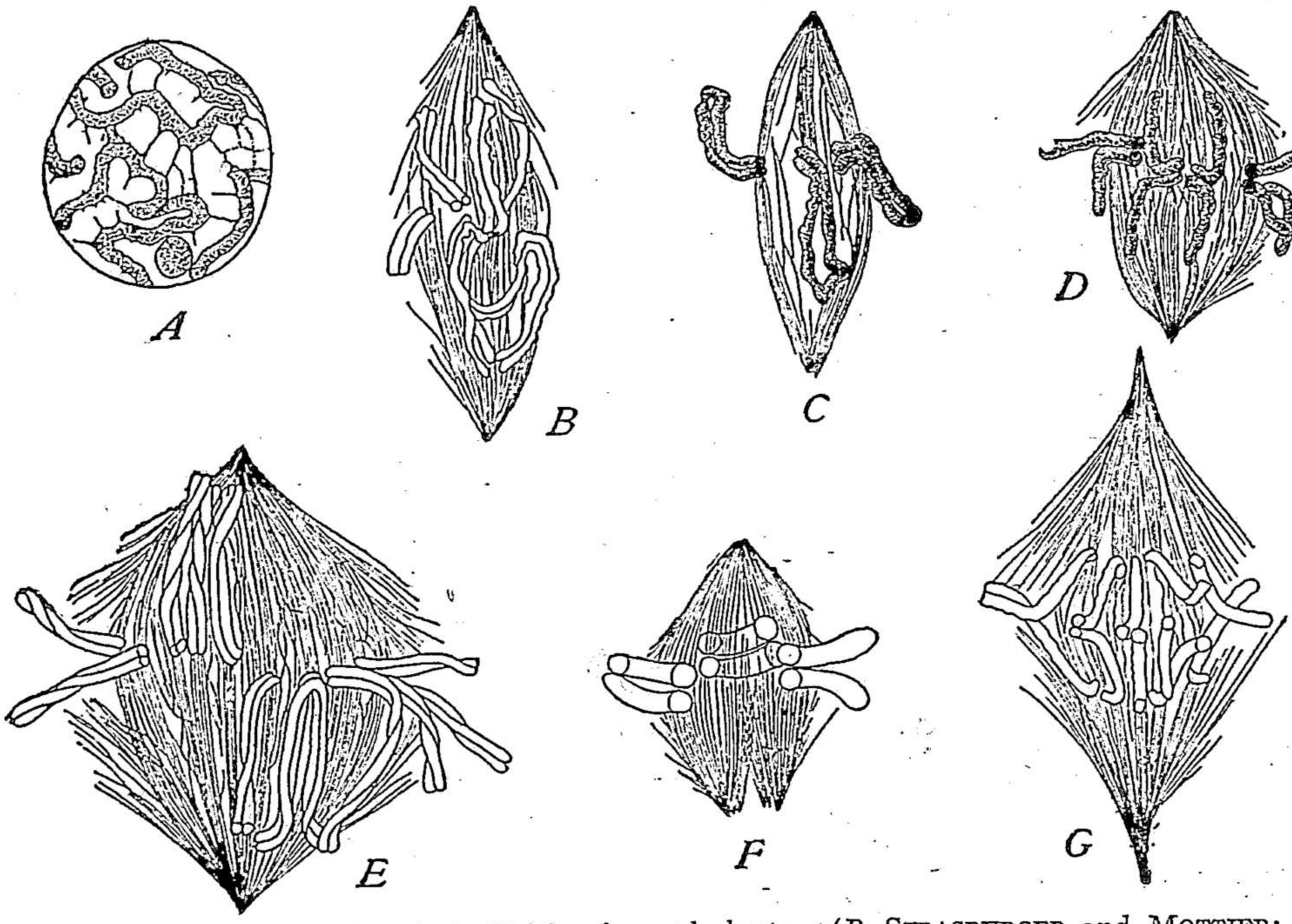

Fig. 261.—The second meiotic division in seed-plants. (*B*, STRASBURGER and MOTTIER; the others from MOTTIER.)

A, nucleus of secondary microsporocyte (*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.

cleavage-clefts of the tetrads are the forerunners of the two actual divisions respectively.

At the end of the interkinesis the chromosomes are bipartite bodies which separate into two single chromosomes in the course of the second division. In the case of compact tetrads they are commonly of a short, dumb-bell shape, and often do not differ markedly in outline from the tetrads of the first division (*e. g.*, in Hemiptera, Fig. 369). When more elongate they have the form of simple rods, J's or V's, longitudinally double, often closely simi-

lar in appearance to the somatic chromosomes (Figs. 242, 261). These forms, as indicated in the preceding section, correspond closely to the original spindle-attachments of the gonial chromosomes, and to those of the tetrads.[1] These facts constitute very strong evidence in favor of the individuality or genetic continuity of the chromosomes; and demonstrate that a complete continuity of organization is maintained throughout the whole process of meiosis and segregation from the diploid gonial groups down to the haploid groups of the gametes.

D. Growth Period of the Auxocytes

1. Introductory

In the foregoing account theoretic prepossessions have, as far as possible, been laid aside except in so far as they might be useful in following an objective description of the observed phenomena. We have thus far simply assumed that the bivalent represents two gonial chromosomes (synaptic mates) in close synaptic association and sooner or later longitudinally split. On what actual evidence does this interpretation rest; and if it be well founded, when and how does the association take place? An immense amount of effort has been put forth in the search for decisive answers to these questions. It has been fully demonstrated that in higher plants and animals the formation of the bivalents occurs during the growth-period of the auxocytes. Most observers are also agreed that the process takes place at a very early period, before the auxocytes have entered upon their most active growth, during the so-called *synaptic period* or *synaptic phase*. It is not yet certain whether synapsis always takes place at this time—certain special exceptions are indeed known (pp. 769, 839)—and some differences of opinion still exist concerning the nature of the process itself. Its effects, however, are unmistakable, as shown by a vast array of evidence, direct and indirect. To its survey we now address ourselves by an examination of the earlier history of the bivalents, and their genetic relations to the gonial chromosomes.

Comparative studies have shown that the events of the growth-period may be grouped in a series of stages which, with many minor variations, display a broad similarity in both sexes of animals and in the spore-formation of plants. The most conspicuous fact in all cases is the formation of a spireme, analogous in many respects to the early prophase of a somatic mitosis, but not at first longitudinally double and not leading directly to a mitosis. This is followed at an early stage by a coupling (synapsis, syndesis) of the spireme-threads or their products two-by-two to form bivalent chro-

[1] For striking examples of this see the observations of Davis ('08), McClung ('05, '14, '17), and Carothers ('17) on *Orthoptera*, and of Agar ('11, '12) on *Lepidosiren*.

mosomes; and the association of synaptic mates thus effected typically persists throughout the whole growth-period until they or their products are disjoined in the reduction-division.[1] It is a remarkable fact, still unexplained, that synapsis and disjunction should be separated by so long a period—in some cases it is measured by years—and by so many cytological events concerned not with meiosis but with the growth and differentiation of the gametes or spores.

2. Outline of the Stages

The stages of meiosis during the growth-period differ appreciably in different species and some of the differences may be of major importance. For the purposes of a preliminary survey we may, however, conveniently recognize eleven successive stages, beginning with the final gonial telophase and extending up to the heterotypic division. Some of these stages may fail to appear in particular cases; others may differ in an important way from that here indicated; but the following outline may serve as a useful guide to the terminology and to the general order of the stages as commonly described. They are illustrated by the accompanying diagram (Fig. 262) based primarily on the conditions observed in animals generally, but also broadly applicable to those of plants. The terminology is based on that of Winiwarter ('00). There is reason to believe that beneath all differences, real or apparent, a fundamental uniformity exists in the most essential of the phenomena, and that the seeming contradictions which in some measure still exist will be cleared up by further investigation.

Of the following stages those inclosed in brackets, including *c*, *d*, *h*, *i*, and perhaps *b*, may be omitted in particular cases.

a. The final gonial telophase. In this, the initial stage of the growth-period, the nuclei are vesicular, rather small, and still show the individual telophase-chromosomes, still more or less compact and deeply-staining (Fig. 265, B, E). It is possible that in some cases this stage passes directly over into Stage *c;* but as a rule it is followed by

b. A "resting" or net-like stage, commonly of rather short duration (as judged by the size of nucleus and cytosome), in which the individual chromosomes are temporarily lost to view in a net-like framework, approaching in this respect to the condition of a somatic nucleus (Fig. 263, A–C). These nuclei (slightly enlarging the application of Winiwarter's term) may be called *protobroch* nuclei. In their later condition, as they prepare to enter the following (leptotene) stage, they were called by Winiwarter *deutobroch* nuclei, but this term, like the preceding one, is not yet in general use. It

[1] Certain special exceptions to this are elsewhere indicated (p. 563, etc.).

is possible that this stage, though of widespread occurrence in both plants and animals, may be suppressed in some cases.

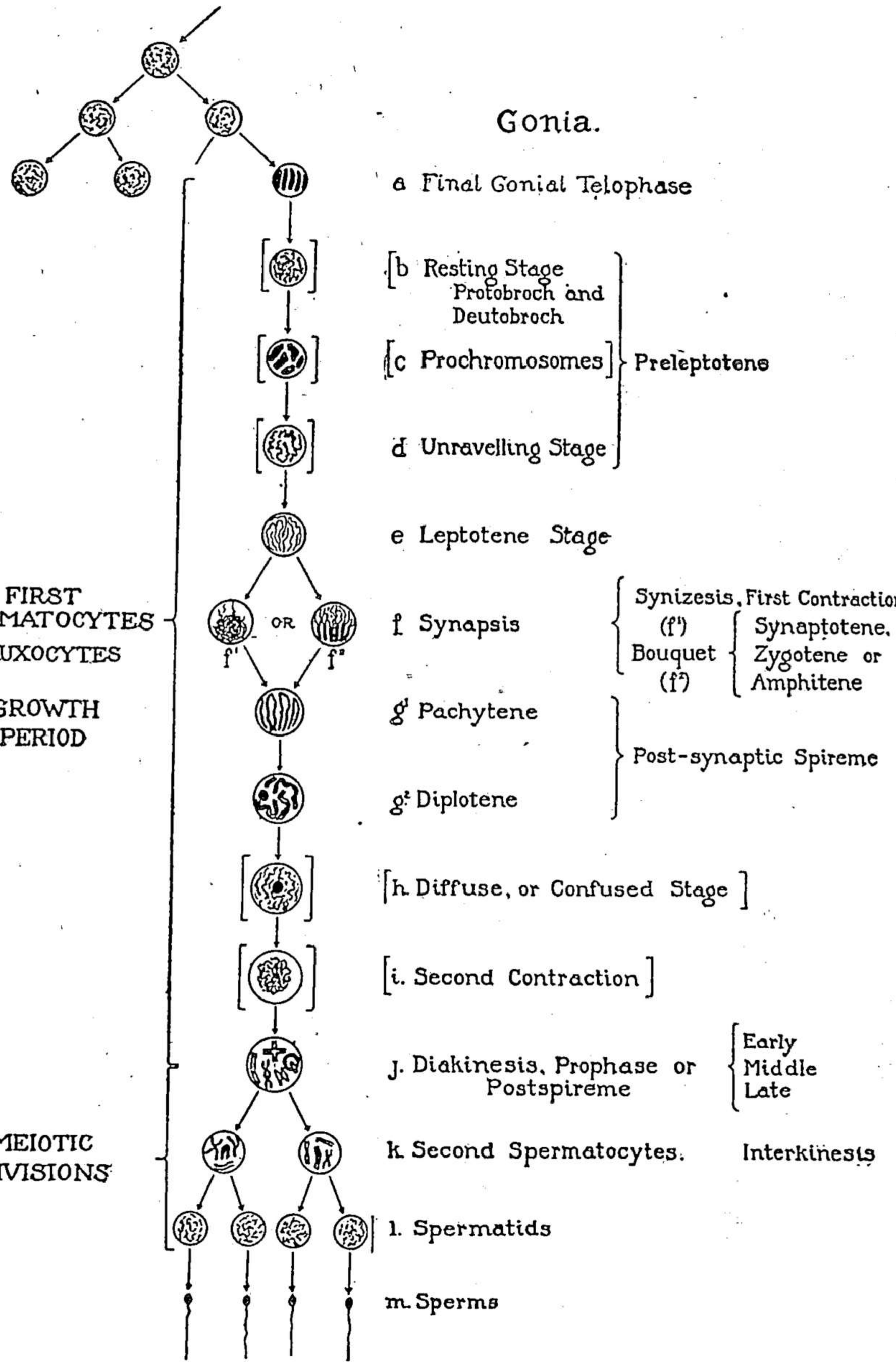

Fig. 262.—Diagram of the stages of maturation and meiosis, to show their order of succession. Stages inclosed in brackets may be lacking in certain cases. The synaptic stage (f) is represented of two different types (f^1 and f^2). Terminology based on that of Winiwarter. Cytological detail roughly indicated in the key-figures.

The changes taking place in the two following stages (*c*, *d*) result in the formation of a fine spireme, the *leptonema* or *leptotene-stage* (Stage *e*); but in

many cases (*e. g.*, in vertebrates generally) the leptonema may be formed directly from the network of Stage *b*, Stages *c* and *d* being omitted.

c. In this, the *prochromosome-stage*, the nuclear framework of Stage *b* again draws together into separate, more or less massive chromosome-like bodies. This stage has been most carefully examined in the insects, but has

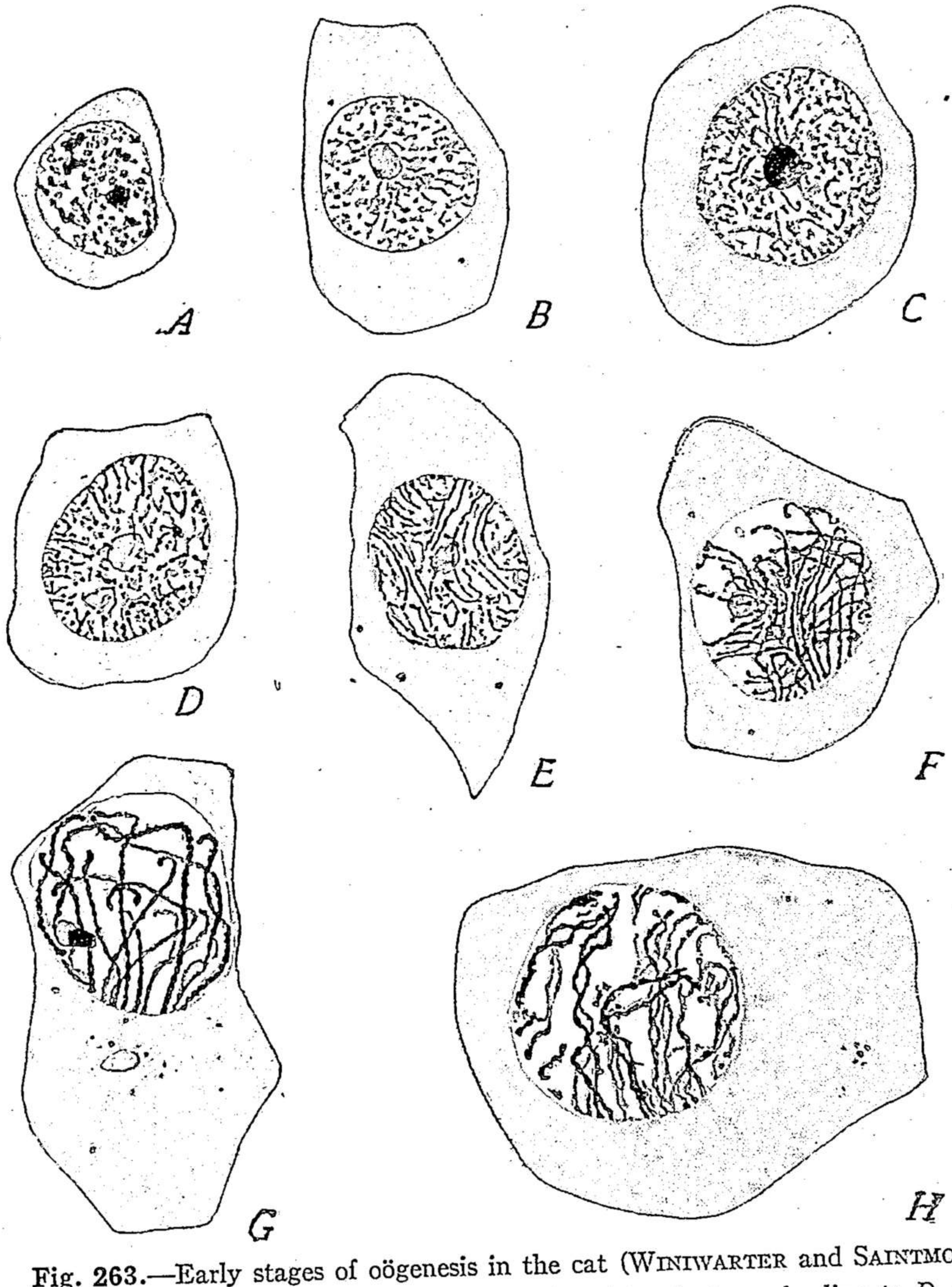

Fig. 263.—Early stages of oögenesis in the cat (WINIWARTER and SAINTMONT).
A, protobroch nucleus, or "resting" stage; *B*, *C*, transitional stages leading to *D*, deutobroch nucleus; *E*, leptonema; *F*, early synaptonema, synapsis; *G*, pachynema; *H*, diplonema, strepsinema.

also been described in some other cases. The form of the prochromosomes varies in different species, but in some degree approaches that of the gonial chromosomes. In the Orthoptera, for instance, they are often elongated and more or less distinctly polarized (Fig. 265, G–I); in the Hemiptera or Coleoptera they are commonly much shorter, often spheroidal tend to

take up a peripheral position, and are not definitely polarized (Figs. 266, 267). Many careful observers have found that their number is nearly, in some cases exactly, equal to the gonial or diploid number; and sometimes they clearly show the same size-relations. Clearly, therefore, these bodies represent a *diploid group of chromosomes corresponding with those of the gonial divisions*. In many cases no trace of this stage has yet been found; typical examples are offered by the vertebrates (urodeles) and platodes (*Dendrocœlum*, Fig. 279).

d. The unravelling stage, during which each prochromosome resolves itself into a closely convoluted or irregularly coiled fine thread which then

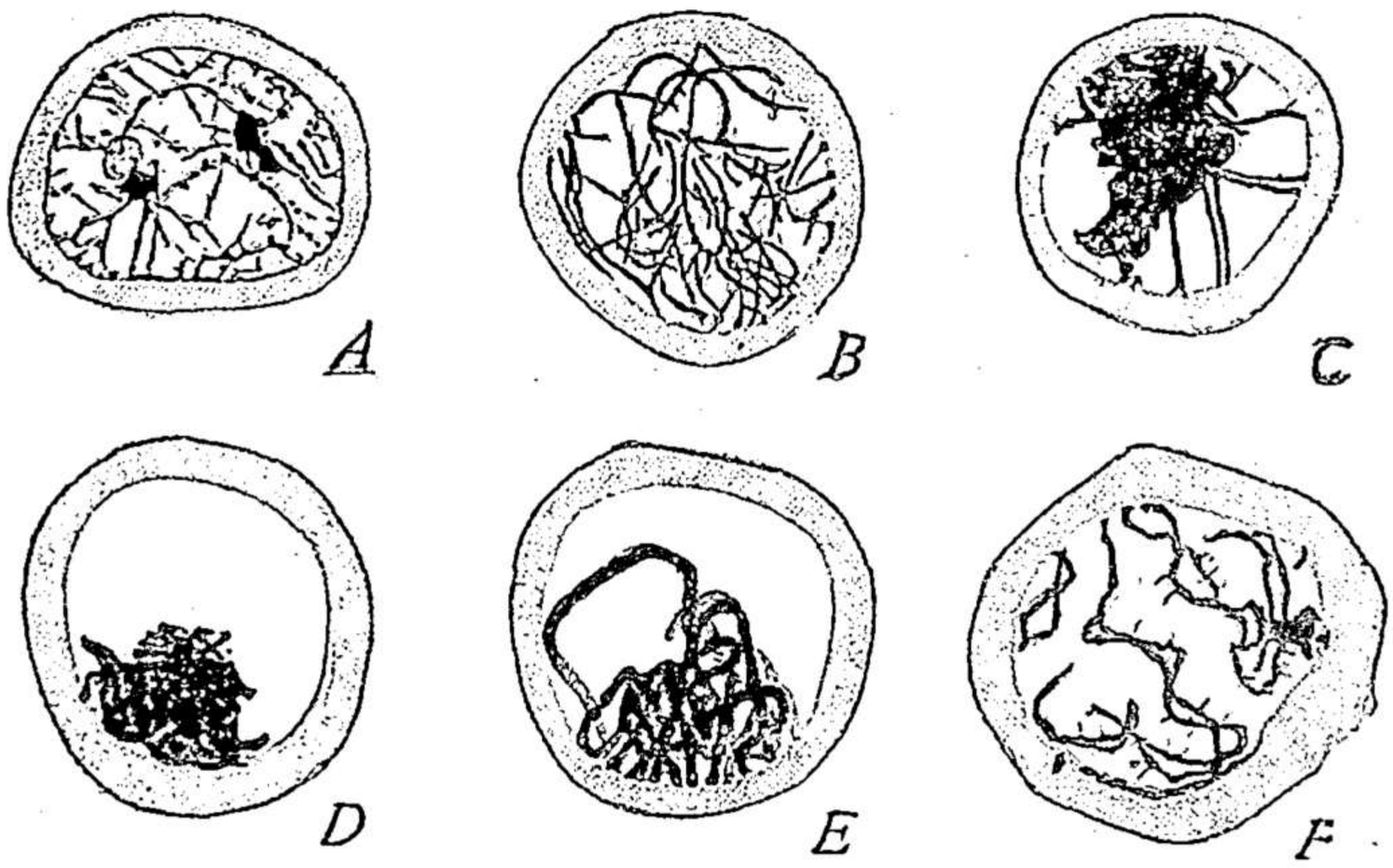

Fig. 264.—Oögenesis in the rabbit (WINIWARTER).

