CHAPTER XI

MORPHOLOGICAL PROBLEMS OF THE CHROMOSOMES

"For every chromosome that enters into a nucleus there persists in the resting-stage some kind of *unit*, which determines that from this nucleus come forth again exactly the same number of chromosomes that entered it, showing the same size-relations as before and often also the same grouping."

BOVERI.[1]

I. THE INDIVIDUALITY OR GENETIC CONTINUITY OF THE CHROMOSOMES

In any general account of the history and genetic relations of the chromosomes in the life-cycle, we inevitably find ourselves speaking of them as if their identity were not really lost when they disappear from view in the resting or vegetative nucleus. The vast literature of the subject is everywhere colored by the implication that chromosomes, or something which they bear, have a persistent individuality that is carried over unchanged from generation to generation. This view has met with some determined opposition;[2] but with the advance of exact studies on the chromosomes scepticism has gradually yielded to the conviction that the chromosomes must, to say the least, be treated *as if they were* persistent individuals that do not wholly lose their identity at any period in the life of the cell but grow, divide and hand on their specific type of organization to their descendants. This does not mean that chromosomes are to be thought of as fixed and unchangeable bodies. Beyond a doubt they undergo complex processes of growth, structural transformation and reduction, in some cases so great that not more than a small fraction of the substance of the mother-chromosomes at its maximum development is passed on to the daughter-chromosomes. Whether we can rightly speak of a persistent "individuality" of the chromosomes is a question of terminology. What the facts do not permit us to doubt is that chromosomes conform to the principle of genetic continuity; that every chromosome which issues from a nucleus has some kind of direct genetic connection with a corresponding chromosome that has previously entered that nucleus.

1. Origin of the Theory

A first hint of the conception appears already in Van Beneden's oft-cited work on *Ascaris* ('83–'84) but the modern theory first took definite

[1] *Zellen-Studien*, VI., p. 229, 1907.

[2] See, for instance, Fick ('07), Meves ('11), Della Valle ('09, '12).

form in 1885 with Rabl's conclusion that the chromosomes lose neither their identity nor their grouping at the close of the division, but are only lost to view by branching out and anastomosing to form the framework of the resting nucleus. Rabl believed that traces of the chromosomes could still be distinguished in the conformation of the nuclear framework during the interphase, the nucleus having a "pole" toward which the apices of the V-shaped chromosomes converge and an "antipole" at the opposite point (Fig. 390). During the ensuing prophases the chromosomes again come into view owing to the fact that "the chromatic substance flows back, through predetermined paths, into the primary nuclear threads." The latter (*i. e.*,

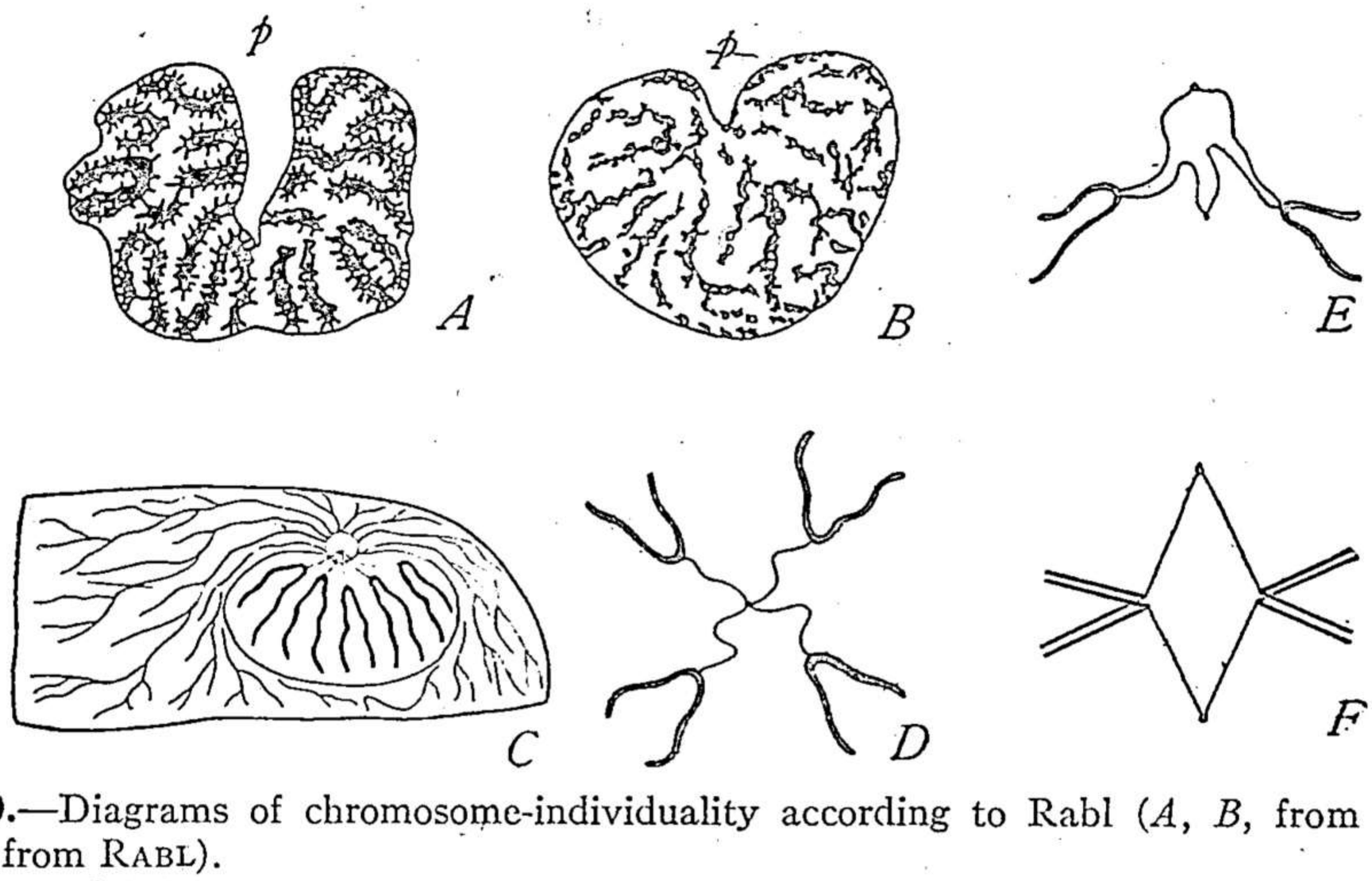

Fig. 390.—Diagrams of chromosome-individuality according to Rabl (*A*, *B*, from HAECKER the others from RABL).

A, earlier, and *B* later telophase-nuclei in epithelial cells of *Siredon* showing branching and vacuolization with retention of polarity; *C*, diagram of interkinesis showing persistent fibrillæ connecting center, chromosomes and general network; *D*, polar view of same (only 4 chromosomes shown); *E*, division of center and of fibrillæ connecting with chromosomes; *F*, fully established spindle.

the chromosomes) accordingly reappear in the same position and number as before.

The further development of this hypothesis was largely due to Boveri, who made it his own by a series of admirable researches extending from 1887 through nearly thirty years. A study of them impresses us both by the solidity of the foundation on which the theory is built and the skill with which its development was worked out. These researches and those that followed showed that the matter is not so simple as it was at first conceived; in principle nevertheless the conclusions of Rabl and Boveri are sustained to-day by a vast and always growing body of data. We need not hesitate, therefore, to accept Boveri's remarkable conclusion, already foreshadowed by Van Beneden, that *in all cells of the offspring produced from the zygote or fertilized egg half of the chromosomes are of maternal ancestry and half of paternal.*

2. General Evidence

Considered as a practical working hypothesis the principle of genetic continuity obviously offers the simplest way of formulating the relations of the chromosomes in the life-cycle generally. In fertilization or syngamy two haploid groups are brought together to form a diploid group, which perpetuates itself by division until the process of meiosis again resolves it into two haploid groups. If the germ-cell after reduction develops without fertilization the haploid number [1] may persist, and thus give rise to a haploid individual, as we see with special clearness in the gametophyte generation of plants and in the haploid type of natural animal parthenogenesis. When numerical differences exist between the gametic groups (as in hybrids) it is their sum that appears in the resulting diploid groups, conspicuous examples