A, early deutobroch nucleus; *B*, leptonema; *C*, synaptic stage (early synizesis); *D*, complete synizesis; *E*, pachynema; *F*, diplonema.

unravels or uncoils to form a single leptotene-thread (Figs. 265, 267). The evidence, though rather scanty, makes it highly probable that only one such thread is formed from each prochromosome [1] and this has been clearly proved in the case of particular prochromosomes, *e. g.*, the large M-chromosome pair in the beetle *Blaps* (Nonidez). This point is of great theoretic interest in contributing to the demonstration that, in some cases at least, *the number of leptotene-threads is diploid* (p. 541).

e. The leptonema or leptotene-stage.[2] This stage is a fundamental and all but universal one from which all later ones take their point of departure. The nuclear substance has now resolved itself into delicate threads which typically show no sign of longitudinal splitting. They are at first irregular, contorted, and when preceded by prochromosomes often clumped in masses corresponding to the bodies from which they have arisen. As above stated,

[1] See especially Davis ('08), Wilson ('12), Nonidez ('20), etc.

[2] It is customary to use the first of these forms as a substantive and the second as the corresponding adjective form; and similarly with pachynema, pachytene, etc.

however, the threads may be formed directly from the nuclear framework of Stage *b* by a process similar to the early spireme-formation in many somatic mitoses (Figs. 263, 279). This has been circumstantially described by various observers in both animals and plants.[1] In a large class of cases

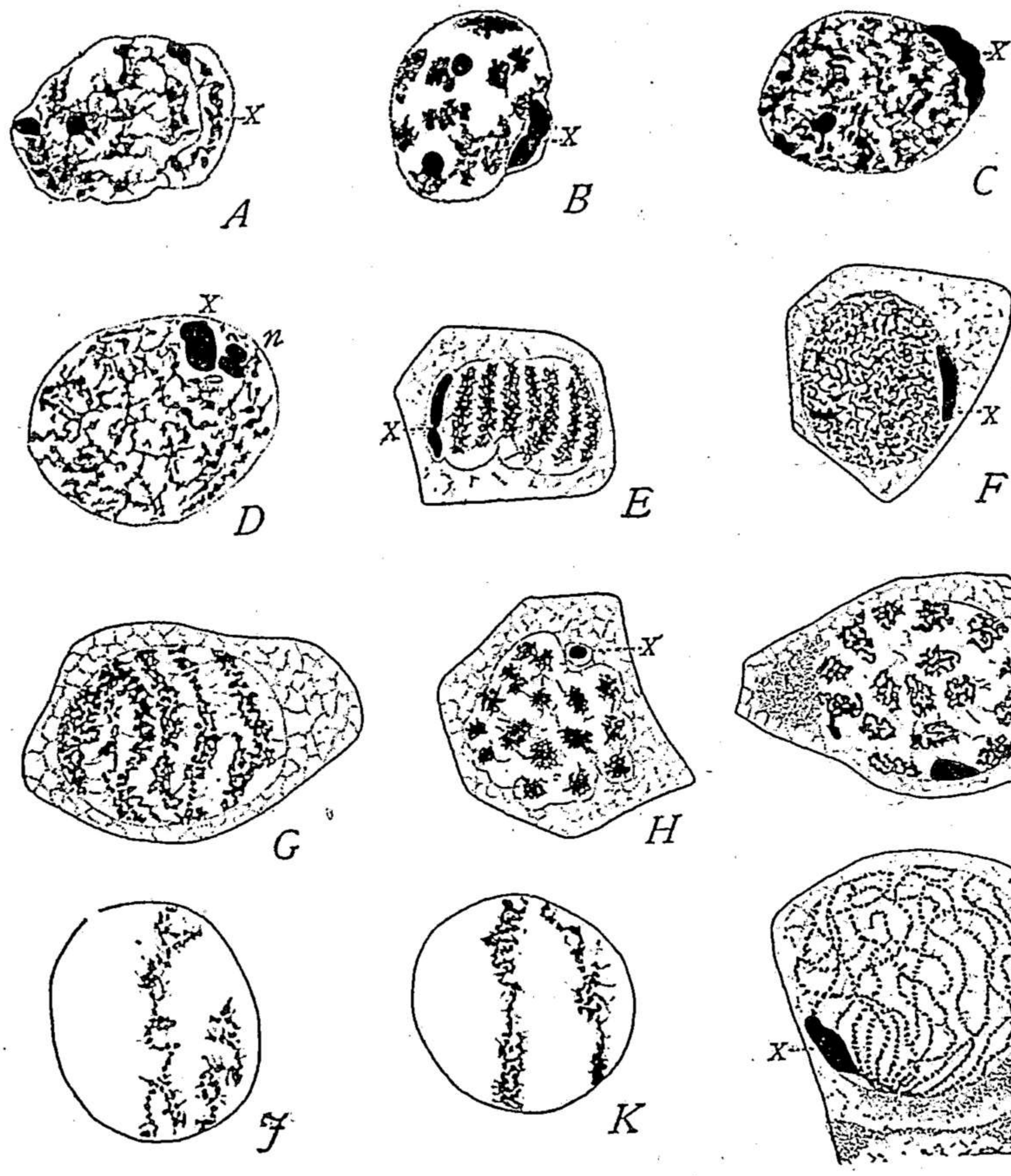

Fig. 265.—Presynaptic stages of meiosis in grasshoppers. (*A–D*, from ROBERTSON, the others from DAVIS).

A–D, *Syrbula; A*, spermatogonial nucleus, separate X-vesicle at X; *B*, spermatocyte-nucleus, just after last spermatogonial telophase, condensed X-chromosome; *C*, *D*, origin of spireme-like structure (leptonema) from same; *E*, last spermatogonial telophase in *Dissosteira*, stage *a; F*, net-like "stage *b*"; *G*, formation of massive polarized prochromosomes (stage *c*) in *Chortophaga; H*, same from pole; *J*, *K*, unravelling of leptotene-threads (stage *d*); *L*, leptonema, in some degree polarized, *X*, the chromosome-nucleolus or X-chromosome (monosome).

the threads gradually become more even and often form loops that are more or less definitely polarized with their ends turned towards that pole of the nucleus near which the centrioles and idiozome lie (Figs. 263, 265, 279). The nucleus thus enters the initial "bouquet-stage," which attains its full development in the ensuing stage.

[1] *E. g.*, in mammals (Winiwarter, '00, Winiwarter and Saintmont, '09), urodeles (Janssens, '01), elasmobranchs (Maréchal, '06) and platodes (Gelei, '13, '21), and in the seed-plants (Mottier, '97, '05, '09, etc., Berghs, '04, '05, Allen, '04, Grégoire, '04, '05, '07, '10, etc., Digby, '10, '14, etc.).

In the case of animals generally evidence has steadily accumulated that *the leptotene-spireme is not continuous but consists of separate segments; and in most well-determined cases these are of the diploid number;* their union to form bivalents has therefore not yet taken place (p. 556). This may be determined with a high degree of probability in Type f^1 by counting the number of prochromosomes from which they arise, in Type f^2 by polar views of the polarized threads, or in certain cases by counting them in side-view (*Dendrocœlum*, p. 555). Among plants, on the other hand, it has not yet been found possible to count the leptotene-threads at this time, and many observers have concluded that the spireme is continuous, only breaking into shorter pieces or segments at a much later period.[1]

The foregoing five stages are preparatory in character and are often designated as *pre-synaptic* or *pre-syndesic*. Now ensues

f. The *synaptic stage* during which, in a large class of cases, occurs the actual association or conjugation, of the chromosomes (in the form of leptotene-threads) two by two to form the bivalents. This process we shall designate as *synapsis* (or syndesis).[2] Nuclei in this stage are of two types, as follows:

f^1. In one of these, widely distributed in higher plants, in arthropods and in various other invertebrates, the leptotene-threads commonly show no definite polarization and become massed together into a more or less dense, intensely staining knot, usually situated towards one side of the nuclear cavity and often inclosing a nucleolus (Figs. 264, 267). This is the contraction-figure or *synizesis* (often called the "synapsis"), which greatly increases the difficulties of observation at this time. Even nearly related forms may differ in respect to the synizesis; for example, it is conspicuously present in Hemiptera or Odonota but absent in most Orthoptera. The synizesis has been supposed by many writers to be an accidental artifact or coagulation product (Meves, Janssen, McClung, Schreiner and others) due to defective fixation; but such is not always the case as is proved by the oft-repeated observation (Sargent, Overton, Grégoire, Vejdovský, Œttinger, Wilson and others) that the contraction-figure may be observed in the living or fresh unfixed material, though it may be accentuated, or even in

[1] See, for instance, the works of Strasburger, Grégoire, Berghs, Allen, Mottier and Digby, cited above.

[2] The term synapsis as thus used is open to some objection, for an important group of cytologists have disputed the conjugation of the chromosomes at this time. The terms *synaptenic* (Winiwarter, '00), and *zygotenic* (Grégoire, '10) are open to the same objection. Janssen's term ('03) *amphitenic* avoids this particular difficulty but is not sufficiently inclusive. A second source of confusion lies in the double meaning attached to the word "synapsis" itself. Though originally applied by Farmer and Moore ('05) to "the temporary union in pairs of premeiotic chromosomes," it later became confused with the contraction figure (synizesis) often associated with this process, so that the word has been widely applied to this figure instead of to the process itself. In the opinion of the writer, the original use of the word should be retained (*cf*. Wilson, '12, p. 349).

some cases artificially produced, by coagulation.[1] Of much interest is the fact that in a few cases the synizesis is foreshadowed already in Stage *c* by a migration of the prochromosomes towards one pole where they become

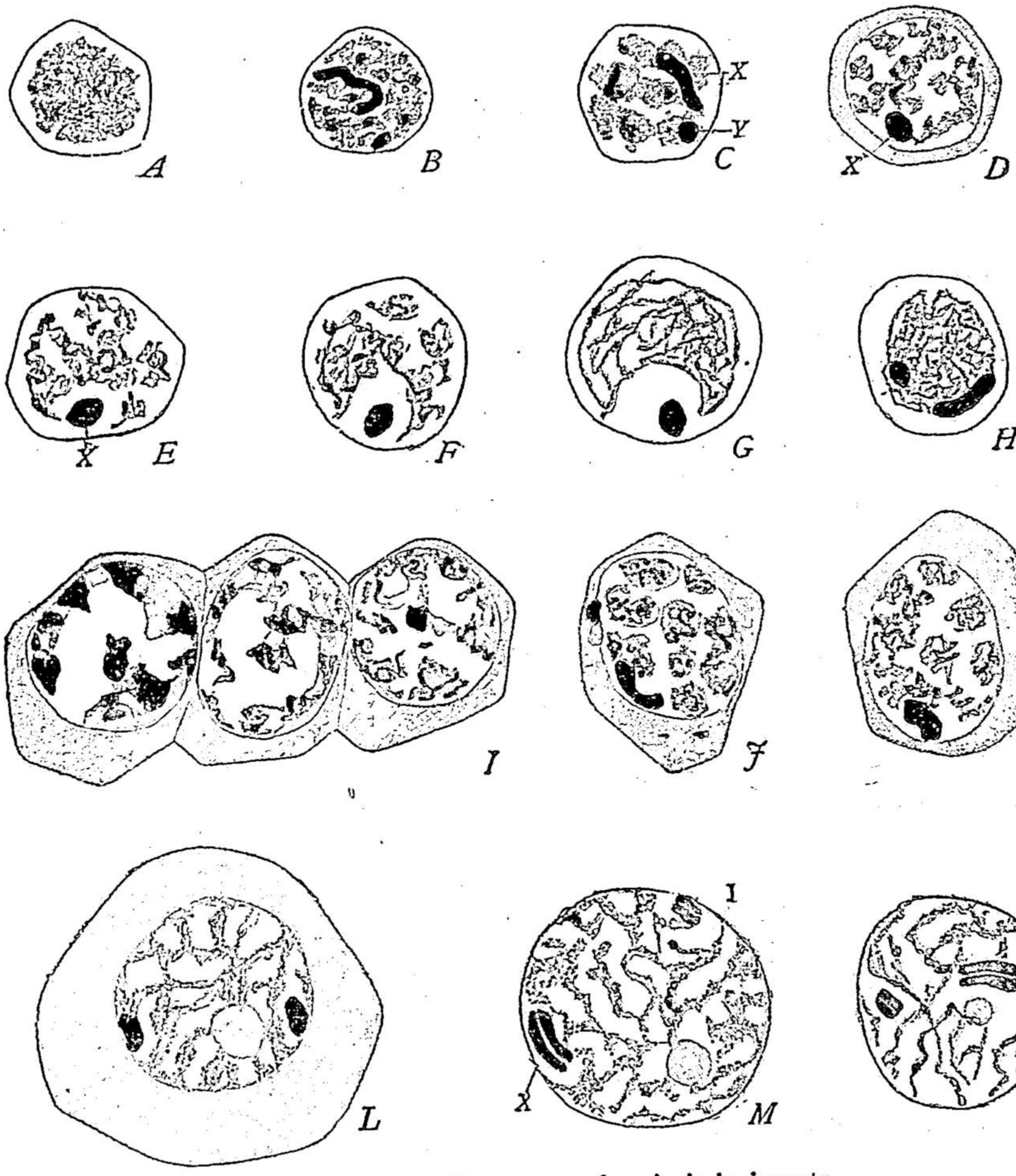

Fig. 266.—Earlier stages of meiosis in insects.

A–C, *H*, *M*, *N*, from the hemipteron *Lygæus bicrucis; D–G*, from *Largus cinctus; I*, from the dragon-fly, *Anax; J*, *K*, from the grasshopper, *Achurum; L*, the hemipter, *Oncopeltus*.

A, Stage *b*, net-like condition; *B*, appearance of the X and Y-chromosomes; *C*, stage *c*, prochromosomes; *D–F*, stage *d; G*, *H*, leptonema; *I*, prochromosomes at left, unravelling at right; *J*, *K*, stage *d*, unravelling; *L*, *M*, stage *h*, diffuse stage; *N*, stage j^1, very early diakinesis.

closely aggregated before the leptotene-threads are spun out from them,[2] so that the synizesis is indicated from the first stages of leptotene-formation.

Many observers, among both botanists and zoölogists, have produced

[1] Sapĕhin ('15) has published photographs of the synizesis from living cells of the mosses *Fissidens* and *Catherinea*. Taylor ('22) has on the other hand found that in *Gasteria* the synizesis may be almost completely eliminated by proper fixation.

[2] This was demonstrated by Nonidez ('20) in the beetle, *Blaps*, though earlier observers had seen something of the sort (Arnold, '08, in *Hydrophilus*).

evidence that as the leptotene-threads draw together to form the synizetic knot they become associated two-by-two and side-by-side (Fig. 264) to form threads that are thicker and at first longitudinally double, thus constituting the bivalent chromosomes. The evidence for this process is, however, less convincing in this case than in the following type.

f^2 In a second type, widely distributed among animals but apparently rare among plants, a contraction-figure or synizesis is usually lacking (there are some exceptions) and the spireme-threads, now having the form of loops, show a more or less pronounced polarization with their ends turned

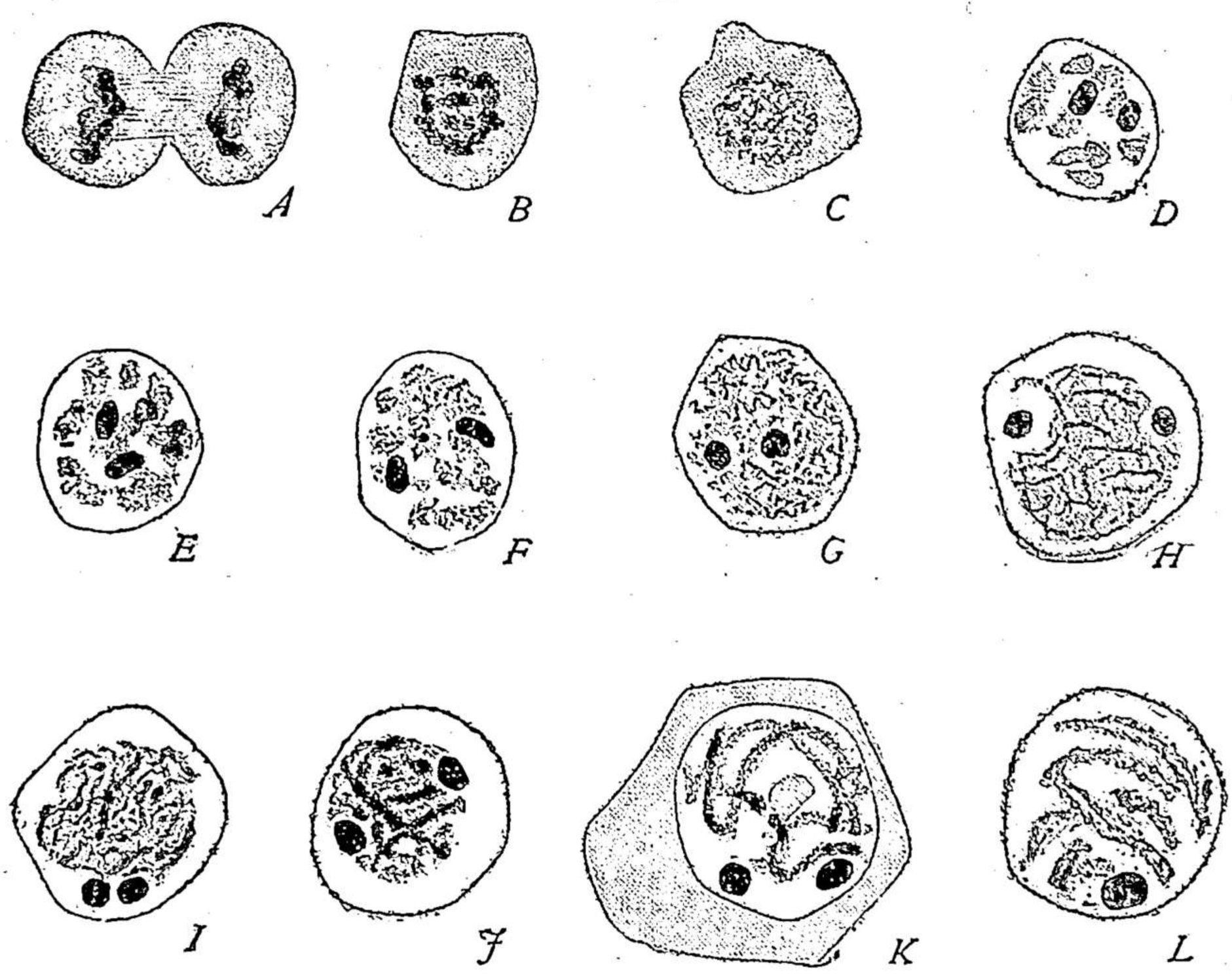

Fig. 267.—Earlier stages of meiosis in spermatocytes of Hemiptera; *A–K*, from *Oncopeltus fasciatus; L*, from *Largus cinctus*.

A, *B*, stage *a*, spermatogonial telophase; *C*, stage *b*, net-like or "resting " stage; *D*, stage *c*, prochromosomes; *E–G*, stage *d*, unravelling of the leptotene-threads; *H*, stage *e*, leptonema; *I*, *J*, stage f^1, synizesis, here not greatly marked; *K*, stage *g*, post-synaptic spireme, pachynema; *L*, diplonema.

From *D* onwards the *X* and Y-chromosomes distinguishable by their compact form (chromosome-nucleoli).

towards the pole of the nucleus near which lie the centrioles surrounded by the idiozome. The polarized threads now progressively thicken and shorten by a process that begins at their polar (free) ends and proceeds towards the opposite pole, so that in the middle part of the period the polar region of the nucleus is occupied by polarized thick threads (*pachytene*), the antipolar by thin ones (*leptotene*), the latter often still irregular in arrangement (Figs. 269, 271, 272). This is the stage often called the *bouquet* (Eisen) or *amphitene* (Janssens),—the latter name in allusion to the presence

of two kinds of threads, thick and thin. The former, growing at the expense of the thin threads and still retaining their polarized grouping, finally occupy the entire nucleus, which thus enters the following or pachytene stage.