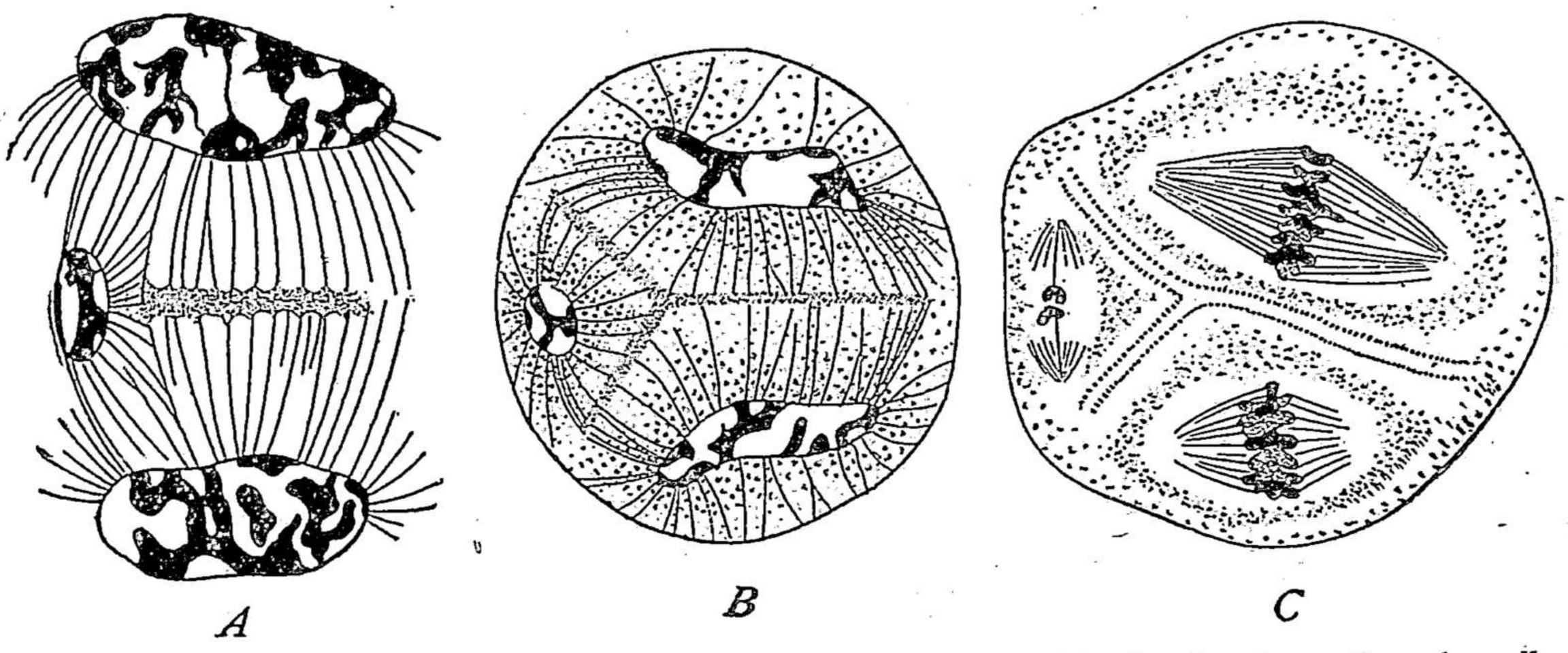

Fig. 391.—Abnormal mitosis in pollen-mother-cells of *Hemerocallis*, showing formation of small nucleus from one or two stray chromosomes and its subsequent division (JUEL).

of which are given by the relations of the chromosomes to sex (p. 751); and here again the diploid group thus established perpetuates itself by division.

The same principle holds for forms which normally have an odd number of chromosomes (irrespective of sex), such as the *lata* types of *Œnothera* with 15 chromosomes. These, though subject to many irregularities, typically produce gametes with 7 and with 8 chromosomes respectively, the sum of which equals the diploid number (p. 944). The same is true of forms in which supernumerary chromosomes occur. Whatever be their number, they appear in the same number in successive generations of cells, both in the diploid groups and during the maturation-process (p. 872). Lastly, when by a natural mutation the number of chromosomes in the zygote is doubled (as in *Œnothera gigas*) this number is retained thereafter.

The foregoing results receive a demonstrative confirmation from the study

[1] In this and other similar statements the occasional formation of double or multiple groups is disregarded (p. 87-).

of abnormal deviations from the typical numbers, whether arising spontaneously or produced experimentally; and here belongs some of the most important of the evidence brought forward by Boveri and his immediate followers. In the polar divisions of *Ascaris*, for example, one or both of the chromosomes destined for the second polar body are sometimes accidentally left in the egg. These chromosomes give rise in the egg to a reticular nucleus, indistinguishable from the egg-nucleus. At a later period this nu-