The nature of the foregoing process has been examined with particular care in the mammals (Winiwarter), urodeles (Janssens), elasmobranchs (Maréchal, Schreiners), and has also been minutely studied in some of the invertebrates, especially in the annelid *Tomopteris* (Schreiners), in the Orthoptera (Wenrich, Robertson), and in the platode *Dendrocœlum* (Gelei). These and many other studies leave no doubt, in the writer's opinion, that the thick or pachytene threads are formed by a union of the thin ones (leptotene) side-by-side (*parasynapsis*) which proceeds from the pole towards the antipole. By this process the pre-synaptic or leptotene-spireme has thus been converted into the much thicker and denser *post-synaptic spireme* of the following stage.

The two foregoing types of synaptic nuclei are connected by various intermediate conditions which prove that they are essentially of the same nature. The polarization, so striking and regular in the forms enumerated above, is much less definite in many of the Orthoptera and disappears in certain of the Hemiptera in which the synizesis is but slightly marked (Montgomery, '11, Wilson, '12). On the other hand, a more or less definite polarization is described by various observers in synaptic nuclei which show a decided synizesis.[1] We are therefore probably dealing with two divergent modifications of a single type, accentuated in some cases, perhaps, by the coagulating effects of the fixatives employed in their study.

g. The *post-synaptic spireme* (sometimes called the *auxospireme*) consists of conspicuously shorter and thicker threads (*pacyhnema*, or *pachytene-spireme*) *of half the original number* (*i. e.*, of the haploid number). In many cases the thick threads show no external sign of duality (Figs. 263, 267, 268, 269), as if a complete fusion of the synaptic mates to form a single pachynema had taken place (*Tomopteris*, urodeles, mammals). In others they seem always to show at least some indication of longitudinal duality (Turbellaria, Orthoptera); and it is probable that such a duality is always present in their internal structure even when they seem externally to have fused (p. 951). Sooner (*Dendrocœlum*) or later (urodeles), however, the threads are plainly longitudinally double (*diplonema*); and the two threads, especially in the later stages, are often spirally twisted about each other to form the *strepsinema* or *strepsitene* (Figs. 272, 273). These various conditions cannot as yet be very logically separated as distinct stages and may better be classed in a single group (*g*, as above).

[1] *E. g.*, by Mottier ('98) in *Lilium*, or by Morse ('09) in the cockroach.

h. Diffuse stage. Wide variations exist in respect to the stage that follows the pachytene or early diplotene; but all agree in the fact that the nuclei recede in greater or less degree towards the condition of a "resting" nucleus. This is shown by a more or less diminished basophily, a loosening up of the spireme-threads during which they acquire rougher contours, often branch more or less, and in extreme cases may thus be lost to view in a general nuclear network. These changes, undoubtedly, are correlated with the processes of cytoplasmic growth; for in general the longer the growth-period and the greater the growth of the auxocytes the greater the nuclear diffusion. The deconcentration of the spireme-threads is thus correlated in some measure with the size of the auxocytes, and goes further in the oöcytes than in the spermatocytes. In some cases the pachytene or diplotene is never lost to view (*Tomopteris*, urodeles, various Orthoptera, copepods, platodes, etc.), the "diffuse" stage being slightly marked or hardly distinguishable as such. The extreme diffuse stage is most typically seen in large oöcytes, heavily laden with deutoplasm (p. 351), but the same condition occurs in the spermatocytes of certain animals (some insects, Fig. 266). Even in auxocytes, that approach the extreme type, however, the chromosomes are sometimes distinguishable at every stage, though in a state of great deconcentration (Figs. 161, 312). It is a noteworthy fact that in some of these cases, probably in all, the diffuse chromosomes are distinctly double, with the halves widely separated but still arranged in pairs.[1] Probably, therefore, the diffuse stage should be regarded as a highly modified diplotene in which the duality of the early diplotene, however it may be obscured, in some manner persists throughout.

The preceding stage, whether in the form of a true diffuse stage or of a more or less evident double spireme, is in some forms succeeded by:

i. The second synizesis or contraction-figure, in which the nuclear substance is again contracted in some degree. This condition, rather rare in animals, more frequent in plants, is most marked when it follows a condition of great diffusion, as is seen for instance in some of the Hemiptera (such as *Pyrrochoris* or *Alydus*) where the second synizesis is almost as marked as the first. In plants the contraction is less marked, the spireme-threads being thrown into loops that radiate irregularly from a central mass in which a plasmosome usually lies (Fig. 275).[2]

j. The *diakinesis*, or prophase in the narrower sense. In this, the final

[1] This fact was first observed by Rückert ('92) in the oöcytes of elasmobranchs (p. 269) and has since been found in many other cases.

[2] A somewhat similar stage occurs in certain fishes (Fig. 277) and other animals, which also show a typical amphitene or bouquet stage. It is at this stage, or that which immediately follows, that Farmer and Moore and their followers believe the equivalent of synapsis to take place, *i. e.*, the establishment of the definitive bivalents. It is important to bear in mind, therefore, that in some cases, (*e. g.*, in many insects) no trace of a second contraction-figure seems to exist.

stage, the bivalents assume their final forms by a rapid process of condensation, during which their quadripartite or tetrad structure usually becomes evident, and the chromatids undergo those various shiftings of position and form by which the different types of tetrads are produced (p. 548). The bivalents or tetrads now appear as unmistakably separate bodies, commonly peripheral in position, and *haploid in number* (there are some special exceptions to this). It is conveniently subdivided into the early,

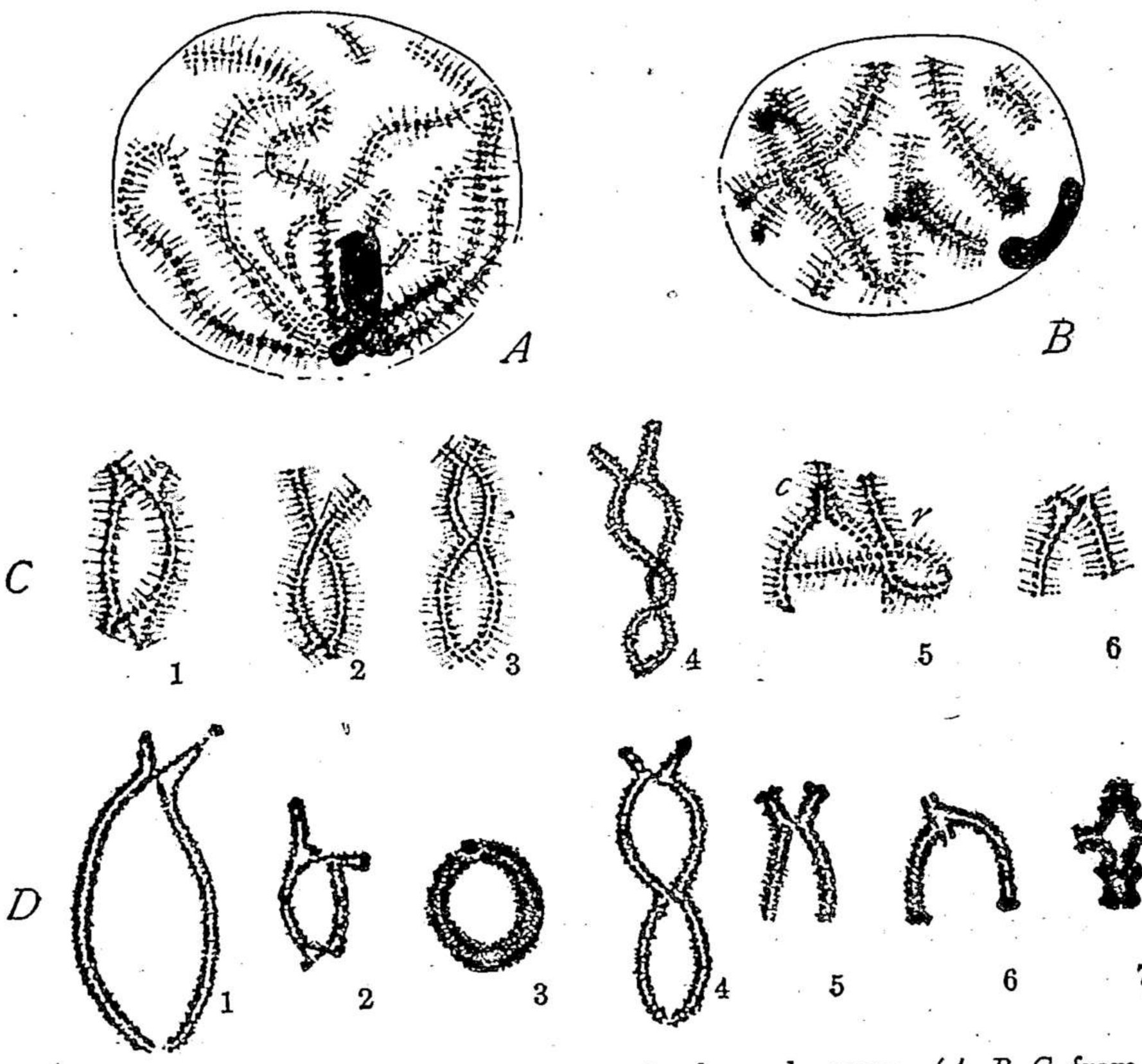

Fig. 268.—Prophase-tetrads in the spermatogenesis of grasshoppers. (*A*, *B*, *C*, from GRANATA; *D*, from WENRICH.)

A, diplotene stage, *Pamphagus; B*, early diakinesis, beginning of the opening-out process; *C*, later diakinesis, *Pamphagus;* 1, early ring with two pairs of lateral arms; 2, the same with one long pair of lateral arms and one short; 3, double ring; 4, twisted ring; 5, *r*, ring with very long lateral arms; *c* doubled cross, 6, double cross, in process of opening out.

D, similar figures from *Phrynotettix;* 1, early single ring, with one pair of arms; 2, ring similar to C_2; 3, condensed ring, no arms; 4, double ring; 5, 6, double cross, opening-out; 7, completed double cross, not yet fully condensed.

middle and late diakinesis (j^1, j^2, j^3). In the early diakinesis (j^1) the bivalents appear in the form of separate more or less elongate spireme-threads, *longitudinally* double and usually from an early period *longitudinally quadripartite*, owing to the appearance of a so-called "secondary split," at right angles to the first (p. 505). The time at which this cleft first becomes evident seems to vary widely in different cases. In *Dendrocœlum* Gelei's careful study ('21, '22) shows that it is first indicated in the early diplotene,

soon after synapsis (Fig. 428, A), though later for a time lost to view. In *Phrynotettix* Wenrich ('16) finds it first appearing in the early diakinesis (Fig. 255, A, 3). In many cases, however, it has not been clearly seen before the anaphases of the heterotypic division.

The shiftings of the chromatids sometimes begin even in the early diakinesis (j [1]) and are continued during the middle period (j [2]) at a period

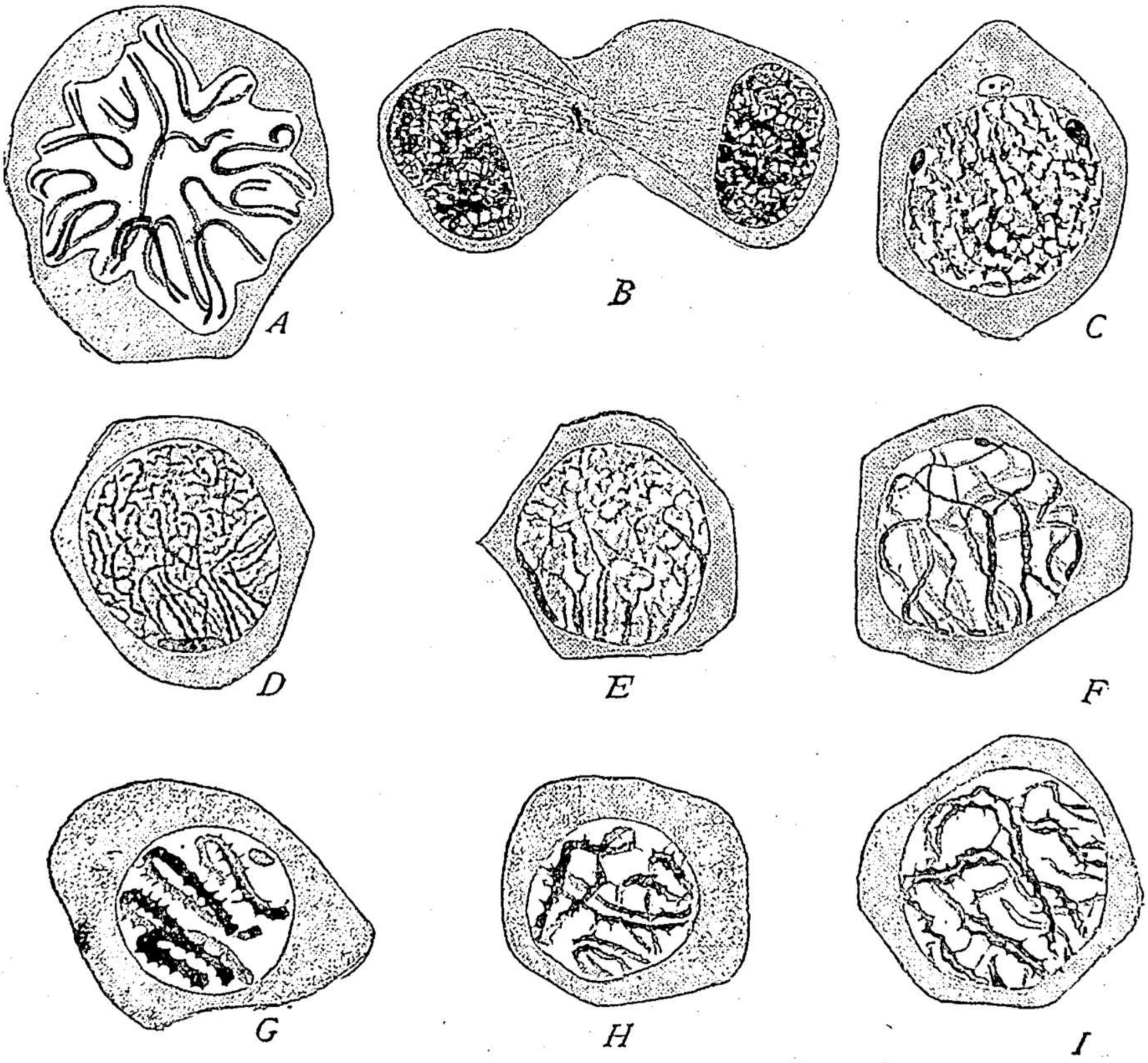

Fig. 269.—Synapsis in the annelid *Tomopteris* (SCHREINER).

A, spermatogonial metaphase; *B*, telophase of last division; *C*, preleptotene; *D*, leptonema; beginning of conjugation; *E*, slightly later stage, amphinema; *F*, late amphinema, the conjugation nearly completed, one Y-figure clearly shown; *G*, pachynema; *H*, *I*, diplonema stages.

when the bivalents are rapidly concentrating; at this time, therefore, many of the characteristic forms of tetrads are seen (rings, double-crosses, transverse tetrad-rods, etc.) in their highest development (Figs. 255, 268). These figures often persist, sometimes in great perfection (*Tomopteris*, etc.) until the late diakinesis (j [3]); but in many cases their relations to the earlier figures are obscured or lost (*Ascaris*, many insects, etc.). All these various forms may be, and in a large number of cases are known to be, derived from threads or rods that are at first longitudinally double (primary or reductional cleft) and later longitudinally quadripartite by the appearance of

a second cleft (secondary or equational) at right angles to the first. To summarize, the principal forms arise as follows:

(1) Longitudinal or anaschistic rod-tetrads by simple shortening of the threads. Spindle attachments terminal, median or intermediate (Fig. 245).

(2) Diaschistic or cross-rod-tetrads, by separation of two halves from one end (most usually along the primary cleft) while remaining attached at the other. Spindle-attachments biterminal or (superficially) median (Figs. 251, 246, 254).

(3) Anaschistic V-tetrads, with median attachment, like anaschistic rods flexed at the middle point (Fig. 250). With subterminal attachment give J-figures (Fig. 252).

(4) Diaschistic V-tetrads, with median attachment, like diaschistic rods flexed at the middle-point (Figs. 251, 253).

(5) Double-crosses, like transverse rod-tetrads with lateral arms drawn out from the middle-point at right angles to the original long axis, often arise by opening apart of the quadripartite rod from one end along the primary cleft, from the other end along the secondary one (Figs. 244, 255, 254, 268).

(6) Single rings by separation of the quadripartite rod along one plane in the central region, leaving the halves attached by their ends; the latter often drawn out laterally to form "lugs" or cross-shaped figures. Spindle-attachments either terminal (Figs. 246, 259) or non-terminal (Figs. 245, 259).

(7) Double rings, from quadripartite rods in which the four components remain attached by their ends but separate along the primary cleft in one half and along the secondary cleft in the other (Figs. 257, 268, etc.).

Other less clearly defined types of tetrads arise by changes of similar type but with minor modifications.

3. General Result

The foregoing facts constitute a solid basis for our earlier assumption (p. 503) that the bivalents or tetrads do, in fact, arise by the association of chromosomes two by two, in pairs, and in many cases side by side; and that the two chromosomes of each such pair persist as the two longitudinal halves of the diplotene-spireme thread. Further, as earlier indicated (p. 505), all the curious shapes and transformations of the tetrads are readily explicable when regarded as modifications of such an original double thread, which has become quadripartite by a longitudinal splitting of each synaptic mate, and has undergone various shiftings of the four chromatids of the tetrad $\frac{A}{-}\Big|\frac{a}{-}$ thus produced. These processes are not a matter of inference but of observed fact. Nevertheless, before we can unreservedly accept

the foregoing interpretation of meiosis, it will be necessary to look more critically at the cytological evidence.

IV. SYNAPSIS AND DISJUNCTION

The Problem of Synapsis

1. Introductory

In its earlier and (superficially) simpler form the theory of synapsis assumed no more than a segmentation of the spireme-thread into the haploid instead of the diploid number of pieces. This conception, which originated with Rückert ('92–'94), Haecker ('92, '95), and Vom Rath ('92), assumed that in mitosis and meiosis alike the chromosomes become aligned end-to-end in a continuous spireme which later segments, in the one case into the diploid number of univalent chromosomes, in the other into the haploid number of bivalents. In meiosis, such a process evidently would involve a primary end-to-end association (telosynapsis or metasyndesis) of the chromosomes but no actual conjugation other than that involved in the spireme-formation. To those who rejected the individuality of the chromosomes accordingly the whole problem of reduction seemed to involve no more than the mode of segmentation of the spireme. This notion has persisted almost down to the present day; [1] but long ago this too simple solution of the problem became untenable.

This theory, obviously, assumed the reduction-division to be a transverse division of the bivalent at the point where the synaptic mates are connected. Evidence quickly was produced, however, demonstrating that both meiotic divisions are often longitudinal (*Ascaris*, urodeles, seed-plants, etc.); hence the earlier scepticism concerning the reduction-division (p. 503). In this conception, nevertheless, investigation of the subject for a long time largely centered, and as remodeled by Farmer and Moore ('03, '05) it is even now upheld by a considerable group of observers. Meanwhile, observations began to accumulate showing that in many cases the chromosomes of the early auxocytes appear at the beginning as separate univalents and of the *diploid number* (as in somatic mitosis) and later conjugate two-by-two in synapsis to form the bivalents.[2] This view later took the dominating position that it now holds. Such a conjugation might conceivably be either end-to-end (telosynaptic) or side-by-side (parasynaptic), and each of these possibilities has been energetically defended.

[1] "In my view, the germ-cells, that is to say their nuclei, inherit the specific peculiarity of producing only the half-number of chromosomes as they enter the growth-period" (Meves, '11, p. 296; also '96, etc.). See also Brauer ('92), Regaud ('10), Champy ('13).

[2] This view first suggested by Henking ('91) and considered by Rückert ('92) and Boveri ('93), first took well-defined shape in the work of Montgomery ('99, '00) and Winiwarter ('00).

On the whole, however, the theory of *parasynapsis* has steadily gained ground since 1900, when the possibility of such a process was first seriously considered. Parasynapsis has, however, been attacked even by recent writers; [1] and we are by no means in a position as yet to assert its universal occurrence.

The issues here raised may conveniently, if not quite logically, be considered under the two heads of *parasynapsis* and *telosynapsis*.[2]

2. Parasynapsis or Parasyndesis

If we except certain casual references by earlier writers (see Fick, '92) the first definite suggestion of a side-by-side conjugation of leptotene-threads came from Winiwarter in 1900, as the result of a study of mammalian oögenesis (rabbit, man), though he did not fully commit himself to this conclusion until several years later (Winiwarter and Saintmont, '09). In the meantime the theory of parasynapsis was placed upon a firm basis, in both animals and plants, by the work of many observers, prominent among them Janssens and A. and K. Schreiner.[3] Since then the theory of parasynapsis has been adopted by many other observers, among them some who, like Montgomery ('11) or Robertson ('16) had long been convinced advocates of telosynapsis.[4]

These observations leave no doubt of the fact that in a large number of cases a side-by-side association of leptotene spireme-threads takes place during the synaptic stage. The general aspect of this process shows wide differences, correlated especially with the presence or absence of a contraction-figure or synizesis. When such a figure is present (most insects and higher plants), the leptotene-threads usually show little or no polarization, and the difficulties of observation are much increased; but even in this case the leptotene-threads are often seen to lie side by side in pairs as they draw

[1] See for example the recent works of Stieve ('18, '20) on *Proteus*.

[2] As will later appear, parasynapsis does not necessarily imply the side-by-side conjugation of single pairs of chromosomes (though it is so described by nearly all zoölogists). It might equally well take place between two continuous spiremes, maternal and paternal, the product later segmenting to form bivalents; and the parasynaptic theory has in fact been advocated in this form by some botanists.

[3] See especially Schönfeld ('01) on the bull, Janssens and Dumez ('03), and Janssens ('01,'05), Wilson ('12), Snook and Long ('14) on urodeles; the Schreiners on *Myxine* ('04, '05) *Salamandra* and *Spinax* ('06a), *Ophyrotrocha* ('06b), and especially on *Tomopteris* ('06, '08); of Bonnevie ('06), *Enteroxenos* ('07); of Maréchal on selachians and other forms ('04, '05, '09); of Vejdovský on annelids ('07) and insects ('11, '12); of Gérard ('09), Morse ('09), Agar on *Lepidosiren* ('11), Montgomery ('11), Vejdovský ('11, '12), Wilson ('12), Stevens ('12), Wenrich ('11, '17), Robertson ('15, '16), Mohr ('16); Hogben ('20, '21) on insects, of Gelei on *Dendrocœlum* ('21, '22), and others; on the botanical side by Berghs ('04, '05), Allen ('04, '05), Grégoire ('04, 'c5, '07), Rosenberg ('05, '07, etc.), Strasburger ('05, 'c7, '08, '09), Cardiff ('06) and others. For a nearly complete list of the literature down to 1910, see the extended review and critique of Grégoire ('05, '10).

[4] For a general critique see Grégoire ('10), Wilson ('12), Gelei ('21, '22).

together (often around the nucleolus) to form the synaptic knot, while their more peripheral portions are still separate. Examples of this are seen in some of the mammals (Fig. 264, Winiwarter) and higher plants. (Berghs, '04, Allen, '04, Cardiff, '06, Digby, '20); and in some of these the paired grouping is more or less clearly seen even before the contraction

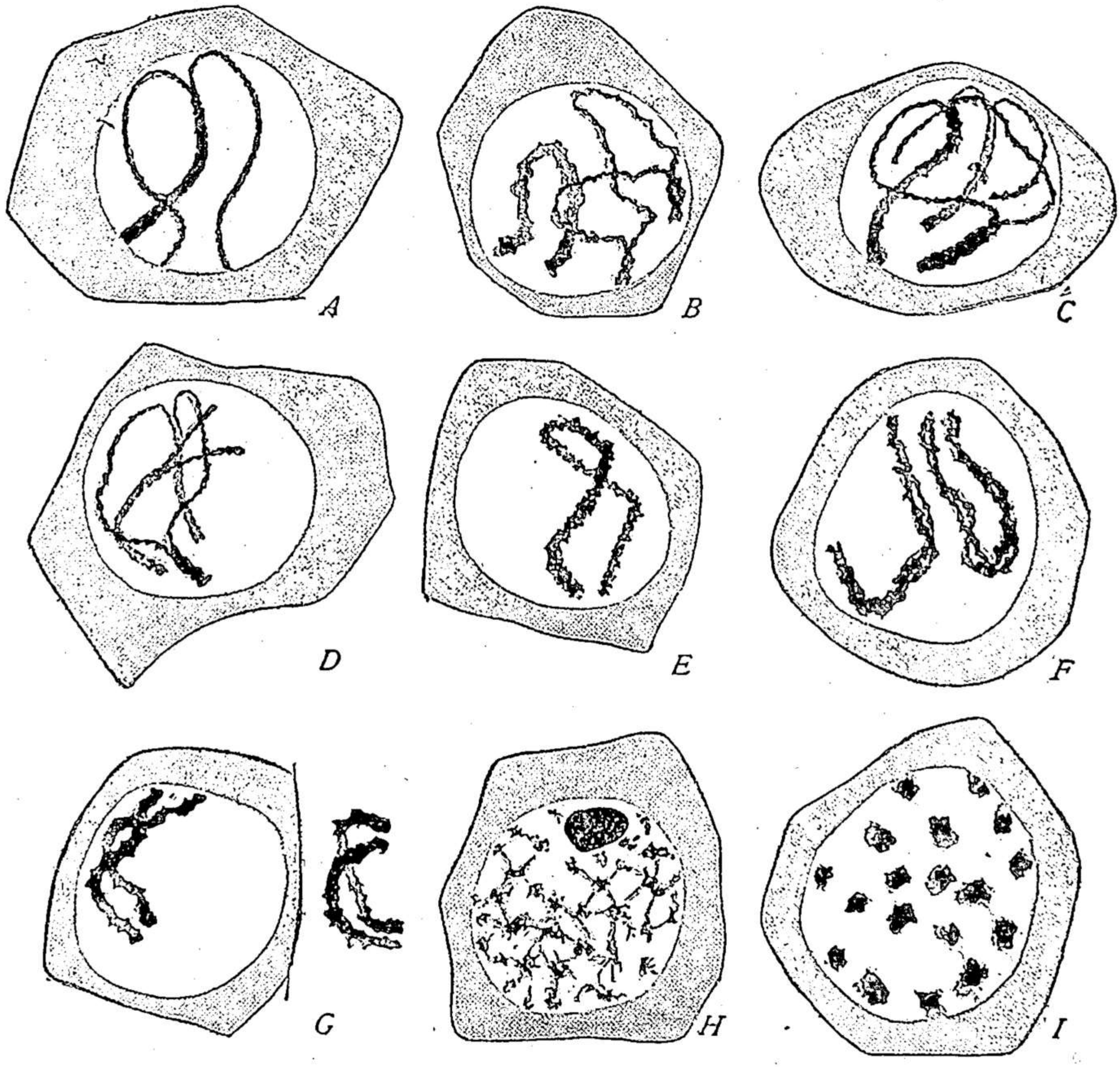

Fig. 270.—Details of synapsis in *Tomopteris* (SCHREINER).

A-D, parallel conjugation; *E*, single pachytene-thread; *F*, diplotene; *G*, the same, later stage; *H*, presynaptic stage in cross optical section, showing about 36 threads (18 loops); *I*, similar section of post-synaptic pachynema, 18 threads (9 loops).

begins. By some writers this has been ascribed to accident; but the weight of opinion is now opposed to this.

A more or less marked synizesis occurs in some of the polarized forms of synapsis, and these are also less favorable for observation,—for instance in some of the mammals (Winiwarter, '00) in the cockroach (Morse, '09, Hogben, '20b) or in the fern *Osmunda* (Grégoire, '07). In forms having no synizesis the leptotene stage is almost always more or less distinctly polarized (bouquet-stage) and the process of synapsis is more readily observed since it begins at one pole and progresses towards the opposite one. The

most typical and convincing examples of this are seen in the urodeles (Janssens) and some of the annelids (*Tomopteris*, Fig. 270) and platodes (*Dendrocœlum*, Figs. 279, 280). In the mammals (Fig. 263) the polarization is somewhat less evident and the process less regular. The same is true in the Orthoptera, though this group has lately offered some of the clearest evidence of parasynapsis (Fig. 271). In the hemipter *Euschistus*,

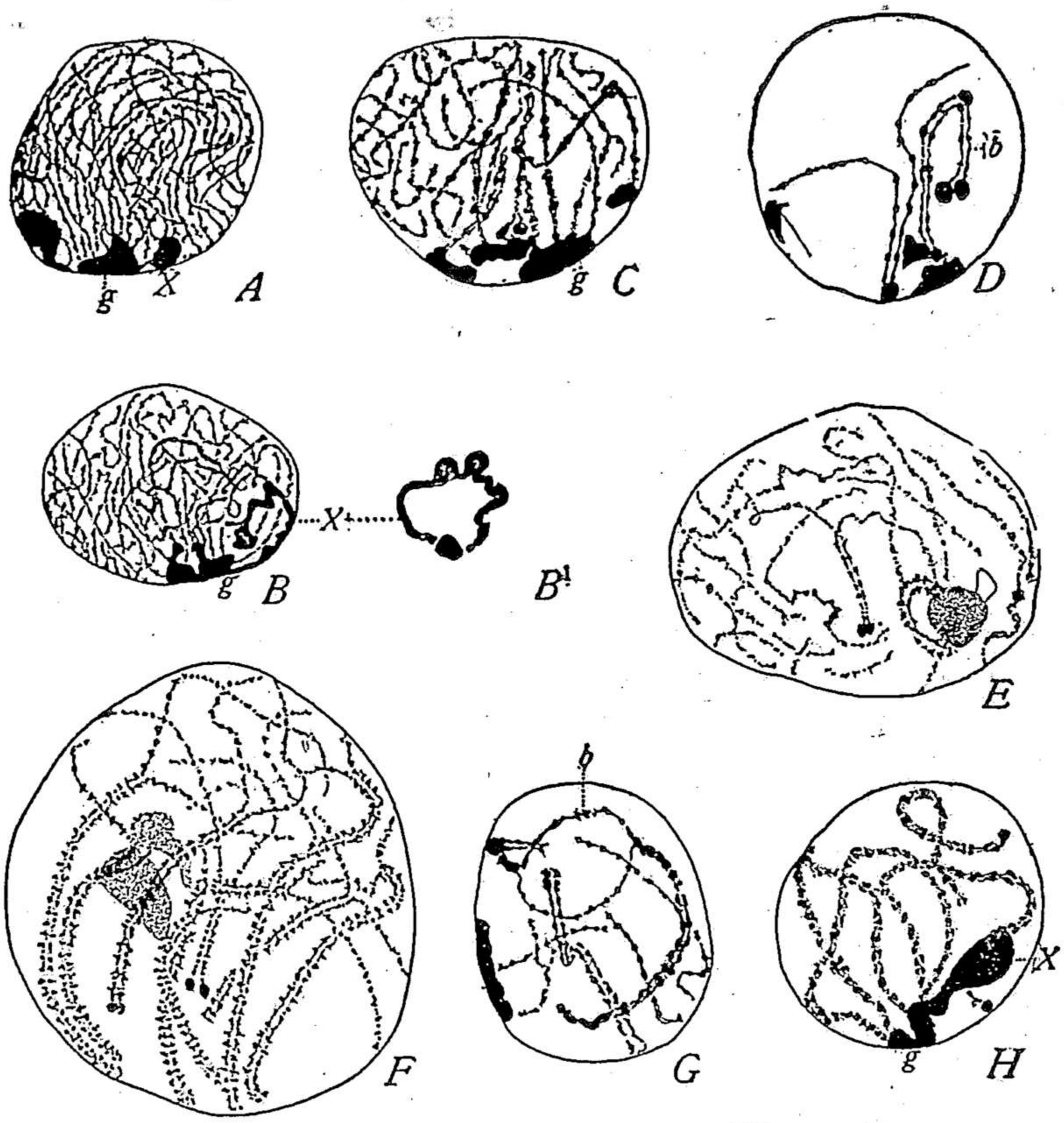

Fig. 271.—Parasynapsis in grasshoppers (WENRICH).

(*E* in *Chorthippus; F* in *Trimerotropis;* the others in *Phrynotettix*.)

A, *B*, leptotene stages, *g* the polar granules, X, the X-chromosome, the latter in greater detail at B^1; *C*, early synaptic nucleus, a few double threads; *D*, detail from similar nucleus, pairing completed in *B; E*, Y-figure and many unpaired letoptene-threads; *F*, amphitene-nucleus, conjugation in full progress; *G*, detail of similar stage, showing at *b* bivalent open in middle region; *H*, completed pachytene-diplotene stage.

as described by Montgomery ('11), neither synizesis nor polarization is present and the process proceeds very irregularly.

With an open and clearly-marked bouquet-stage the process of conjugation advances with considerable regularity from the nuclear pole, nearest the central bodies and idiozome, so that a very definite amphitene-stage may be recognized (Figs. 269, 271). Among the finest examples of this are those offered in the spermatogenesis of the urodeles *Batrachoseps*

and *Plethodon* and of the annelid *Tomopteris*, made classical by the works of Janssens and of the Schreiners, as cited above. Even more striking are the phenomena as shown in the oöcytes of *Dendrocœlum lacteum* of which Gelei ('21) has made a detailed and careful study.[1] In cases of this type the spireme-threads are most commonly, and perhaps always, loop-shaped with both free ends directed towards the pole. In either case side-by-side union of the threads begins at their free ends, nearest the pole, and proceeds thence step by step towards the opposite pole. Thus arise char-

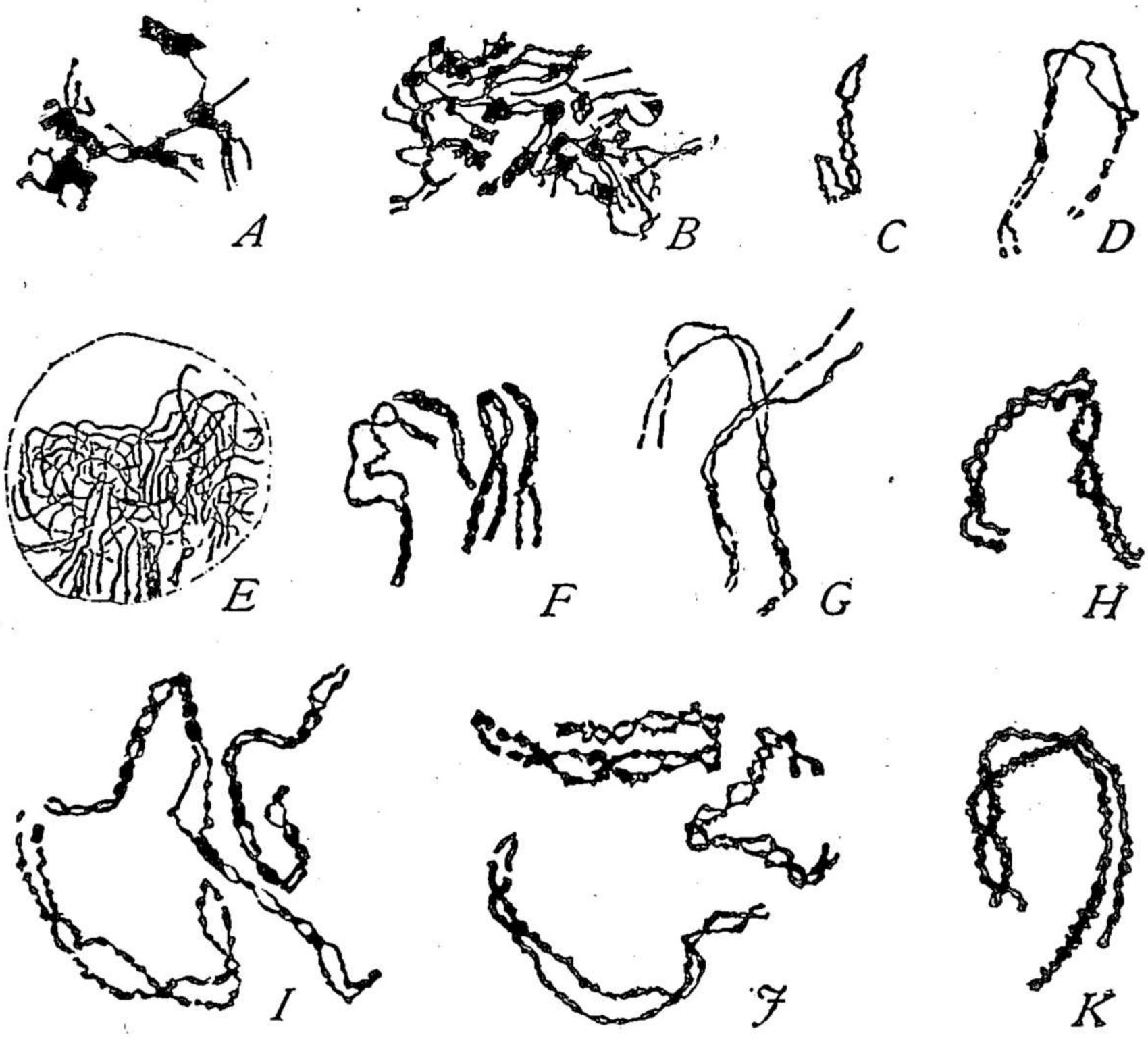

Fig. 272.—Earlier stages of meiosis in plants (mainly from GRÉGOIRE).

A, *B*, formation of leptotene-threads in *Lilium; C*, *D*, parasynaptic pairing of the threads; *E*, synaptic nucleus, *Osmunda; F*, early diplonema; *G–K*, twisted or strepsitene stages in *Lilium* (*K* from BERGHS).

acteristic Y-shaped figures, with thick longitudinally double stems, from which diverge the two halves to form the single branches of the Y. In many cases this process advances with considerable regularity, so that in its middle stages one-half the nucleus is occupied by thick and more or less parallel double threads, the other by single, thin and often contorted single threads; hence Janssens' term *amphitene*.[2]

When, as is usually the case, the two leptotene-threads have the form of

[1] See also Bordás, '21.

[2] Gelei ('21) has clearly shown that in *Dendrocœlum*, though a typical polarized bouquet is present, conjugation takes place irregularly, often being completed in some bivalents at a time, when in others it has only just begun.

loops, the conjugation proceeds from the free ends towards the middle point,[1] giving rise to the curious figures shown in Figs. 270, B–D; 271, G; 280 E, F; which may be likened to a pair of Y-figures united by their divergent branches. These forms, obviously, represent two leptotene-loops, united for a certain distance near their free ends, but still wide apart in the central region. Such forms have been clearly demonstrated by several observers, in particular by the Schreiners in *Tomopteris*, by Wenrich in *Phrynotettix*, by Robertson in *Chorthippus*, Mohr in *Locusta* and Gelei in *Dendrocœlum*. They offer very convincing evidence of parasynapsis and are probably of widespread occurrence, but may readily escape detection because of the confusion of the leptotene-threads. In the Amphibia these figures are also obscured by the fact, described by Janssens and readily verifiable in such urodeles as *Batrachoseps* or *Plethodon*, that many of the leptotene-threads run into a large chromatin-nucleolus or "chromoplast" situated towards the antipole.[2]

In some cases the stem of the Y-figure, during the amphitene-stage continues to show a distinct longitudinal cleft representing the plane of lateral apposition; and in such cases the two halves, in some cases at least, show each a series of very definite granules or chromomeres, which lie opposite one another in the two threads (Figs. 271, 428). This fact, of the highest theoretical interest (p. 952), is clearly shown in the figures of many observers, for instance in those of Mohr ('16), on *Locusta*, of Wenrich ('16, '17) on *Phrynotettix* and *Chorthippus*, or of Gelei ('21 '22) on *Dendrocœlum*.[3]

In other cases the stem of the Y shows no clear evidence of longitudinal duality, a classical example of which is seen in the urodeles as figured especially by Janssens, whose observation the writer can fully confirm in both *Batrachoseps* and *Plethodon*. This appearance may be due to an intimate fusion of the conjugants, to inappropriate fixation, or to other causes. Many interesting possibilities in this direction are suggested by Gelei's studies on *Dendrocœlum*, a very favorable object. This work, carried out with an improved technique, offers a remarkable demonstration of parasyn-

[1] An exception to this seems to occur in *Chorthippus* and *Trimerotropis* according to Wenrich ('17) who found some reason to conclude that pairing of the V-shaped and other atelomitic chromosomes here first begins at the apices of the V's and proceeds thence towards the free ends. A similar conclusion was earlier indicated by Gérard ('09).

[2] It seems possible that some of the figures here described do not belong to the synaptic period but to the early diakinesis and are early stages in the formation of rings; *i. e.*, the threads are not coming together but separating at this time. In such cases the central regions of the threads may have remained separate from the beginning.