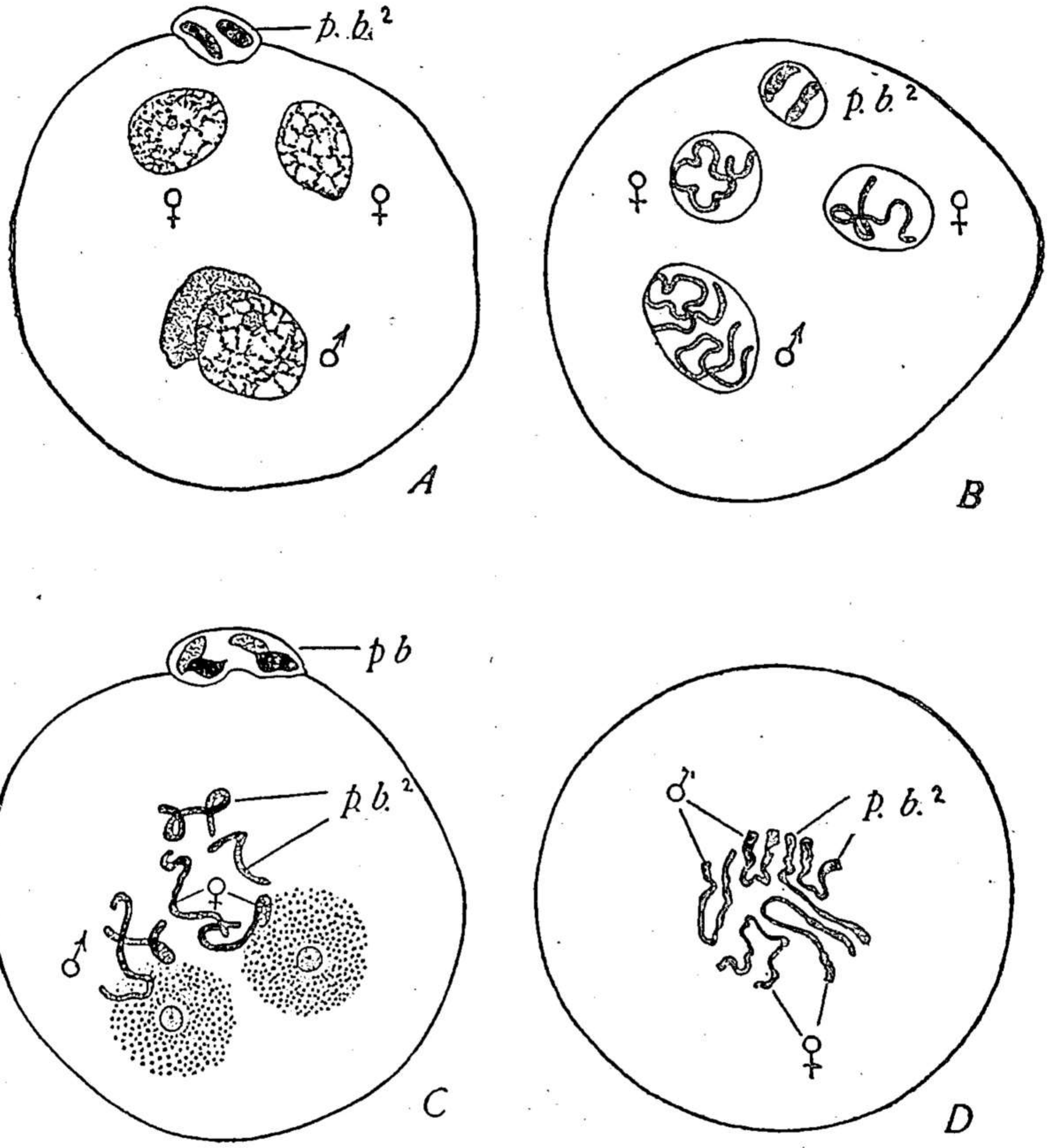

Fig. 392.—Evidence of the individuality of the chromosomes. Abnormalities in the fertilization of *Ascaris* (BOVERI).

A, the two chromosomes of the egg-nucleus, accidentally separated, have given rise each to a reticular nucleus (♀, ♀); the sperm-nucleus below (♂); *B*, later stage of the same, a single chromosome in each egg-nucleus, two in the sperm-nucleus; *C*, an egg in which the second polar body has been retained; *p. b.*², the two chromosomes arising from it; ♀ the egg-chromosomes; ♂ the sperm-chromosomes; *D*, resulting equatorial plate with six chromosomes.

cleus gives rise to the same number of chromosomes as those that entered into its formation, *i. e.*, either one or two. These are drawn into the equatorial plate along with those derived from the pronuclei, and mitosis proceeds as usual, the number of chromosomes being, however, abnormally increased from four to five or six (Fig. 392). Again, the two chromosomes left in the egg after removal of the second polar body may accidentally

become separated. In this case each chromosome gives rise to a reticular nucleus of half the usual size, and from each of these a *single* chromosome is afterward formed (Fig. 392). The same general result was given by Zur Strassen's ('98) studies on the history of giant embryos in *Ascaris*. These embryos arise by the fusion of previously separate eggs, and have been shown to be capable of development up to a late stage. The embryos from such eggs show an increased number of chromosomes proportional to the number of nuclei that have united. Thus in monospermic double eggs (variety *bivalens*) the number is triploid (six instead of four); in dispermic double eggs the number is tetraploid, being increased to eight (Fig. 393).