[3] This fact has been urged by opponents of the theory of parasynapsis in favor of the contention that the two opposed threads result from longitudinal splitting of a single thread; but many facts are opposed to this. Wenrich has emphasized the fact, which may be clearly seen in Fig. 428, that the two opposed granules are sometimes unequal in size, a fact hard to reconcile with such an interpretation.

apsis. The number of leptotene-threads (which are of different lengths) is definitely 14, the diploid number, and of post-synaptic bivalents, 7. The pre-synaptic threads show very clearly a beaded structure, consisting of definite basichromatic granules (chromomeres) in a single series connected by a more lightly staining substance (linin?). During the conjugation the threads are brought together two by two in parasynaptic association and in outward appearance completely fuse to form a pachytene. *The chromomeres, however, remain distinct* and after suitable extraction of the dye are found lying in two distinct and separate series, *lying opposite each other two by two* in the pachytene thread and afterwards in the diplotene (Figs. 279, 280, 428). This makes it probable that the seeming fusion of the conjugants

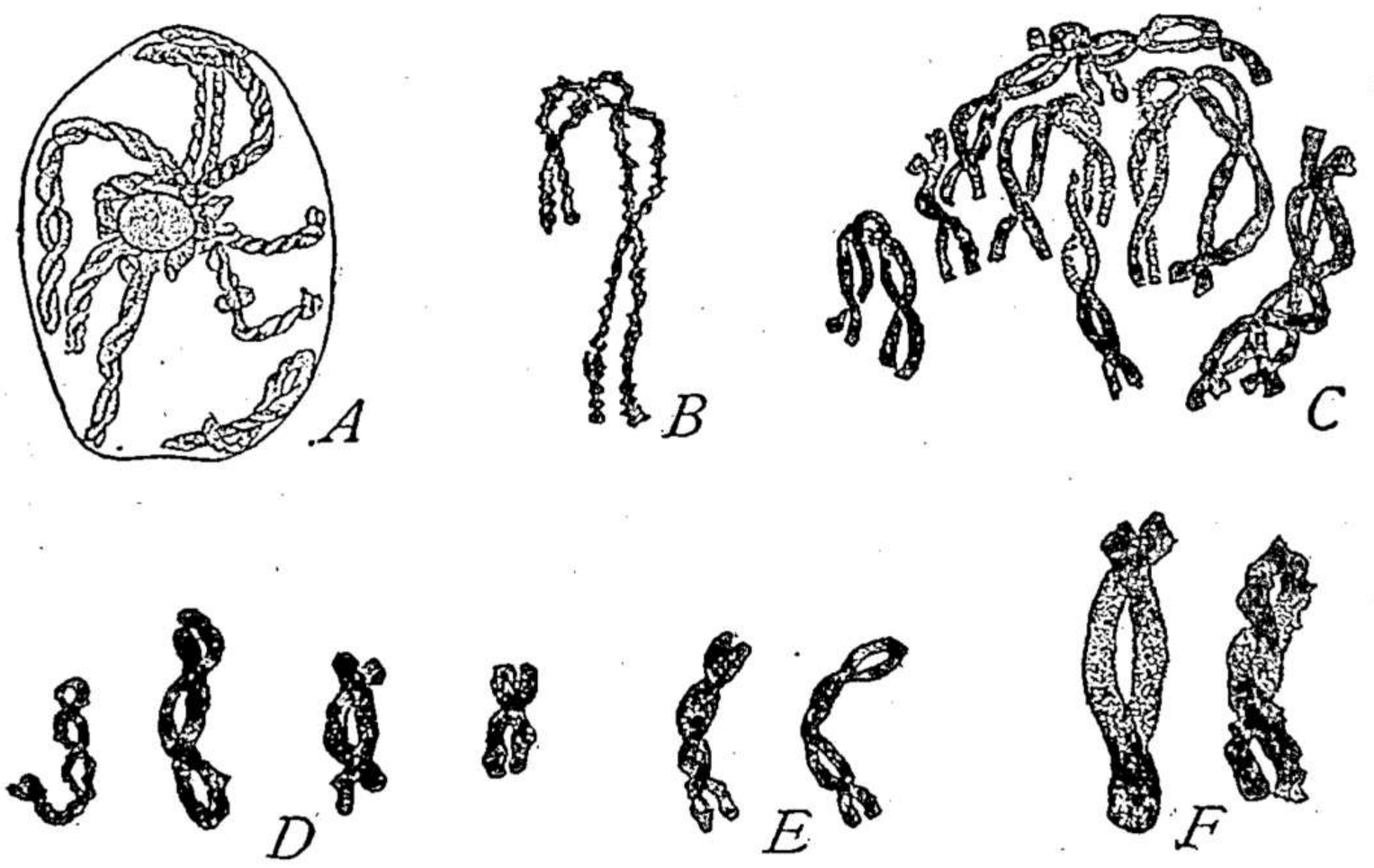

Fig. 273.—Later stages of meiosis, especially strepsinema stages (*A*, from OVERTON, *B*, *D*, *F*, from BERGHS, *C* from JANSSENS).

A, second contraction-figure in *Podophyllum; B*, earlier strepsinema in *Lilium; D*, *F*, later stages, twisted loops and double rods; *E*, similar figures, *Convallaria; C*, late strepsinema in the salamander *Batrachoseps*.

is deceptive, and that in internal structure the bivalents are always double structures.

Another interesting possibility is that the apparent fusion of the conjugants may in some cases be due to a close twisting together of the two leptotene-threads, a process which is clearly indicated (though not described) in Janssens' figures of *Batrachoseps* ('06). Other observers who have figured or described a similar torsion at this time include Grégoire ('07) in *Osmunda* and *Allium*, Agar ('11) in *Lepidosiren*, Bolles Lee ('11) in *Helix*, and Gelei ('21) in a few cases in *Dendrocœlum*. This point calls for the closest investigation because of its bearing on the chiasmatype-theory (p. 954); but the evidence in its support is very inadequate. Both Stevens and Lee believed the double spiral to persist from the time of synapsis through all the ensuing stages up to the period of diakinesis, but this is urgently in need

of confirmation. Most observers, including Winiwarter, the Schreiners, Wenrich, the writer, and many others, have found no evidence of a synaptic twisting. In *Dendrocœlum*, Gelei found twisting only in rare cases (Fig. 428); and it seems possible that this may be an accidental product of the technique. On the whole, therefore, there is little to support the hypothesis of a synaptic twisting.

In any case the result of the synaptic process is the complete replacement of the leptotene-threads by the pachytene. There is no doubt in many cases that the number of pachytene-threads is haploid, *i. e.*, that the pseudo-reduction has been accomplished during the synaptic stage, as is demonstrated with certainty by endwise or polar views or the polarized loops during the bouquet-stage. In *Tomopteris*, for example (as is clearly figured by the Schreiners, '08) the post-synaptic or pachytene-bouquet shows 18 threads, the pre-synaptic twice this number (Fig. 270). Since each loop-shaped thread appears as two in polar view the actual numbers are 9 (18) and 18 (36) corresponding to the haploid and the diploid numbers respectively. An example of the facts in species showing a synizesis is shown by the hemipter *Largus cinctus*, in which the male diploid number is 11, including an unpaired X-chromosome and five autosome-pairs. Here the number of post-synaptic pachytene-threads is five (with one unpaired condensed X-chromosome, Fig. 267, L), while the pre-synaptic number (of prochromosomes) is 11.[1] A considerable number of such cases have now been determined.

The evidence thus briefly reviewed seems to the author to leave no doubt that in a large class of cases pseudo-reduction is accomplished during the synaptic stage by a side-by-side union of leptotene threads, each of which represents a single or univalent chromosome. This conclusion has, however, met with energetic opposition on the part of some recent writers, even in case of the urodeles. Champy ('13) could find no evidence of any kind of synapsis and, like Fick, Meves, Della Valle and others practically abandons the whole problem of reduction as insoluble. Stieve ('20), in two lengthy papers on *Proteus*, contradicts all of the essential results of Janssens, Schreiner, Snook and Long, the writer, and other observers of the urodeles, finding a continuous spireme up to and through the pachytene bouquet; the diploid number of loops throughout both the leptotene and pachytene bouquet; complete absence of an amphitene stage or of other evidence of parasynapsis; the segmentation of the pachytene-spireme into the *diploid* number of univalent chromosomes; and finally a telosynaptic union of the latter two-by-two to form the bivalents. The present writer, who has examined the original preparations of the Schreiners (*Tomopteris*)

[1] Wilson, '12.

and of Janssens (*Batrachoseps*),[1] supplemented by subsequent repeated study of other preparations of urodele material, is of the opinion that Stieve's results on all of these points are erroneous.

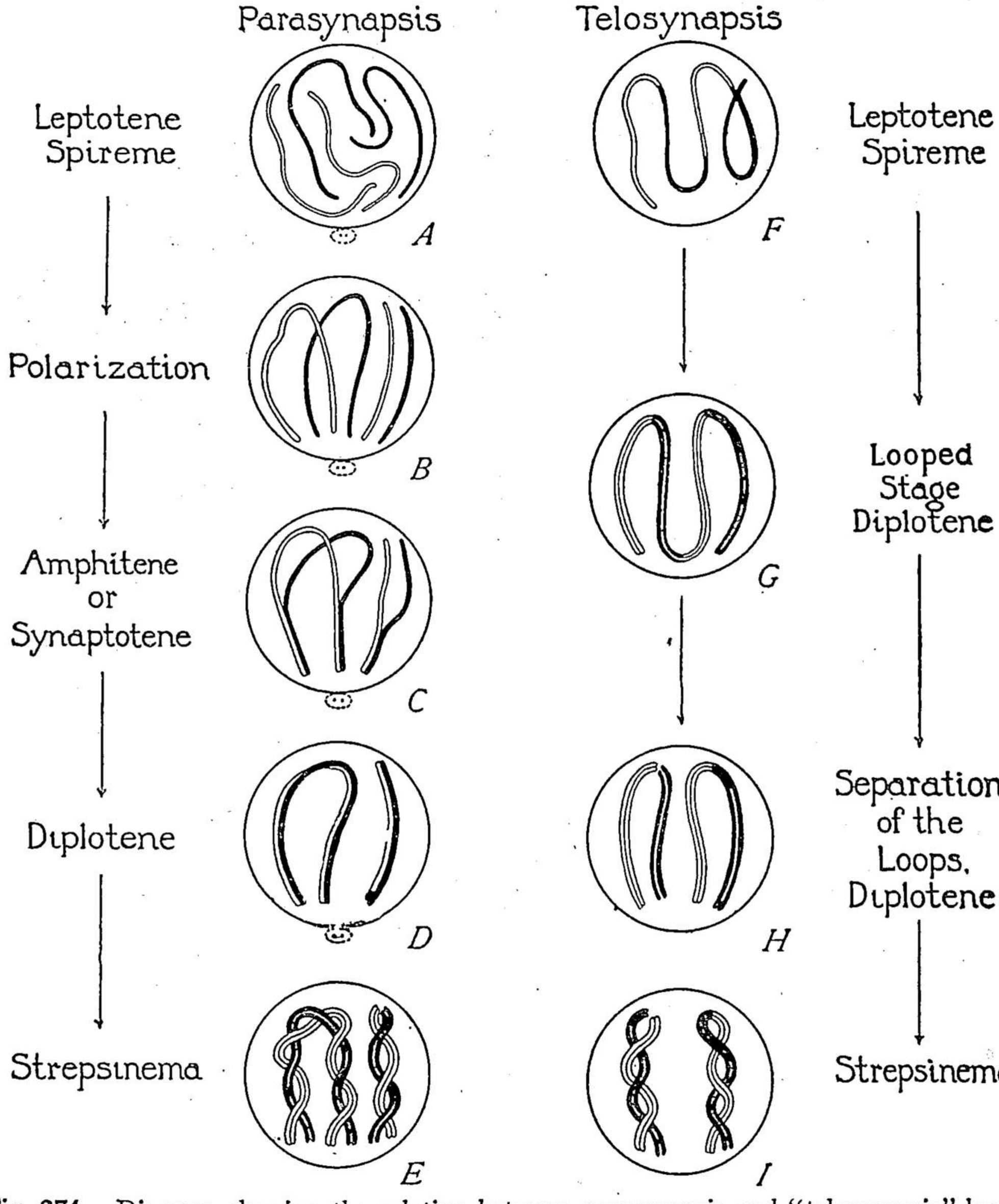

Fig. 274.—Diagram showing the relation between parasynapsis and "telosynapsis" by loop-formation. In the parasynaptic series one pair of loops and one pair of rods are shown. The final stages are much alike in effect (parasynaptic association of the synaptic mates), but the early stages are widely different.

3. Telosynapsis or Metasyndesis. End-to-end Union and the Theory of Loop-formation

Though telosynaptic conceptions have lost ground in recent years they still have the support of some competent observers. The theory of Rückert and his followers received its first detailed development by Montgomery

[1] *Cf.* Wilson ('12).

('00, '03, '05) and by Farmer and Moore ('03, '95). Though differing somewhat in detail, these interpretations (like Rückert's) alike assume primarily that upon segmentation of the spireme the synaptic mates of each pair remain attached at one end, either lying in a straight line, or, more commonly, flexed at the synaptic point to form a loop, and longitudinally split. By closure of the loop the two mates may finally come to lie side by side and by twisting together may give rise to the strepsinema (Fig. 275). In such cases, as Farmer has pointed out ('13) the cytological distinction between telosynapsis and parasynapsis almost disappears. Genetically, on the other hand, the distinction is of fundamental interest especially for the group of problems that center in the phenomena of crossing-over (p. 955). It is clear that according to this view the original cleft of the diplotene does not represent the plane of side-by-side apposition, but that of an ordinary equation-division.

Montgomery originally assumed (in case of *Peripatus*) an end-to-end conjugation of rod-shaped chromosomes two-by-two to form V-shaped bivalents *in the telophases of the last gonial division*, the V's thus produced giving rise directly to the polarized loops of the synaptic stage. This view never received much credence, though there is now some reason to reconsider its possibilities (p. 562).[1] As developed by Farmer and Moore ('03, '05) on the other hand, the theory of loop-formation has had many adherents, especially among investigators of the phenomena in plants.[2] In this form the theory assumed no actual conjugation of chromosomes but a looping and subsequent segmentation of a continuous spireme; taking place in the second synizesis or contraction-stage (Stage *i*) immediately preceding diakinesis. At this time the pachytene spireme (commonly, but not always, showing a longitudinal split) is in fact in many objects thrown into loops, often disposed radially about a central knot in which lies the nucleolus (Fig. 275). The spireme now segments transversely so as to separate the loops (or straight single pieces which subsequently bend into loops) which constitute the bivalents. Meanwhile the two branches of each loop often approximate until they lie side by side and often twist about each other to form 8-shaped figures or short double spirals. The bivalents thus formed may subsequently undergo the various changes of form already described.

This interpretation agrees with the parasynaptic in the conclusion that the synaptic mates in many cases *ultimately* do come to lie side by side but

[1] Montgomery's conception of the composition of the synaptic loops, apart from their mode of origin, was the same in principle as that adopted by Paulmier, McClung, Sutton, Wassilieff, Stevens and some other investigators of the time.

[2] See Strasburger ('04) and especially Mottier ('05, '07, '14) on *Lilium*, *Podophyllum*, *Acer*, and other forms; Gates ('08, '09), B. M. Davis ('09, '10, '11), Geerts ('08), and Cleland ('22) on *Œnothera;* Lewis ('08) on *Pinus* and *Thuja;* Digby ('10, '14, '20) on *Gallonia*, *Crepis*, etc.; Frazer and Snell ('11) and Sakamura ('14) on *Vicia*.

through a secondary process. In all other respects it involves a fundamentally different conception of the organization of the spireme; for the longitudinal cleft of the diplotene is considered as a simple equational split (like

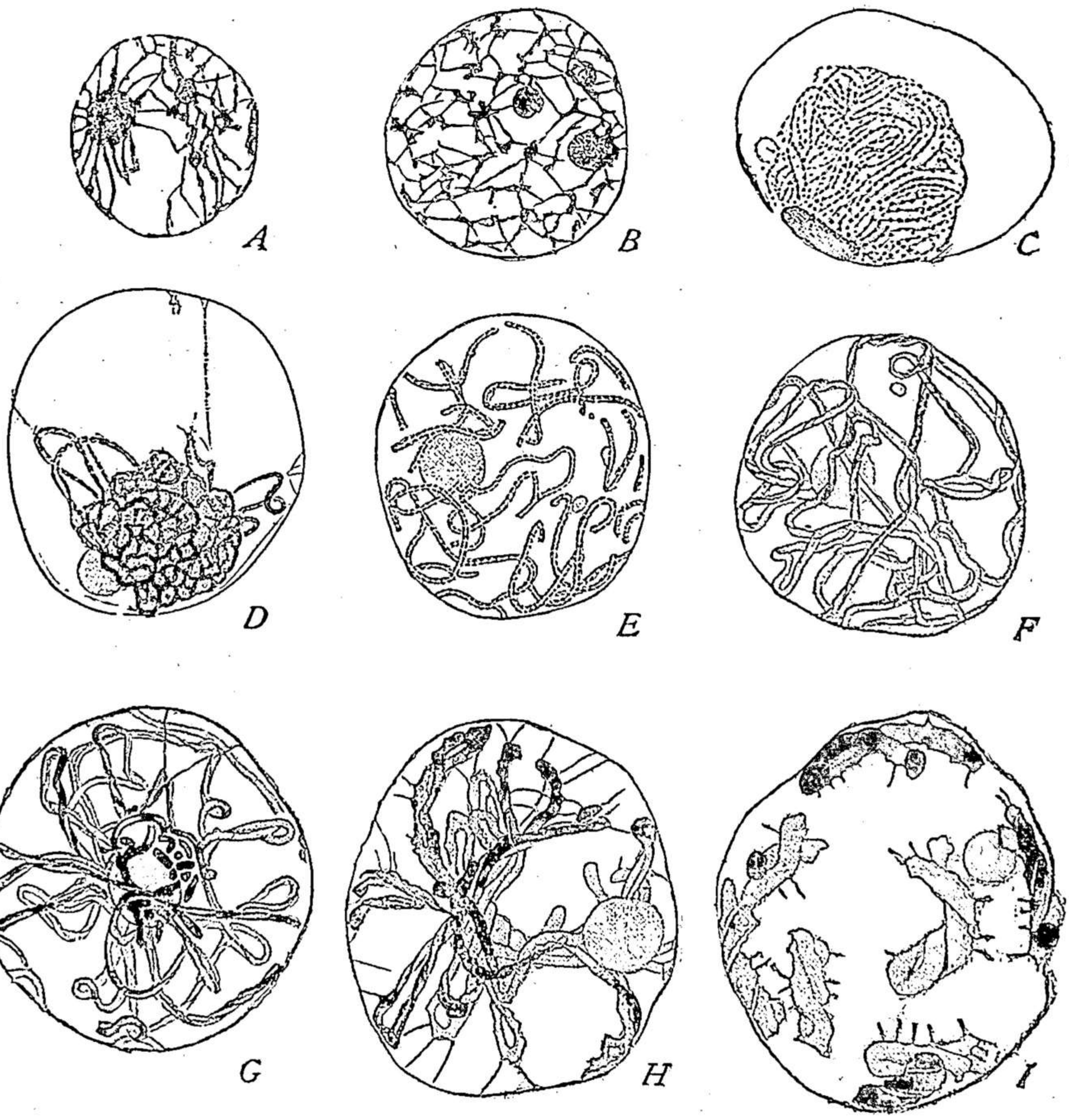

Fig. 275.—Meiosis by loop-formation in the pollen mother-cells of *Lilium*, as described by MOTTIER (FARMER and MOORE mode).

A, *B*, presynaptic net-like stages; *C*, early synizesis ("synapsis") of the leptotene-threads; *D*, loosening of the synizesis, spireme longitudinally double (diplonema); *E*, "hollow," segmented, double spireme (diplonema); *F*, similar or slightly later stage, twisting; *G*, looping of the twisted and longitudinally double threads; *H*, later looped stage, second contraction, segmentation of the threads in progress; *I*, diakinesis, loops separate, shorter and thicker, near periphery.

that of a somatic prophase) instead of the apposition-plane of two synaptic mates (or spiremes).

If therefore we accept the conclusion that the synaptic mates in each pair are respectively of maternal and paternal ancestry (p. 505) it must be assumed that in the original spireme paternal and maternal chromosomes regularly alternate and in such a way that synaptic mates always adjoin. In apparent harmony with this are the facts described in *Œnothera*, where just prior to the diakinesis the full diploid number of chromosomes (14)

are said to be visible, most of them aligned end to end in the pachytene spireme (Fig. 276), though a few may already be free. By segmentation of the spireme seven bivalents are formed, each consisting of two synaptic mates attached end-to-end. During the diakinesis the two mates usually fold together so as to lie side by side, or even to form rings; but they may remain end to end in telosynaptic union. A similar alignment in the spireme is seen in *Bufo* (King, '07) and in *Carex* by Stout ('12) though these observers leave the mode of synapsis undetermined. Too much importance

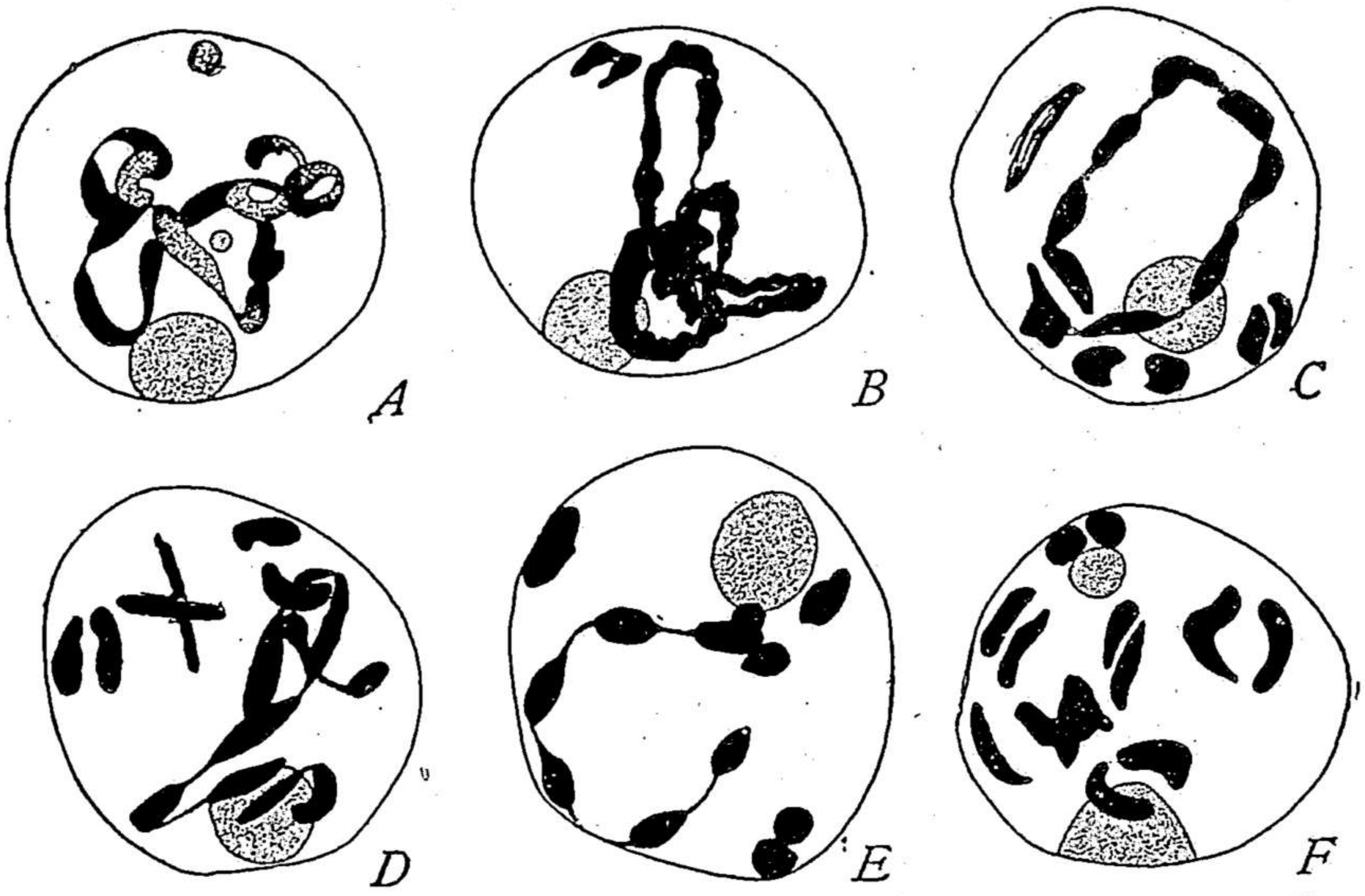

Fig. 276.—Meiosis in *Œnothera* (*A*, *Œ. lamarckiana*, DAVIS; *B–F*, *Œ. rubrinervis*, GATES).

A and *B* partly segmented pachynema; *C–E*, later stages, serial alignment of chromosomes with several pairs separate; *F*, the chromosomes separate and in part paired.

should not be ascribed to these facts, however, in view of the diakinetic phenomena later to be described.

Farmer and Moore's interpretation still has the support of some able observers,[1] but has of late lost ground. In case of the cockroach, for instance (Moore's object), both Morse ('09) and Hogben ('20) have produced strong evidence in favor of the parasynaptic theory, while Digby ('20), still a convinced supporter of the loop-theory, has recently admitted the side-by-side union of leptotene-threads at the synaptic stage. In *Spinacea*, *Smilacina* and some other seed-plants according to Stomps ('10) and Lawson ('12) the spireme is not continuous at any period, but consists of separate *univalent* threads, each of which is longitudinally split from an early period.

[1] "In the entire history of the nucleus from the stage of rest to the formation of the twelve bivalents, nothing is clearer to the writer than the fact that all of the bivalents are derived from the spireme; that no spireme is formed previous to synapsis (synizesis); that there is no union of spiremes, either before, during or after synapsis, and that the spireme is composed of the somatic chromosomes placed end to end" (Mottier, '14, p. 120).

These threads, according to Lawson's very specific account, conjugate sidewise in pairs at a stage nearly corresponding to the second synizesis or the early diakinesis, the original longitudinal fission of the threads meanwhile becoming less evident or wholly obscured. With this may be compared the phenomena in *Euschistus* (according to Montgomery, '11) where the spireme is likewise segmented from the very beginning and the parasynaptic pairing of the chromosomes occurs step by step in rather irregular fashion as the growth-period advances. Were this process deferred until a later period a condition much like that described by Lawson would exist.[1]

4. Synapsis in Relation to the Anaphasic Duality

Certain attempts have been made to reconcile the side-by-side association of leptotene-threads in the synaptic stage with telosynaptic conceptions. It is hardly necessary to consider seriously the earlier crude notion that this association is merely an accidental result of the drawing together of polarized leptotene-threads towards one pole. More careful consideration is due to the conception of Meves ('98) that it represents a kind of precocious longitudinal fission, in which the spireme is formed progressively as a double structure from the beginning. Advocates of the loop-theory of telosynapsis have given a certain vogue to the related notion that parasynapsis is no more than a reunion of sister-threads that have resulted from an earlier longitudinal fission and have temporarily separated. This fission has for the most part been referred to the final gonial anaphase, the sister chromosomes then produced, often widely separated, being assumed to have persisted throughout all the following stages until their reunion in the synaptic stage.[2] The meiotic prophase is thus treated as merely a special modification of the anaphasic splitting in the somatic mitoses (p. 138), and the parasynaptic pairing of leptotene-threads loses all significance for the reduction-problem.

Advocates of the loop-theory of synapsis have thus sought to reconcile their own conclusions with the positive observation of parasynaptic pairing described by so many competent observers.[3] To cite Brunelli: "Step by step the two longitudinal halves of the individual chromosomes place themselves side by side; wherefore the intermediate appearances that have been described as the fission of a single thread or as the reunion of two threads having the value of two separate chromosomes (zygotene hypothesis)"

[1] For more recent accounts of telosynapsis see Nothnagel, '16 (*Allium*), Nakahara, '19 (*Perla*) Gates and Rees, '21 (*Lactuca*).

[2] This possibility is clearly suggested by Rückert ('92a, p. 149, '92b, p. 51) in his remarkable papers on elasmobranch oögenesis, in which are foreshadowed so many later conclusions concerning the history of the chromosomes (p. 924).

[3] See especially Digby ('10) on *Galtonia* and ('19) on *Osmunda*, Fraser and Snell ('11) and Frazer ('14) on *Vicia*, Brunelli ('11) on *Trixalis*.

(*op. cit.*, p. 9). This interpretation deserves careful attention but has encountered fatal difficulties. The *status* of the so-called anaphasic "splitting" in the somatic mitoses has itself become extremely dubious (p. 139); but a still more serious difficulty appears in the numerical relations. Since the gonial number is diploid the anaphasic split should give the tetraploid number, and parasynapsis should reduce this number again to the diploid (of pachytene threads); but both these demands of the hypothesis are contrary to fact,[1] at least in some cases. Direct counts of the leptotene-threads are sometimes practicable; and when such is not the case, accurate counting of the prochromosomes from which the threads arise may still be possible. Both methods show conclusively that the number is *diploid*. Especially clear cases of direct counting are offered by the Schreiners' studies on *Tomopteris* ('96, '08) (haploid 9) and the more recent ones of Gelei ('21) on *Dendrocœlum* (haploid 7). Enumerations of the prochromosomes are especially convincing when certain of them are recognizable individually by their size or otherwise. In *Lygæus bicrucis*, for example, their number, like that of the spermatogonia, is 14; and two of these are at once recognizable by their denser and more basophilic character and their unequal size (p. 542). Again, in the beetle *Blaps lusitanica* Nonidez ('20) found 33 spermatogonial chromosomes including constantly three large ones, readily recognizable. In Stage *c* the prochromosomes show the same number and character; and as in other cases one leptotene thread is formed from each.

Finally, Robertson ('19), who himself accepts the anaphasic splitting, has briefly announced that in grasshoppers of the family Tettigidæ the presynaptic-threads in the male are of the diploid number (13) and *longitudinally split*, the 12 autosomes pairing side-by-side to form six bivalents, each of which is presumably already a tetrad. This, if well founded, is evidently fatal to the interpretation of Digby, Brunelli and others as above indicated. Still a different condition (still unpublished) has been found by McClung in the grasshoppers (*Leptisma* and *Mecostethus*)[2] in which the number of prochromosomes is *haploid*. Here the chromosome-conjugation seems to be at least initiated in the gonial telophases or a little later, the telophase-chromosomes becoming associated side by side in pairs. Such a mode of synapsis, evidently, approximates to Montgomery's original conception of an anaphasic conjugation. These observations evidently are no more favorable to the interpretation in question than are those of Robertson.

Taken together the foregoing facts appear to be decisively against the theory of anaphasic duality as applied to parasynapsis, and equally opposed to the earlier telosynaptic conception of Montgomery.

[1] Wilson, '12.
[2] The writer has had the privilege of examining the original preparations. See McClung, '24.

5. Late Conjugation. Diakinetic Synaptic Phenomena

Certain accounts of chromosome-conjugation taking place late in the growth-period, or even at its close, open interesting possibilities concerning the phenomena already considered. That excellent observer Henking ('91) found evidence in *Pyrrhocoris* of a diakinetic conjugation following the second contraction-figure; and a similar phenomenon has been described more in detail by Gross ('04, '06) in *Syromastes* and *Pyrrhocoris*. In the elasmobranch *Pristiurus* Rückert ('92, '93) found the full diploid number

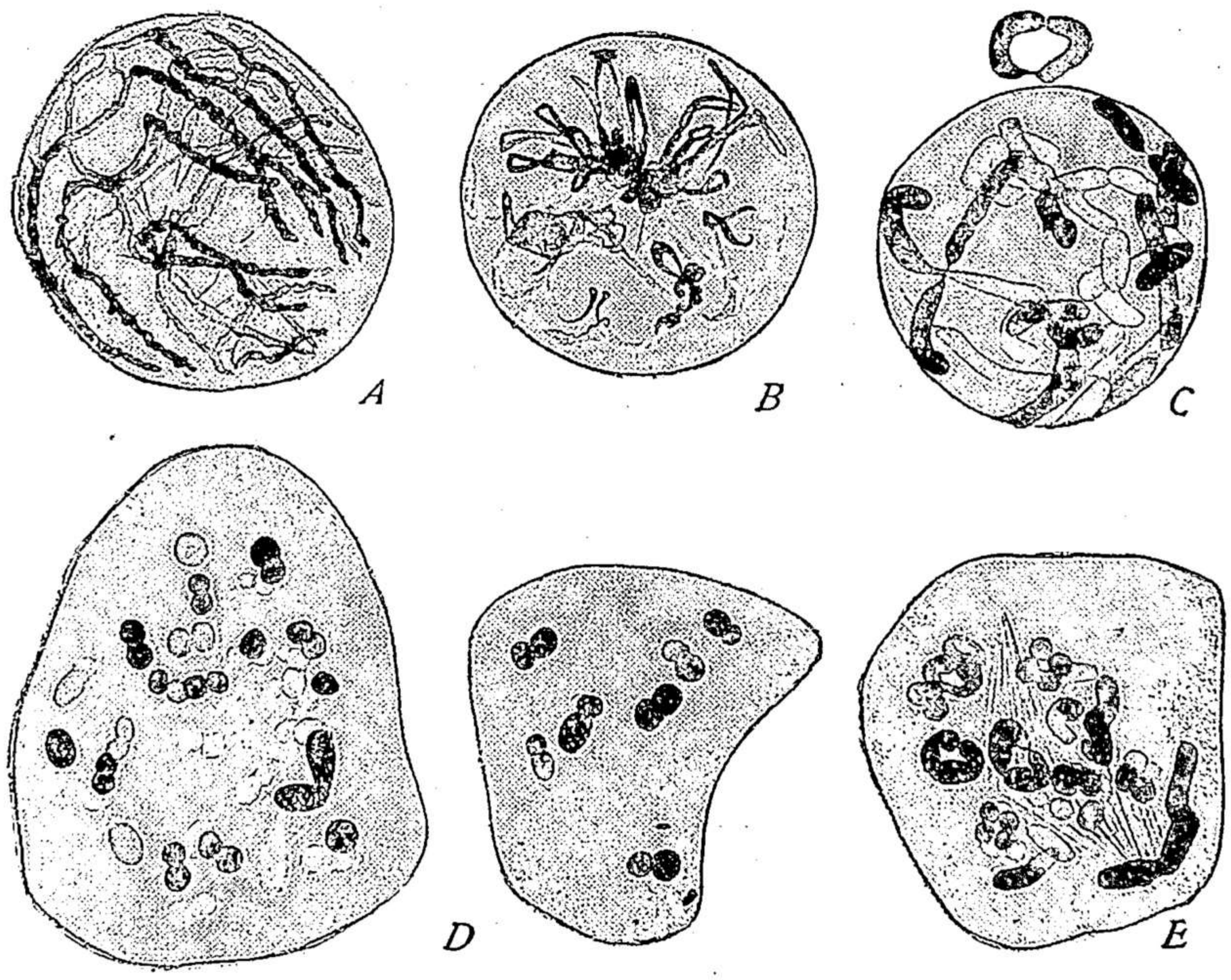

Fig. 277.—Later stages of spermatogenesis in *Lepidosiren* (AGAR).

A, late pachynema, with haploid number (19) of loops; *B*, second contraction-figure, strepsinema, loops formed by separation of the ex-conjugants; *C*, diakinesis, shortening, thickening and separation of the ex-conjugants, a ring-tetrad shown separately above; *D*, final diakinesis (in two sections), nuclear membrane disappeared, 38 univalent chromosomes, each transversely constricted; *E*, late prophase, secondary pairing of the chromosomes to form rings or tetrad-shaped bodies.

of chromosomes (36), arranged in pairs in the middle growth-period of the germinal vesicle, the haploid number appearing at a later period.[1] A more recent example is offered by the works of Stieve ('18, '20a, '20b) on the spermatogenesis and oögenesis of *Proteus;* but this account as above stated is, in the author's opinion, open to serious question.

There are certain well-established cases of chromosome-conjugation at a late stage—in the diakinesis or even later. For example, the *m*-chromosomes of coreid Hemiptera regularly conjugate in the final prophases of the

[1] See also Born ('93), Wilcox ('95), Korschelt ('95).

heterotypic division (p. 839); while the XY-pair of sex-chromosomes of Hemiptera generally do not conjugate until the final anaphases of that division (p. 769). In some of these cases the conjugation in question seems undoubtedly to represent *a secondary coupling that has been preceded by a typical synapsis at the usual time and a subsequent deconjugation.* One of the clearest of these cases is described by Agar ('11) in *Lepidosiren.* In this case the diploid divisions show 38 chromosomes, which give rise in the pre-synaptic period to typical leptotene-threads. In a typical amphitene or synaptotene bouquet-stage these conjugate side-by-side, the synaptic mates often being more or less twisted about one another. Thus are formed 19 pachytene loops; but after a second contraction-figure or synizesis a disjunction occurs to form short, thick chromosomes of the *diploid* number (38) which show no sign of having been previously coupled. In the final stages of diakinesis, as the chromosomes are actually passing upon the spindle, the univalents again conjugate two-by-two to form the 19 bivalents of the meiotic divisions (Fig. 277).

Results similar to the above in many respects have been reached in some of the gall-flies by the recent work of Hogben ('20a). In *Rhodites* (p. 803), the somatic number in various kinds of cells is uniformly 18. In synapsis the leptotene-threads (presumably also 18 in number) conjugate *parasynaptically* to form 9 bivalents; but in the diakinesis reappear 18 single threads which are said to conjugate *end-to-end* to form the 9 bivalents that pass upon the spindle. The facts reported in *Cynips* are quite similar save that the respective chromosome-numbers are 20 and 10. The diakinetic telosynaptic pairing observed by Hegner ('14) in *Copidosoma* is very probably a secondary conjugation of similar type, and Hogben believes that a similar process occurs also in *Orthopelma.* A similar explanation undoubtedly applies to the above cited case of the elasmobranchs as described by Rückert. Here the later work of Maréchal and of the Schreiners demonstrated a typical parasynapsis at the usual time; and the later appearance of the diploid number is clearly owing to the wide temporary separation of the halves of the diplotene, which finally reunite side-by-side. The meaning of these singular manœuvers of the chromosomes is almost unknown; but they show how readily we may fall into error concerning both the mode of synapsis and the time at which it occurs if every stage of meiosis be not closely scrutinized. They are also of much interest in relation to diploid parthenogenesis, which in some cases is likewise preceded by a process of conjugation and pseudo-reduction, only to be undone by a disjunction prior to the single maturation-division (p. 793).

6. Critical

The parasynaptic and telosynaptic hypotheses, as outlined above, do not differ in respect to the final result of maturation; but from a theoretical point of view it is important to determine the precise *modus operandi* of synapsis because of its bearing on "crossing-over" (p. 952). It is possible that both types of synapsis may actually occur; but to the writer this seems improbable. We may admit that to some extent the time and mode of synapsis may not be the same in all objects; but no explanation can here be found for the contradiction in case of the same objects; in the lily, for example, diametrically opposing results have been reached by such competent observers as Allen and Grégoire on the one hand, and Farmer, Moore, and Mottier on the other. Grégoire ('07, '09) after a critical reëxamination of the phenomena in the seed-plants most positively reaffirmed the parasynaptic conclusions of Allen, Berghs and others in opposition to Farmer and Moore; while the opposing hypothesis in its turn received fresh support from the studies on other seed-plants of Mottier ('14) of Digby ('10, '14, '20), Frazer and Snell ('11), Frazer ('15) and others. In the case of *Œnothera*, as already indicated, a "telosynaptic" association of the chromosomes in early diakinesis seems indubitable. Among zoölogists, on the other hand, the drift of opinion has been steadily towards the parasynaptic conception. Montgomery himself, after a renewed and extended study of the spermatogenesis of *Euschistus* ('11) definitely accepted this conclusion in opposition to his earlier conclusions. The results of Moore ('05) on the cockroach have been shown to be almost certainly untenable by Morse ('09) and Hogben ('20) in later studies on the same object. The present writer ('12) after long study of the problem in the Hemiptera, and especially on original preparations of *Batrachoseps* by Janssens, of *Tomopteris* by the Schreiners, and on numerous additional preparations of *Plethodon* and *Batrachoseps*, likewise became convinced of the reality of parasynapsis. McClung ('14, '20) long favorable to a telosynaptic conception in the case of Orthoptera, has at length accepted as most probable the parasynaptic one, which also finds strong support in the recent work on this group of Robertson ('15, '16), Wenrich ('16, '17) and Mohr ('16), of Gelei on the Turbellaria, and that of Metz and others on the unquestionable side-by-side pairing of the chromosomes in Diptera, even in the somatic divisions (p. 837).

Some of the existing divergence of interpretation has, no doubt, arisen from errors of observation in this difficult field. To the writer, however, it seems probable that the divergence may also be due in part to a failure to reckon with all the cytological phenomena and in particular with possible secondary modifications. Interesting possibilities in this direction are

suggested by the phenomena of diakinetic deconjugation and reunion reviewed in the last section; and it seems possible that important further light may be thrown on the subject by more adequate studies on the relation between the synaptic stage, the second contraction, and the diakinesis. There is increasing reason to believe that the serial alignment of chromosomes sometimes seen in the later stages, may in some cases be a secondary association quite different from the original one. Perhaps we may find in this direction a common ground on which parasynapsis, telosynapsis and loop-formation may come together. For parasynapsis begins by the union of the chromosome-ends; and we might further conceive that the looping process as described in higher plants was originally (perhaps still is) preceded by an early side-by-side association that is undone in later stages preceding the loop-formation. The latter process would then restore the original side-by-side association.

7. The Mechanism of Synapsis

The causes that determine the pairing of the synaptic mates, are wholly unknown. We think naturally of a chemical or physical difference of sign or potential between the maternal and paternal homologues; but every such hypothesis stumbles against the fact that maternal chromosomes of one generation may become paternal in the following one (or *vice versa*). The difficulties increase when we consider synapsis as observed in triploid or tetraploid cells. In such cases the process is of especial interest since three or four synaptic mates are present instead of the normal two. Certain tetraploid forms, such as some of the *gigas* forms of *Œnothera* or *Primula*, breed approximately true without splitting up to any large extent into other forms; and from this we may infer that during meiosis the chromosomes at least tend to mate in pairs and to disjoin in typical fashion.[1] It is certain, also, that such a mode of pairing takes place in the meiosis of particular lobes or cysts of the testis that are abnormally tetraploid in individuals otherwise diploid[2] (see Bowen, '22).

Such cases would seem to suggest that some sort of "affinity" exists between the synaptic mates—such as a difference of electric charge or of chemical nature—that is satisfied by their union; and the same view is suggested by the behavior of certain triploids or other forms having an odd

[1] Gates found, however, that the synaptic pairing in *Œ. gigas*, as often in other Œnotheras, is very loose and irregular in appearance. See Gates, '09, '13, '15, '24.