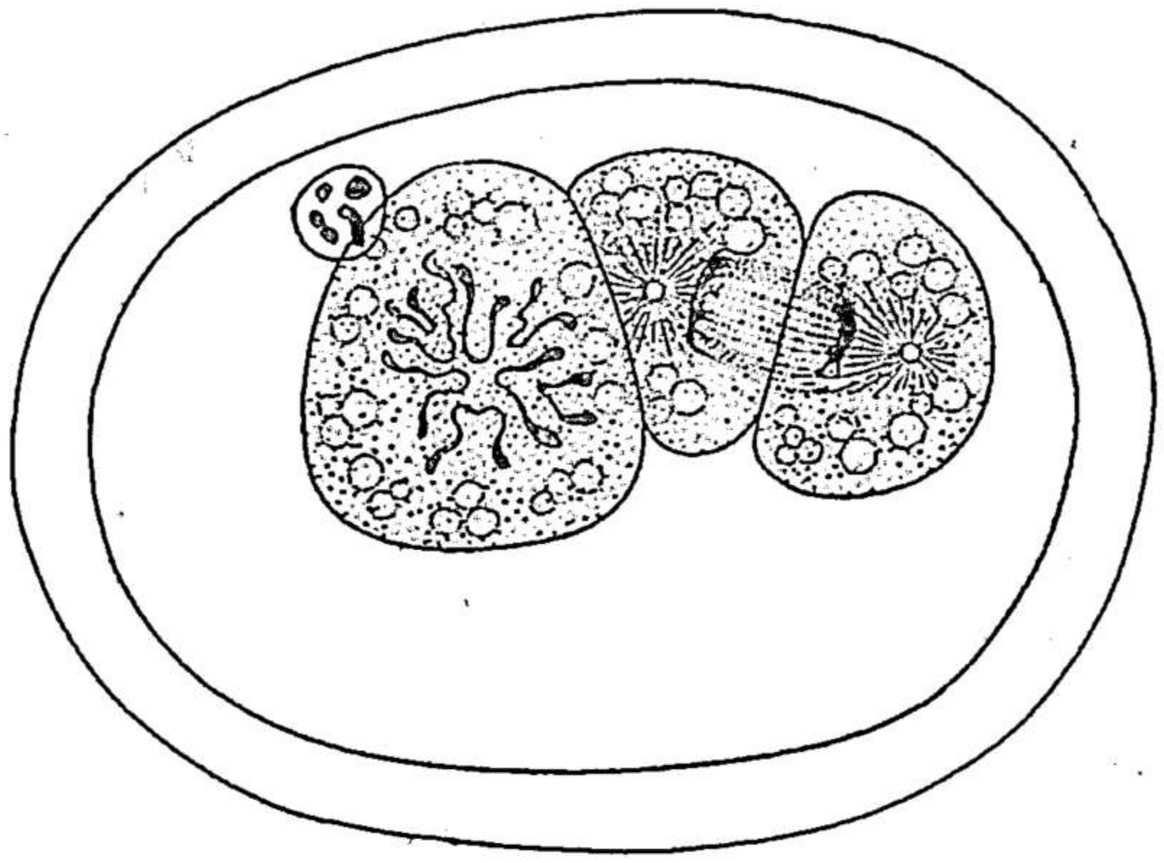

Fig. 393.—Giant-embryo of *Ascaris, var. bivalens*, arising from a double-fertilized double egg, showing eight chromosomes (*Zur Strassen*).

Later researches have afforded a mass of confirmatory data. Among the most striking are the experimental modifications of number in the eggs of sea-urchins and other animals. It is possible by various methods to cause the egg (after maturation) to develop without union with a sperm-nucleus, for instance by artificial parthenogenesis (p. 472), or by slight etherization of the egg (p. 447). In such cases the egg-nucleus divides with the haploid number of chromosomes (pp. 447, 476). In merogonic fertilization the nuclei of the segmenting germ-cell are derived from the sperm-nucleus alone, and as before they divide with the haploid number.[1] Conversely, the diploid number of the zygote may by artificial means be doubled so as to produce a tetraploid group. In the resulting embryos, as Boveri showed (p. 729), the tetraploid number thereafter persists.

Essentially the same result is given by the experimental results of Gerassimoff on *Spirogyra* and of the Marchals on mosses, an account of which is given at p. 730. A parallel to all these cases is given by the recent observations of G. and P. Hertwig ('20), which show that even in animals as highly organized as frogs development is possible with either the haploid (12), diploid (24) or triploid (36) number of chromosomes. The eggs of the frog *Rana esculenta* fertilized by sperm of the toad *Bufo viridis*, in certain cases produce two kinds of embryos, larger and more vigorous diploid ones and smaller and less vigorous ones which, because of their small nuclei, are believed to be of haploid constitution. This probably means that both are cases

[1] This was first proved by Boveri ('93, '95a) and Morgan ('95d).

of gynogenesis (p. 460), the haploid larvæ arising from eggs that have undergone complete reduction, the diploid from such eggs that have subsequently doubled their number (*e. g.*, by monocentric mitosis). This was tested by fertilizing frog's eggs showing this behavior with sperm of its own species, which produced triploid larvæ (up to 51 days old), in which the chromosomes were actually counted. The original eggs of this type were thus proved to have been diploid after maturation, and to have been fertilized by normal sperm, giving the triploid condition. Even more conclusive are those cases in which different numbers are experimentally produced in different nuclei of the same embryo, as in Boveri's dispermic sea-urchin larvæ or the hybrid sea-urchin larvæ of Baltzer and Herbst (pp. 917, 963). In these cases irregularities of chromosome-distribution, due to multipolar mitosis or the like, produce initial inequalities of chromosome-number which apparently cannot be equalized by regulative processes. The size of these nuclei depends upon the number of chromosomes which they receive (p. 730); and these differences, once established, seem to be irremediable. We thus see in the same larva patches of tissue showing mitoses with different chromosome-numbers and nuclei of different sizes, or larvæ with diploid hybrid nuclei on one side and purely maternal haploid nuclei on the other (p. 966).

Facts of this type demonstrate that *the number of chromosomes issuing from a resting-nucleus is determined by the number of chromosomes that have entered into its formation.* Opponents of the theory of genetic continuity, in particular Fick and Della Valle, have sought to interpret this as a simple quantitative effect, the size of the chromosomes being fixed by the physico-chemical quality of the chromatin and their number by its quantity. Fick urged that chromosomes are merely temporary packets of chromatin, "tactical formations" produced by a process comparable to the manœuvers of a military body. Della Valle compares chromosome-formation to that of liquid crystals and argues that their identity is wholly lost in the resting-nucleus.[1] The weakness of all such views lies in treating the chromosomes *en masse* without regard to their individual characteristics. The constant differences of the chromosomes in size, and often also in form and behavior, persist from one generation to another, whether the chromosome-group be haploid, diploid, triploid or tetraploid or broken up into other numbers by multipolar mitosis (p. 917).

[1] For criticisms of this view see Wilson ('09, '10, etc.), Montgomery ('10), McClung ('17), Tischler ('17), Parmenter ('19), Enriques ('21).

II. DIFFERENTIATION WITHIN THE CHROMOSOME GROUPS

That the chromosomes may show differences of size and shape in the same species was noted by Flemming, Strasburger and other earlier observers, but it did not at first occur to cytologists that such differences were other than fortuitous variations or fluctuations. Montgomery ('01) recognized the constancy of the differences of the chromosomes in respect to size and shape and in some cases also of behavior. His work in this field, carried out especially on the germ-cells of insects, formed the morphological counterpart of Boveri's epoch-making experimental demonstration of the physiological and qualitative differences of the chromosomes (p. 917) and thus contributed in an important way towards the demonstration of the genetic continuity of the chromosomes and the cytological explanation of Mendel's law (p. 926).

1. Differences in Size and Form

Constant differences of size and form among the chromosomes have now been found in so many groups of animals and plants, including even the Protista, as hardly to require enumeration here. They are illustrated by many figures throughout this work, especially in Chapters XI and XII, especially selected examples being shown in Figs. 394, and 395.[1] As before indicated (p. 127) the size-differences are in considerable measure due to the length rather than the diameter of the chromosomes, a point of much theoretical interest for various reasons. Meek ('12) ingeniously endeavored to prove that the transverse diameter of the chromosomes is constant throughout very large animal series, and that the observed variations have a far-reaching phylogenetic significance; but Farmer and Digby ('14) have shown that these relations are much less constant than found by Meek, whether in the individual or in the group; and this is in accordance with the observations of many other cytologists. Nevertheless Meek's observations are of considerable interest in their bearing on the variation of chromosome-number in the individual and in the species (p. 868).

Constant differences of shape among the chromosomes are often correlated with corresponding differences in mode of attachment to the spindle-fibers (p. 130). This is seen among both plants (Figs. 252, 395) and animals (Figs. 394, 396); conspicuous examples are offered by the acridian grasshoppers. In this group all the chromosomes most commonly are rod-

[1] For animals, see especially the works of Sutton, McClung, Robertson, Wenrich, Carothers, on Orthoptera; those of Paulmier, Montgomery, Wilson and Morrill, on Hemiptera; of Stevens and Nonidez on Coleoptera; of Stevens, Metz and Bridges on Diptera;—to all of which more special reference is elsewhere made. See also for plants C. Müller ('10, '12) with earlier literature, Stomps ('10), Wisselingh ('10), Strasburger ('10), Tischler ('17), Belling and Blakeslee ('22), etc.

shaped and have terminal attachments (Fig. 413), but in certain species, or even in different individuals of the same species, certain particular chromosomes may be V-shaped or J-shaped. The constancy of these relations has strongly impressed all observers who have studied them critically, not