[2] This gives substantial ground for the conclusion that mutants or species that are "tetraploid" as compared with original or related forms are really such—*i. e.*, that each specific type of chromosome is present in quadruplicate instead of in duplicate. This conclusion explains the otherwise puzzling fact that in hybrids between diploid or tetraploid forms (as in *Drosera*, p. 846) synapsis produces a number of bivalents equal to the fundamental haploid number, the remaining chromosomes being univalent.

number of chromosomes, where the unpaired chromosomes find no mates in meiosis (p. 848). Unluckily, however, this seems to be contradicted by the synaptic phenomena in certain other triploid and tetraploid forms where the synaptic mates conjugate by threes or fours. A demonstrative example of this is offered by the trivalent *m*-chromosome of *Metapodius* (p. 876); and more recently the same fact has been clearly shown by Belling and Blakeslee ('23) in both triploid and tetraploid *Daturas*. In the latter cases synapsis leads to the formation of trivalent or quadrivalent heterotypic chromosomes, followed by a disjunction that involves a random assortment of the chromatids and consequent splitting up of the original groups. In harmony with this are the results of Holt ('17), Bridges ('22) and Metz ('22) on the association of homologous chromosomes in triploid, tetraploid, and polyploid somatic cells of *Drosophila*, which indicate that in such cells the synaptic mates tend to an association in groups of three, four or more, instead of in pairs as in the normal diploid individuals. In

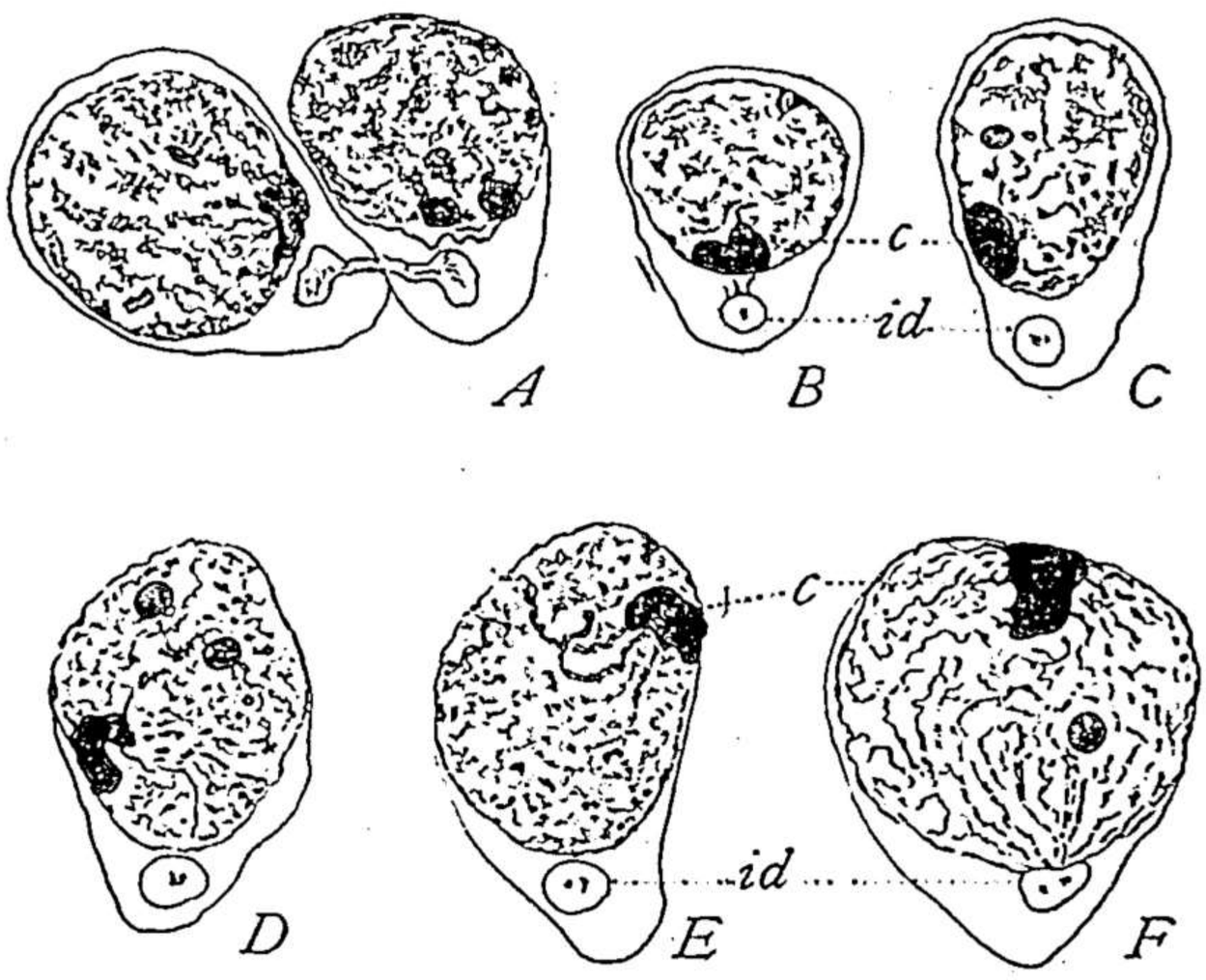

Fig. 278.—Telokinetic movement of the nucleus in very young spermatocytes of the salamander *Batrachoseps* (JANSSENS).

A, early stage, sister-cells still connected by spindle-bridge, chromoplasts near the idiozome; *B*, slightly later stage, chromoplast close to idiozome; *C*, *D*, *E*, successive stages in the rotation of the nucleus, leading to *F*, leptotene, already slightly polarized, with chloroplast opposite to the idiozome.

view of all this, we can only record the observed facts, admitting our present inability to find their physical explanation.

Undoubtedly the side-by-side conjugation of long thread-like loops from both ends towards the center involves some difficult mechanical problems. The difficulty is to some extent lessened by the preparation for the process that begins in the pre-synaptic stages and may be more extensive than has been suspected. In animals, at least, the central bodies evidently play an important part in this process; for it is towards them (*i. e.*, the idiozome-

pole of the nucleus) that the free ends of the leptotene threads or loops are drawn during the polarization; and it is here that their union two by two typically begins. Rod-shaped chromosomes with the spindle attachment at one end seem to become looped during synapsis with both ends towards the pole, as clearly seen (for example) in the "conflexion" of the X-chromosome in Orthoptera (p. 761). The behavior of V-shaped chromosomes (*Tomopteris*, urodeles), is of especial interest; for here the spindle-attachment is at the apex of the V, yet in the bouquet-stage it is the free ends that are turned towards the idiozome-pole (Janssens, '05). This observer has

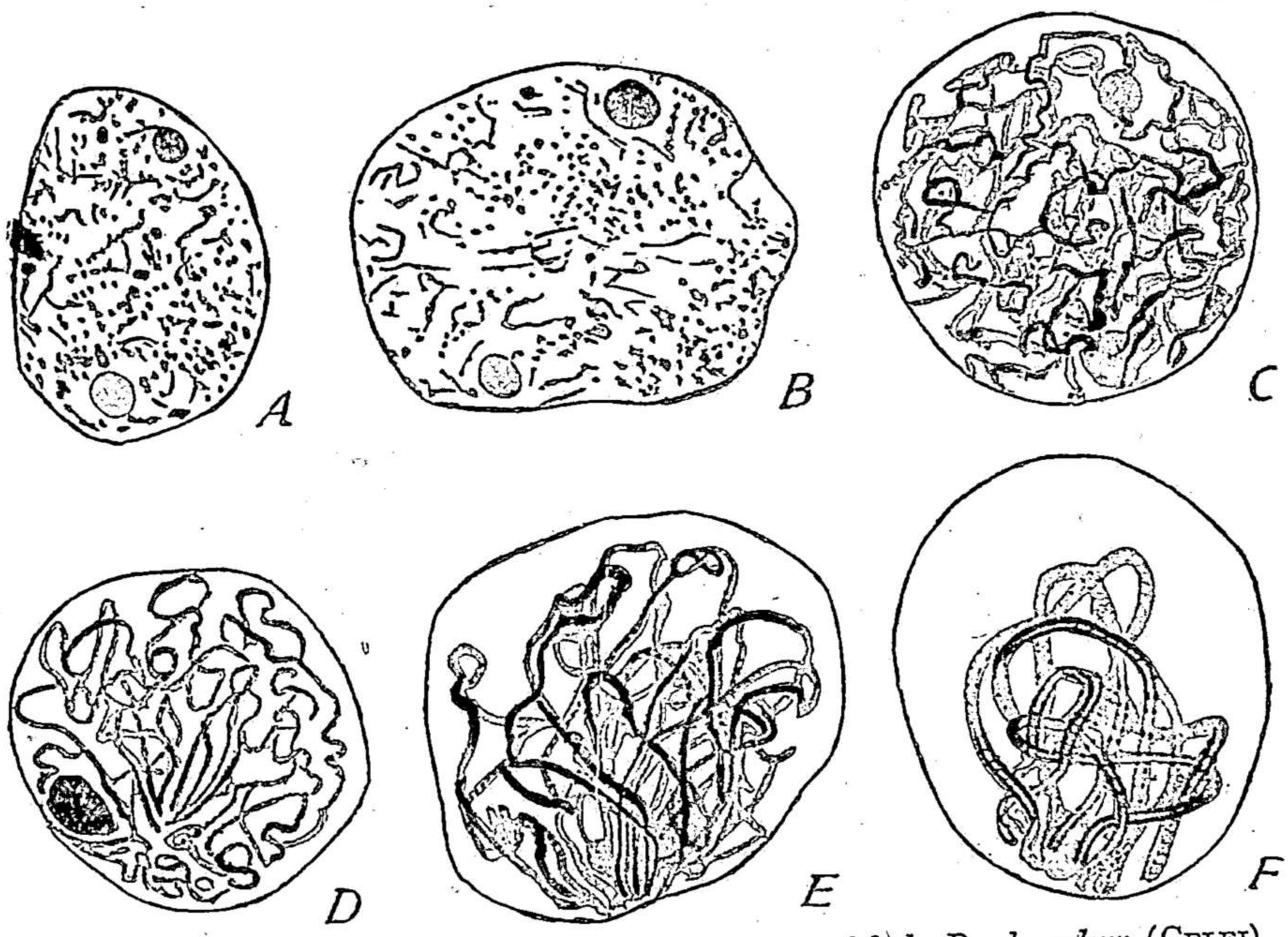

Fig. 279.—Stages of meiosis in the oögenesis of the triclade *Dendrocœlum* (GELEI). *A*, netlike stage (protobroch); *B*, beginning of the spireme-formation (deutobroch); *C*, fully formed but still unpolarized leptonema, free ends of the threads marked by crosses; *D*, beginning of the leptotene polarization; *E*, polarized leptotene-bouquet stage, with seven pairs of loops; *F*, polarized diplonema, seven double loops.

produced apparently strong evidence that during the telokinesis of the last gonial division in urodeles the nucleus rotates through 180°, so that the original relations of the loops to the central bodies are reversed (Fig. 278). A similar telokinetic transposition was indicated by the Schreiners ('06) in the case of *Tomopteris*, and is also stated by Gelei ('21) to take place in *Dendrocœlum*, though its exact *modus operandi* was not determined. This clearly shows that the relation between chromosome and center is not due to a persistent attachment between them.

Gelei has demonstrated, further, that before the polarization the free ends of the leptotene loops lie upon the nuclear membrane, at first quite irregu-

larly scattered, but later gliding towards the pole until they finally come into contact with their mates as the conjugation begins (Fig. 279). Gelei believes these movements to result from an active motility of the chromosomes; but this is hypothetical. In any case it is evident that they prepare the way for a conjugation that begins with the free ends and gradually draws the synaptic loops together towards the central points. We can thus in a measure understand how the loops disentangle themselves from the spireme; and we even may suspect that the seeming labyrinth of threads is an orderly system the nature of which is determined at a still earlier period. Of much interest in connection with this is the occasional occurrence of two or even three ring-shaped bivalents linked together like links in a chain, of which several cases have been observed by McClung. This obviously might result from an entanglement of the leptotene-threads such that one or more of them were caught between the two synaptic mates of another conjugating pair. Such conditions actually occur, as is clearly shown by Gelei (Fig. 280, F). This observer believes such entangled threads to be subsequently liberated by pulling through the ring; but the occasional occurrence of interlocking rings shows that such is not always the case. The parasynaptic theory, evidently, gives a simple explanation of such cases.

B. Disjunction and Segregation

The purely sceptical attitude towards both synapsis and disjunction formerly taken by some writers [1] is now possible only for those who have not troubled themselves with the progress of modern cytological research. On the other hand, the question whether the synaptic mates that couple in synapsis retain their identity as such, to be disjoined as such in the reduction-division, has found a definite answer only in the case of particular chromosomes (p. 571).

1. The Reduction-division

In many objects, including those classical ones *Tomopteris* and *Batrachoseps* (p. 551), it has not been possible to demonstrate with certainty any longitudinal duality in the pachynema for a certain period following synapsis and prior to the appearance of the diplonema (a period very short in *Tomopteris* but extending through a large part of the growth-period in urodeles). An important group of observers (p. 506) were thus led to a position of great reserve concerning the reduction-division, concluding that synapsis leads to a complete fusion of the synaptic mates to form "mixochromosomes" or "zygosomes" in which the identity of the original

[1] *E. g.*, Meves, or Fick (p. 506).

conjugants may be wholly lost (Winiwarter, Bonnevie and others). So far as the visible phenomena in these cases go, there seems externally to be nothing to distinguish the formation of the diplonema from an ordinary longitudinal or equational split, and hence no ground for assuming the occurrence of a reduction. On the other hand, a considerable number of good observers have emphatically maintained that in some objects the longitudinal duality produced by parasynapsis is never at any period wholly lost to view,[1] at least in portions of the pachynema; while, as earlier indicated, Gelei has shown that in *Dendrocœlum* a union of the synaptic mates that externally seems to involve complete fusion may leave intact the two separate

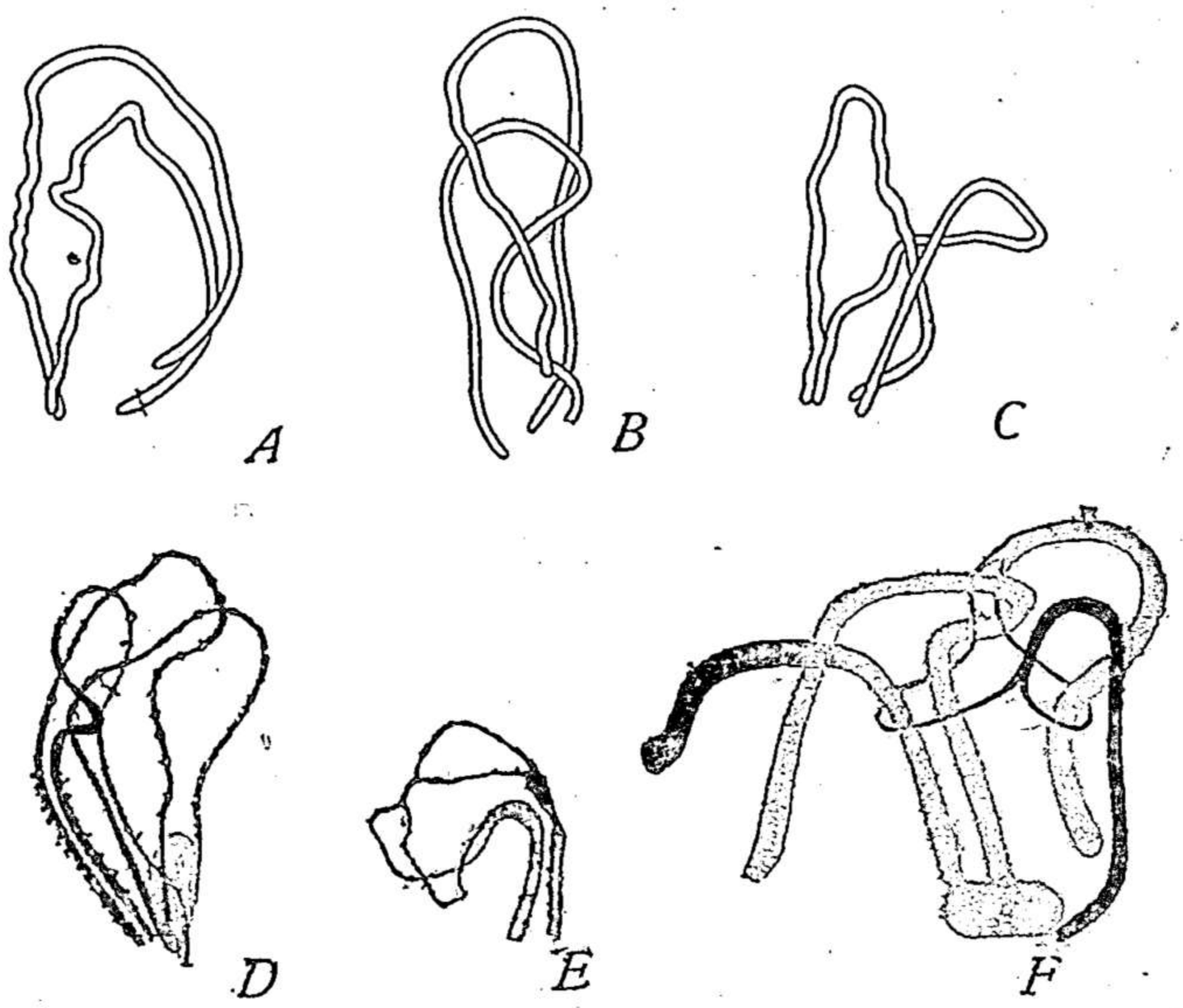

Fig. 280.—Details of parasynapsis in *Dendrocœlum* (GELEI).

A–C, three pairs of leptotene-threads (from one nucleus) at the beginning of conjugation; *D*, *E*, middle stages of conjugation, entanglement of the loops in *D*; *F*, diagram showing entanglement of the loops during conjugation.

series of chromomeres derived from each (Fig. 428). But apart from this direct evidence the indirect evidence from other sources is so strong as to remove every doubt concerning the reality of the reduction-division or the fact that in some sense or other a duality of the post-synaptic spireme persists throughout the pachytene stage.

The special and indirect evidence of the reduction-division is of widely varied nature. It is most demonstrative in the case of certain kinds of chromosomes which do not spin out into leptotene-threads before synapsis but conjugate and disjoin at a late period in the form of condensed chromosomes of the ordinary type. An example of these is offered by the micro-

[1] See especially Grégoire ('07, '10), Montgomery ('06, '11, etc.), McClung ('14, etc.), Wenrich ('16, '17).

chromosomes or "*m*-chromosomes" of certain Hemiptera (p. 839). These chromosomes ordinarily remain separate in the diakinesis and only couple to form a bivalent as the chromosomes are actually grouping themselves to form the equatorial plate.[1] Their conjugation is always immediately followed by disjunction, the process being one of "touch-and-go" which seems merely to serve the purpose of ensuring a definite segregation of the synaptic mates. Not the smallest doubt can here exist of the reality of synapsis and disjunction without intervening fusion of the synaptic mates or loss of their identity.

In this case the process might indeed be merely a secondary one, preceded by an earlier primary synapsis and disjunction (p. 793). This possibility is, however, excluded in a second case offered by the XY-pair of sex-chromosomes in certain Hemiptera, which are recognizable already in the pre-synaptic period (Stage *c*) by their condensed form which is retained throughout all the succeeding stages. In some of these cases, it is true, these chromosomes conjugate, deconjugate, and again conjugate at a later period (p. 769), though their identity never is wholly lost.[2] In others conjugation often wholly fails in the earlier stages, and both synaptic mates fully retain their identity at every period without the least sign of fusion.[3] In all cases these chromosomes divide separately in the heterotypic mitosis, though usually lying side by side, and conjugate in its final anaphase to form a bivalent in most cases unequal or heteromorphic (Fig. 369). Without fusion of its two components this bivalent enters the second mitosis and immediately disjoins. In this case, which may be taken as a crucial one, both synapsis and reduction-division are plain to demonstration. This is even more strikingly shown in case of the compound sex-chromosomes (p. 772).

A third decisive demonstration of the reduction-division is offered by the so-called *heteromorphic* chromosome-pairs in which the synaptic mates are visibly distinguishable by the eye by differences of size, form, mode of spindle-attachment or structure. The most remarkable cases of this kind are offered by the XY-pair, just referred to, in which Y is almost always smaller, often much smaller, than X (p. 767). This case is of crucial importance, because we know that the Y is of paternal ancestry and the X of maternal (p. 767), this case having first substantiated Montgomery's general hypothesis that the synaptic mates are respectively of maternal and paternal origin.[4] Since this case was made known heteromorphic pairs of ordinary chromosomes (autosomes) have been demonstrated by Carothers, Robertson and Wenrich in several genera of *Orthoptera*. In some of these

[1] Gross, '04, Wilson, '05b, etc.
[2] Wilson, '05b, etc.
[3] *Oncopeltus*, Wilson, '12.
[4] Stevens, '05, Wilson, '05.

cases the synaptic mates differ only in size (*Arphia*, *Phrynotettix*), in others in mode of spindle-attachment, as in *Trimerotropis* or *Circotettix*, where one may have a terminal attachment, the other a non-terminal (p. 934).