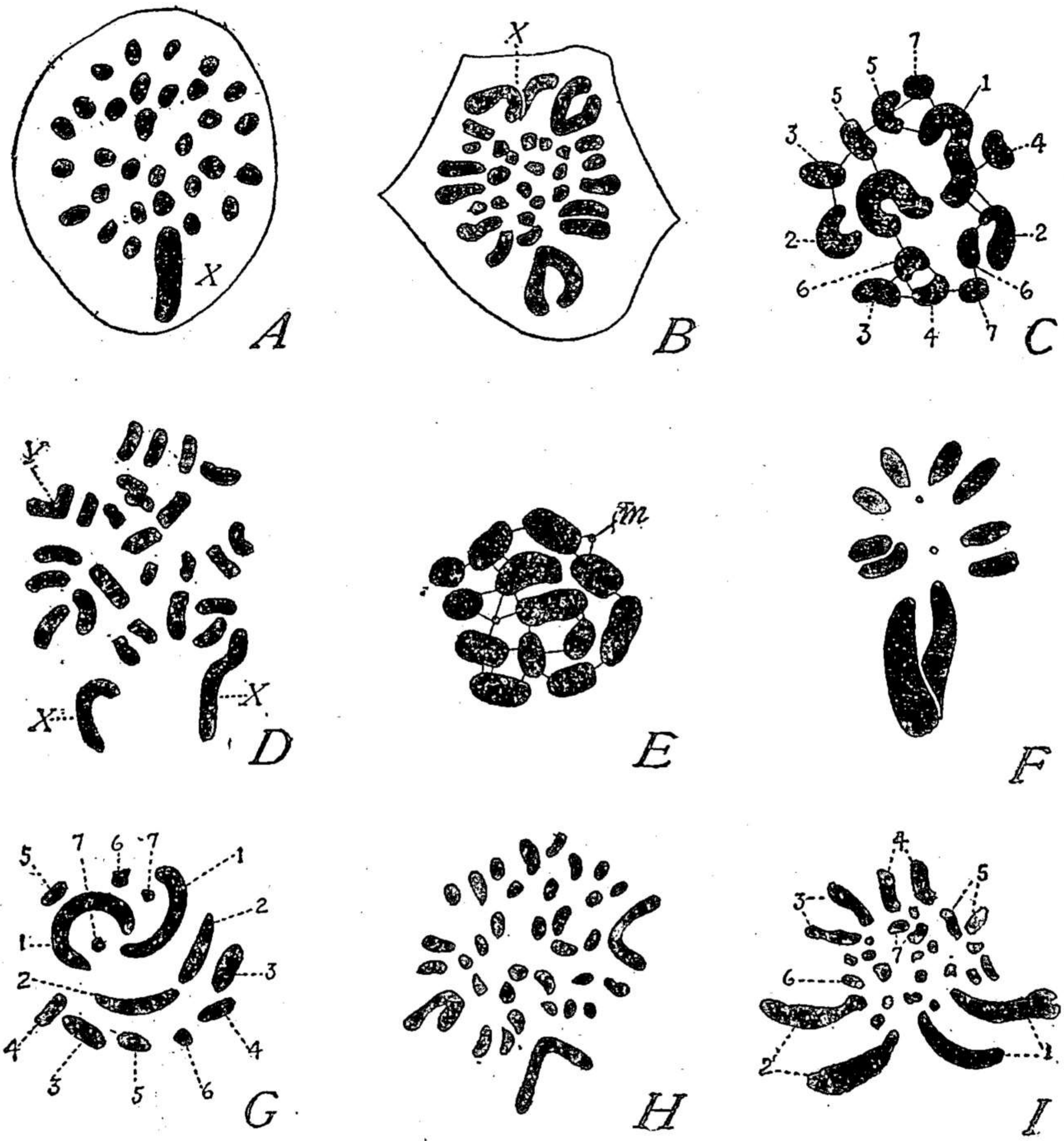

Fig. 394.—Size-differences of the Chromosomes. (All except *E*, *G*, and *I* are spermatogonial metaphases.)

A, the locustid *Orphania denticulata*, 31 chromosomes with one large *X*-chromosome (SINÉTY); *B*, *Locusta viridis*, 29 chromosomes with 3 V-shaped (MOHR); *C*, the hemipter *Protenor belgica*, 14 chromosomes; *D*, the mantid *Tenodera superstitiosa*, 27 chromosomes (OGUMA); *E*, the hemipter *Pachylis gigas*, with very small *m*-pair (WILSON); *F*, the fly *Drosophila funebris; G*, cleavage-nucleus of *Aphis rosæ* (STEVENS); *H*, the beetle *Blaps lusitanica*, 33 chromosomes, 3 atelomitic (NONIDEZ); *I*, root-tip of the seed-plant *Eucomis bicolar* (MÜLLER).

alone in the Orthoptera (Acrididæ, Locustidæ), but in other insects.[1] A remarkable case is that of the grasshopper *Trimerotropis*, as described by Carothers ('17) in which most of the chromosomes are rod-shaped with terminal attachments but a certain number usually are V-shaped or J-

[1] See for example Sinéty ('01), McClung ('14, '17), Robertson ('16), Wenrich ('16), Mohr ('14) Metz ('14, '16). For similar differences in the chromosomes of echinoderms see Baltzer ('09, '10, '13), Heffner ('10), Pinney ('11), Tennent ('11).

shaped. The number of the latter varies in different individuals *but is constant in the individual, and always affects the same particular chromosomes*, as is demonstrated both by the size-relations and by critical comparison of the diploid (spermatogonial) groups and those of the spermatocyte-divisions (Figs. 439, 440). Very striking cases of constant differences of both size and shape are also seen among the Diptera, which may be exemplified by *Drosophila melanogaster*, as described by Bridges ('16). The diploid groups here show eight chromosomes (Figs. 396, 415), four V-shaped (median at-