In the face of such facts scepticism must give way to the conviction that whatever changes of reorganization the synaptic mates may undergo during the meiotic cycle their identity is not lost. The cytological phenomena of synapsis in these cases have not yet been sufficiently followed out. Wenrich ('16) carefully studied the earlier history of an unequal autosome-tetrad in *Phrynotettix* and found that the unequal mates originally lie side by side in the *diplonema* (Fig. 255),[1] subsequently opening apart to form an unequal double cross. If this is correct, it seems fatal to the assumption that synapsis is followed by total fusion and a subsequent new splitting of the mixochromosome thus produced.

We here again emphasize the striking fact that while every bivalent (or tetrad) resulting from the conjugation of synaptic mates, undergoes two divisions during meiosis, a chromosome having no synaptic mate *divides but once*.[2] Remarkable examples of this are offered by the maturation-divisions of organisms having only a haploid group of chromosomes, such as the males of Hymenoptera (p. 797) or the haploid mutants of *Datura* recently described by Blakeslee and Belling ('22). In such cases synapsis fails to occur, and the univalents pass singly upon the spindle. Though each is at this time longitudinally double (equation-split) the halves do not separate in the first division but in the second. In the first division of these *Daturæ* the twelve double chromosomes (dyads) are distributed at random to the poles (3 and 9, 8 and 4, etc.) *without division;*[3] while the second division is quite normal apart from the diminished number of chromosomes. In the bee or wasp the first division is abortive and though the spindle forms, the dyads do not pass to its poles. The second (equational) division, as before, is normal. Evidence of the same type, though less spectacular, is afforded by organisms having an odd number of chromosomes, such as various mutants of *Œnothera* or *Datura* (p. 942), the males of many insects (p. 751), or individuals having supernumerary chromosomes (p. 872). The validity of the conceptions of synapsis and disjunction is thus fully demonstrated; for obviously the "reduction-division" is not properly such but only the separation of two associated synaptic mates (p. 505).

2. Order of the Divisions

In the foregoing pages no attempt has been made to discuss the order of succession of the reduction- and the equation-divisions. An answer to

[1] *Cf.* also Robertson. [2] Certain exceptions to this statement are considered at pp. 847, 852.
[3] All pollen grains with less than twelve seem to be abortive.

this long-disputed question must obviously rest upon our means of identification of the reduction-division and, as will be evident from the foregoing, *such identification can only be made with complete certainty in cases where the synaptic mates are visibly distinguishable* by differences of form, size, structure, or mode of attachment. A sufficient number of such cases are now known to demonstrate that *the two divisions do not in all cases follow the same order, and that even in the same division the bivalents may differ individually in this respect.* Weismann's early assumption that the first division, considered as a whole, is equational, and the second reductional ("post-reduction") led to a tedious controversy as to the order of the two divisions. Weismann's conclusions were adopted by Rückert, Haecker, Van der Stricht, Griffin, McClung and many others. The reverse order ("pre-reduction") was advocated by Henking, Korschelt, Paulmier and Montgomery, and ultimately by Strasburger, Mottier, Farmer and Moore, the Schreiners and most of the later students of the problem. As recently as 1910 Grégoire, in an important review, leaned strongly towards the conclusion that pre-reduction would prove to be the prevailing and perhaps the universal order of division. This conclusion was based especially on the conclusion that the first division takes place through the "primary" longitudinal cleft of the bivalent, and that this represents the plane of parasynaptic conjugation on either side of which lie the homologous conjugants or synaptic mates. This interpretation seemed to be supported by the strong tendency of the two primary halves to early separation (as early emphasized by Flemming) and the consequent formation of rings, crosses and other peculiar forms.

There is some strong additional special evidence in favor of a general pre-reduction. In the haploid *Datura* mutants or in male Hymenopt as indicated above (p. 572) it is obviously the first division that re ts the reduction-division. In the heteromorphic tetrads of *Tr otropis* and other Orthoptera, it is always the first division in whic junction of the synaptic mates occurs (p. 933). In 15-chromosome mutants of *Œnothera* (*lata* type, p. 944) or in 25-chromosome mutants of *Datura* (p. 944), it seems to be always the first division in which the unequal distribution occurs.

Nevertheless it is certain that this order is not invariable, as is proved especially by the sex-chromosomes. The heteromorphic XY-pair, for example, always divides pre-reductionally in Coleoptera and Diptera, so far as known, while in the Hemiptera heteroptera, it follows the reverse order. The same is true with the unpaired X-chromosome (p. 756). A remarkable demonstration of such differences is seen in the heteropter *Metapodius*, where, in the first spermatocyte-division, the *m*-chromosome pair and the

XY-pair may be seen side-by-side in the same mitosis, the former manifestly dividing reductionally, the latter equationally. Finally, in the grasshopper *Phrynotettix* one of the heteromorphic bivalents ("pair C") was found by Wenrich ('16) to divide in either order, even in the same individual.

From the foregoing we may conclude that pre-reduction probably constitutes the general rule, but that changes in the order may readily occur. In such cases both divisions may be of mixed type, and the old distinction between the reduction- and the equation-divisions can only apply to the tetrads considered individually. This fact, evidently, has an important bearing on the genetics of parthenogenetic animals (p. 962). In practice, however, it is often difficult to distinguish between the "primary" and "secondary" clefts of the tetrads and hence between the reduction-division and the equational. In the formation of the double crosses for instance, both clefts open out nearly or quite at the same time, though from opposite ends (p. 523); so that in the fully formed cross it is often impossible to distinguish certainly between the two. The case is precisely similar with the double rings (p. 527) which arise by the opening out of the primary cleft in one-half of the original rod, of the secondary cleft in the other; or in case of the transverse rod-tetrad (which is equivalent to a double cross devoid of lateral arms). The Schreiners ('06, *Tomopteris*), Montgomery ('11, *Euschistus*), Robertson ('16, *Syrbula*) and most others have concluded that the original quadruple rod opens out along the primary cleft, the resulting "cross-division" being reductional. Wenrich ('16) on the other hand produces some evidence in grasshoppers (*Phrynotettix*) in favor of the contrary conclusion that the primary cleft closes up while the secondary one opens so that the "cross-division" is here equational. It is entirely possible that both sides are right and that different species may vary in this respect as they undoubtedly do in the order of the divisions (p. 572).

V. INDIRECT EVIDENCE. GENERAL ASPECTS. SUMMARY

The general conception of synapsis and reduction is supported indirectly by a great body of indirect evidence, of which the cumulative force is irresistible and leads us to the confident expectation that the remaining difficulties will sooner or later be overcome. The most convincing of this evidence includes the size-differences and pairing of the chromosomes in the diploid groups, and their relation to the tetrads; the chromosomes of hybrids; the history of the sex-chromosomes; and the cycle of the chromosomes in the antithetic alternation of generations of plants. Since these phenomena will be more fully considered hereafter we will here only briefly emphasize a few of the more important facts. Prominent among them is the fact that in some plants and animals, notably in Diptera, the synaptic mates of the

diploid groups are arranged in pairs in the somatic or diploid divisions (Fig. 396). In some of these cases, as shown especially by Metz ('14, '16), the synaptic mates of each pair are so closely associated in the somatic prophases as to appear exactly like the products of longitudinal fission in the spireme-threads; and they have actually been described as such by some observers, but this proved to be an error (p. 837). The fact that paternal and maternal homologues may pair so closely, side-by-side, when in the

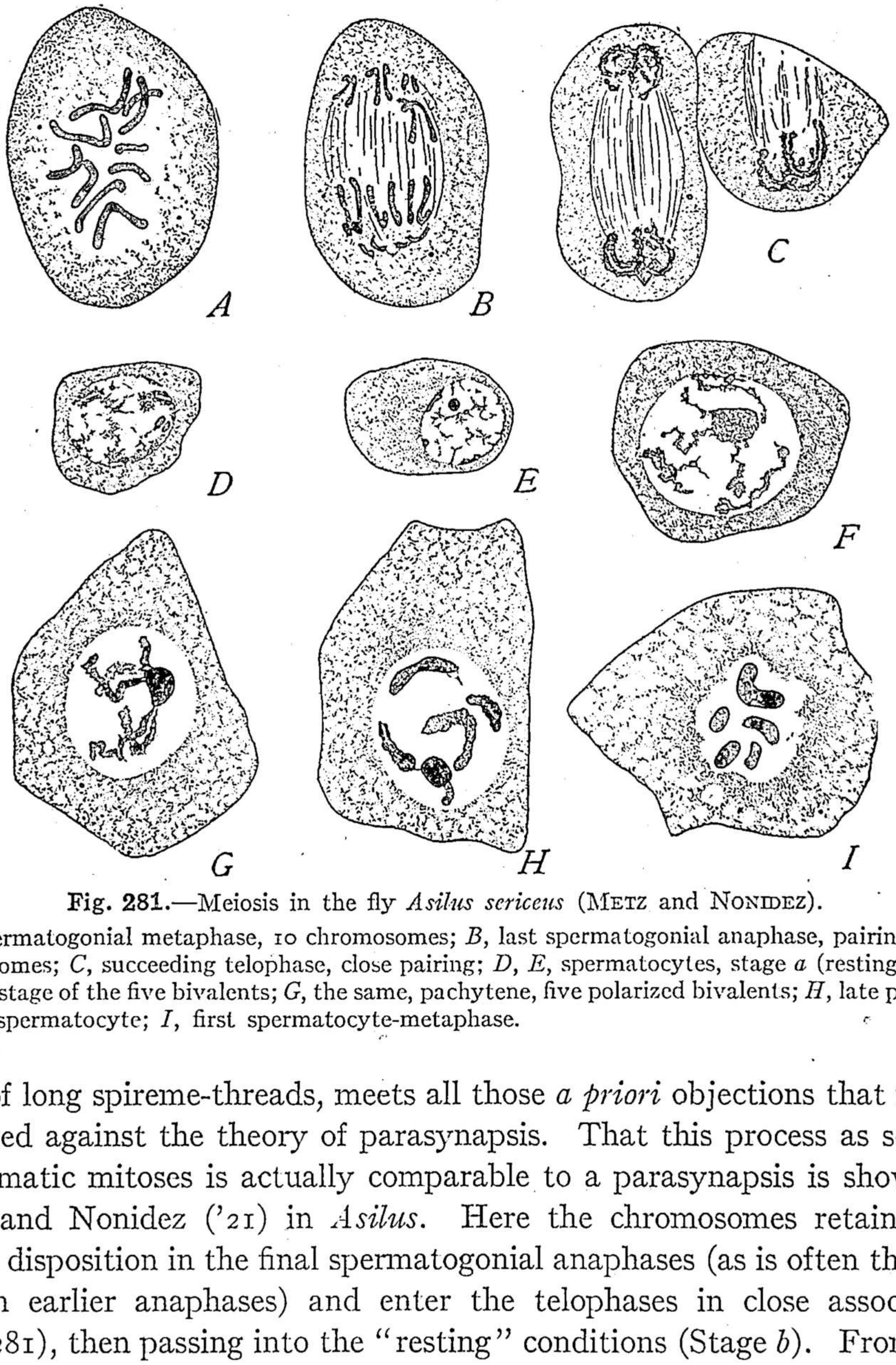

Fig. 281.—Meiosis in the fly *Asilus sericeus* (METZ and NONIDEZ).

A, spermatogonial metaphase, 10 chromosomes; *B*, last spermatogonial anaphase, pairing of the chromosomes; *C*, succeeding telophase, close pairing; *D*, *E*, spermatocytes, stage *a* (resting stage); *F*, early stage of the five bivalents; *G*, the same, pachytene, five polarized bivalents; *H*, late prophase of first spermatocyte; *I*, first spermatocyte-metaphase.

form of long spireme-threads, meets all those *a priori* objections that might be urged against the theory of parasynapsis. That this process as seen in the somatic mitoses is actually comparable to a parasynapsis is shown by Metz and Nonidez ('21) in *Asilus*. Here the chromosomes retain their paired disposition in the final spermatogonial anaphases (as is often the case also in earlier anaphases) and enter the telophases in close association (Fig. 281), then passing into the "resting" conditions (Stage *b*). From this

stage *they emerge in the form of typical pachytene-bivalents of the haploid number* (Stage *g*), Stages *c*, *d*, *e*, and *f*, including the leptonema and synaptic stages, being omitted. Here, evidently, pseudo-reduction is initiated by an anaphasic parasynapsis, similar in principle to the anaphasic or telophasic conjugation assumed by Montgomery (p. 558). It seems, therefore, a reasonable view that in animals generally the paired union of chromosomes in synapsis is usually long delayed, but may be foreshadowed by a more or less definite paired association that takes place early in the diploid cycle, thus giving some suggestion of an approach to the zygotic type of meiosis (p. 491).

Another striking fact is that true tetrad-formation and heterotypic mitosis are seen only in bivalent chromosomes resulting from the union of synaptic mates, and hence does not take place in the haploid phase of organisms but only in the diploid, however brief the latter may be. It is for this reason obviously, that in all plants having an antithetic alternation of generations tetrad-formation does not occur in the gamete-producing divisions, since the latter takes place in the haploid generation and by a simple mitosis of the ordinary type, while heterotypic mitosis appears only in the diploid generation during the process of spore-formation (pp. 491, 619). So-called "tetrads" and "heterotypical mitosis," have, it is true, been described in the somatic mitoses; but these appearances have a totally different significance from that so manifest in the meiotic divisions. They do not result from a process of synapsis; they do not lead to a reduction of chromosome-number; and they divide through only one of the tetrad-sutures (p. 904).

In conclusion it may be said that a vast and always growing body of data, both cytological and genetic, supports the general conclusions drawn by Weismann thirty-five years ago. Some perplexing cytological difficulties, indeed, still remain; but they are difficulties of detail which, we may confidently expect, will sooner or later be cleared up. The most obvious effect of meiosis is to sort out the diploid chromosome-group into two haploid ones. Karyogamy and meiosis are thus opposite and complementary processes; but it must be borne in mind that the haploid groups brought together by karyogamy do not remain long separate as such (gonomery), since the paternal and maternal chromosomes soon become indistinguishably mingled; nevertheless the diploid chromosome-group as a whole, when once established, is maintained intact by mitosis throughout the whole diploid cycle.

Meiosis brings about two additional results, less obvious but fundamentally important. One is to establish *new haploid combinations* of the original maternal and paternal chromosomes in the germ-cells. The

genetic evidence demonstrates that the haploid groups produced by meiosis are in most cases not purely maternal or paternal (though they may be so). Most of them represent regroupings of the original chromosomes, always such as to retain the essential character of the haploid group but differing in respect to the parental source of the individual chromosomes (Fig. 105). This reorganization of the haploid groups results from a very simple mechanism later to be considered (p. 927).

Not less important is the reorganization of the chromosomes, individually considered, that takes place during meiosis, by means of " crossing-over," *i. e.*, of orderly exchanges of material between the synaptic mates during the period of their association. This process, thus far certainly known only from the genetic evidence, is of unknown physiological significance. As earlier mentioned, and will later be shown in greater detail (p. 956), crossing over is often of such a type as to render both divisions of a given tetrad in part reductional, in part equational (*i. e.*, in the so-called " two-strand chiasma," Fig. 451). In such cases both divisions are necessary for complete reduction of the chromosome-components, and the distinction between reductional and equational division *of the chromosomes as such* cannot strictly be maintained. This, however, leaves untouched the fact that in the processes of meiosis lies the explanation of the main phenomena of Mendelian heredity, including segregation, random assortment of the linkage-groups and recombination by "crossing-over," as will be more fully indicated in Chapter XII.

LITERATURE VI

(See also IV, V, VII, X, XI. For abbreviations see General Literature List.)

Agar, W. E., '11. The Spermatogenesis of *Lepidosiren: Q. J.*, LVII.
Dalc, A., '21. La spermatogénèse chez l'Orvet (*Anguis*): *A. B.*, XXXI.
Davis, H. S., '03. Spermatogenesis of Acrididæ and Locustidæ: *B. M. Z.*, LII.
Digby, L., '10. The somatic, premeiotic and meiotic nuclear Divisions of *Galtonia candicans: A. Bot.*, XXIV.
Farmer and **Moore,** '05. The Meiotic Phase in Animals and Plants: *Q. J.*, XLVIII.
Fick, R., '06. Vererbungsfragen, Reduktionstheilung, etc.: *E. A. E.*, XVI.
Gates, R. R., '08. A Study on Reduction in *Œnothera rubrinervis: B. G.*, XLVI.
Gates and **Rees,** '21. A cytological Study of Pollen Development in *Lactuca*: *A. Bot.*, XXXV.
Gelei, J., '21, '22. Weitere Studien über die Oögenese von *Dendrocœlum*, II, III: *A. Zf.*, XVI, 1, 3.
Granata, L., '10. Le cinesi spermatogenetiche di *Pamphagus marmoratus: A. Zf.*, V.
Grégoire, V., '05. Les resultats acquis sur les cinèses de maturation dans les deux régnes, I: *L. C.*, XXII.

Grégoire, V., '10. Les cinèses de maturation dans les deux régnes: *Ibid.*, XXVI.
Henking, H., '91. Ueber Spermatogenese, etc., bei *Pyrrhocoris apterus: Z. W. Z.*, LI.
'92. Untersuchungen über die ersten Entwicklungsvorgänge in den Eiern von Insekten: *Ibid.*, LIV.
Hertwig, O., '90. Vergleich der Ei- und Samenbildung bei Nematoden. Eine Grundlage für cellulare Streitfragen: *A. M. A.*, XXXVI.
Janssens, F. A., '01. La spermatogénèse chez les *Tritons: L. C.*, XIX.
'05. Évolution des auxocytes mâles du *Batrachoseps attenuatus: Ibid.*, XXII.
Janssens, F. A., et Dumez, R., '03. L'élément nucleinien pendant les cinèses de maturation des spermatocytes chez *Batrachoseps attenuatus et Plethodon cinereus: L. C.*, XX.
Kœrnicke, M., '04, '05. Die neueren Arbeiten über die Chromosomen-Reduktion im Pflanzenreich und daran anschliessende Karyokinetische Probleme: *B. Z.*, LXII.
Maréchal, J., '07. Sur l'ovogénèse des Selachiens: *L. C.*, XXIV.
Matschek, H., '10. Ueber Eireifung und Eiablage bei Copepoden: *A. Zf.*, V.
McClung, C. E., '14. A Comparative Study of the Chromosomes in Orthopteran Spermatogenesis: *J. M.*, XXV.
Meves, F., '08. Es gibt keine parallele Konjugation der Chromosomen: *A. Zf.*, I.
Mohr, Otto L., '14. Studien über die Chromatinreifung der männlichen Geschlechtszellen bei *Locusta viridissima: A. B.*, XXIX.
Montgomery, T. H., '04. Some Observations and Considerations upon the Maturation Phenomena of the Germ Cells: *B. B.*, VI, 3.
Mottier, D. M., '05. The Development of the Heterotypic Chromosomes in Pollen Mother-cells: *B. G.*, XL.
'07. The Development of the Heterotype Chromosomes in Pollen Mother-cells: *A. B.*, XXI.
'09. On the Prophases of the Heterotypic Mitosis in the Embryo-sac Mother-cell of *Lilium; Ibid.*, XXIII.
'14. Mitosis in the Pollen Mother-cells of *Acer* and *Staphylea; A. B.*, XXVIII.
Platner, G., '89. Ueber die Bedeutung der Richtungskörperchen: *B. C.*, VIII.
Rückert, J., '92a. Zur Entwicklungsgeschichte des Ovarialeies bei Selachiern: *A. A.*, VII.
'92b. Ueber die Verdoppelung der Chromosomen im Keimbläschen des Selachiereies: *A. A.*, VIII.
'93. Die Chromatinreduktion der Chromosomenzahl im Entwicklungsgang der Organismen: *Merkel and Bonnet, Erg.*, III.
Schleip, W., '09. Vergl. Untersuchungen der Eireifung bei . . . Ostracoden: *A. Zf.*, II.
Schreiner, A. and **K. E.**, '06a. Neue Studien über die Chromatinreifung der Geschlechtszellen. I. Die Reifung der männlichen Geschlechtszellen von *Tomopteris onisciformis: A. B.*, XXII.
'06b. II. Reifung der männlichen Geschlechtszellen von *Salamandra maculosa, Spinax niger* und *Myxine glitinosa: A. B.*, XXII.
'08. Gibt es eine parallelle Konjugation der Chromosomen?: *Videnskabs-Selskab. Skrifter.* I. *Math.-Natur. Klasse*, IV.
Stomps, T. J., '10. Kerndeeling en Synapsis bij *Spinacia:* See *B. C.*, XXXI.
Strasburger, E., '05. Typische und allotypische Kernteilung: *J. W. B.*, XLI.

Vejdovský, F., 07. Neue Untersuchungen über die Reifung und Befruchtung: *Königl. Böhmische Ges. d. Wiss., Prag.*

Wenrich, D. H., '16. The Spermatogenesis of *Phrynotettix magnus*, etc.: *B. M. Z.*, LX.

'17. Synapsis and Chromosome Organization in *Chorthippus* (*Stenobothrus*) *curtipinnis* and *Trimerotropis suffusa: J. M.*, XXIX.

Wilson, E. B., '12. (See X.) Studies on Chromosomes, VIII: *J. E. Z.*, XIII.

Winiwarter, H. de, '01. Recherches sur l'ovogénèse, etc.: *A. B.*, XVII.

Winiwarter and **Saintmont,** '09. Nouvelles recherches sur l'ovogénèse, etc.: *Ibid.*, XXIV.