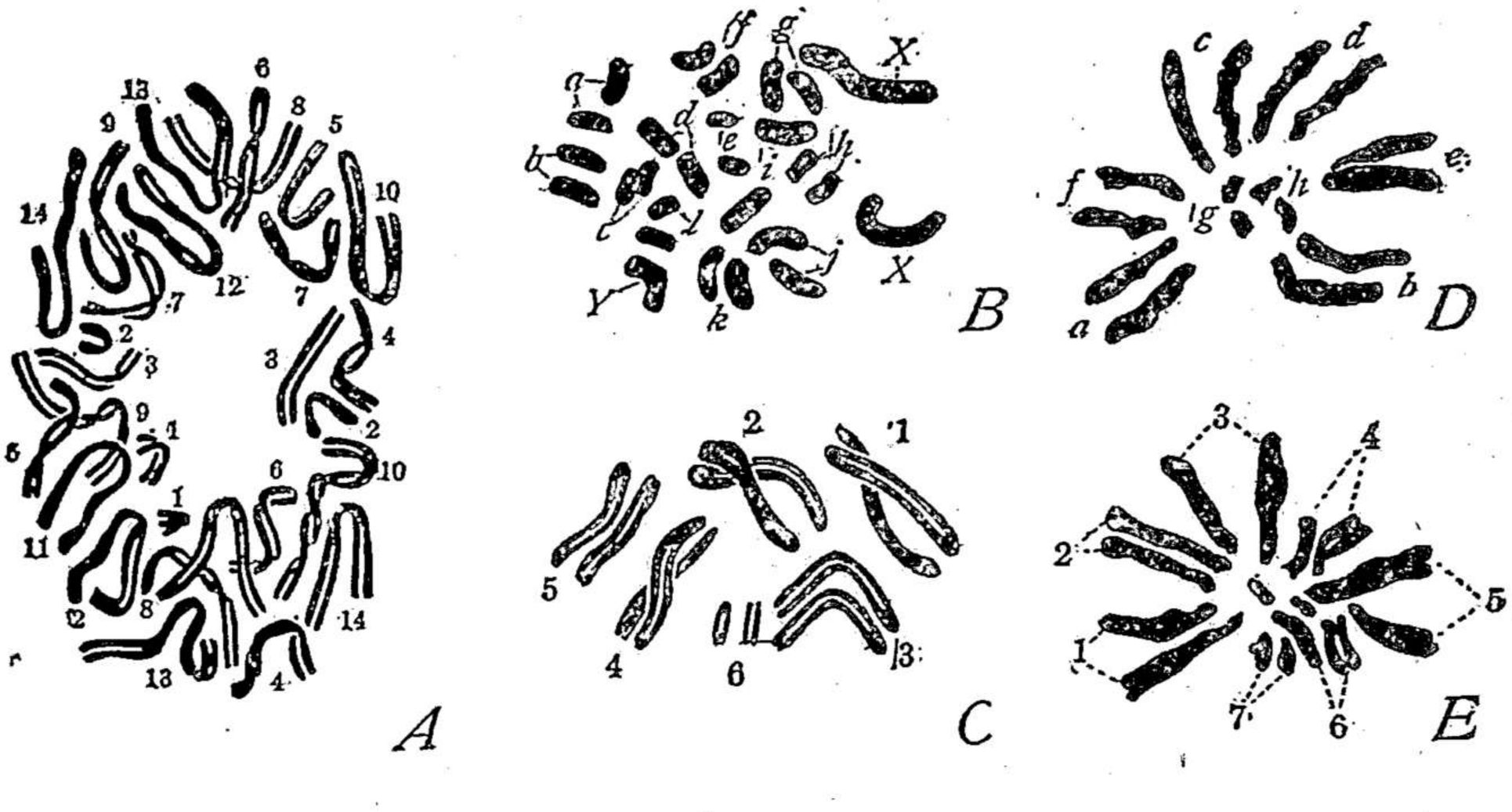

Fig. 395.—Chromosome-pairs in the diploid mitoses of animals (*A–C*), and plants (*D–H*).

In *A* there are 14 pairs, numbered according to size, but not actually grouped in pairs. The paired grouping is more or less clearly evident in all the others, and is perfect in *C*.

A, prophase of peritoneal cell, salamander, *Amblystoma tigrinum* (PARMENTER); *B*, spermatogonial group of mantis, *Tenodera superstitiosa* (OGUMA), the three sex-chromosomes (*X*, *X* and *Y*) not symmetrically paired; *C*, oögonial group of fly *Scatophaga pallida* (STEVENS); *D*, from root-tip of seed-plant *Galtonia* (STRASBURGER); *E*, same (MÜLLER); *F*, same of *Albuca; G*, of *Bulbina; H*, *Eucomis* (MÜLLER).

tachment), one rod-shaped with terminal attachment (the X-chromosome), one hook-shaped, with sub-terminal attachment (the Y-chromosome), and two very minute spheroidal ones. Constant differences of similar type in other species of Diptera have been observed by Stevens, Metz ('14, '16), and other observers. Differences in the shape of chromosomes are by no means always directly due to differences of spindle-attachment (*cf.* the ring-tetrads of *Tomopteris* and of Orthoptera, p. 530); and the point of

attachment, though on the whole highly constant, is not absolutely invariable.

2. Paired Condition of the Chromosomes in the Diploid Groups

Conclusive proof of the validity of the foregoing conclusions is afforded by the fact that in all cases where clearly marked differences of size are shown by the chromosomes the diploid groups contain two chromosomes of each recognizable size, the haploid groups but one, a fact first indicated by Montgomery ('01) and more fully studied by Sutton ('02), who found eleven recognizable pairs of chromosomes in the diploid groups of the male grasshopper *Brachystola* besides one unpaired X-chromosome. In many cases the chromosomes show no definite order of grouping; in others the synaptic mates show a certain tendency to approximate two by two in pairs;[1] while in a few cases *all or nearly all the chromosomes are thus arranged in pairs.* The most remarkable of these cases occur in the Diptera where all the chromosomes, apart from occasional irregularities, are unmistakably grouped in symmetrical pairs, the two members being of equal size and lying side by side, sometimes more or less twisted about each other as in a *strepsinema* (Figs. 395, 396). In the prophases, particularly, as shown by Metz,[2] the synaptic mates are so closely associated as to simulate closely the two halves of a longitudinally split chromosome, and as such they have actually been described by Lomen ('14) and Dehorne ('14). These observers were thus led to consider the somatic groups of some of these insects (*Culex*, *Corethra*) as haploid instead of diploid. That this is an error has been conclusively proved in *Drosophila* by Metz, and by Taylor, Whiting and Hance in *Culex.*

Some writers [3] too hastily accepted the probability that an actual pairing of the chromosomes is a general characteristic of the diploid nuclei; but this clearly goes too far; the opposite statement indeed would seem to be nearer the facts. The Diptera thus far stand alone in respect to both the regularity and the intimacy of the pairing; and even here it often fails in case of certain chromosomes. The most that can be said of organisms generally is that there is a rather widespread tendency for such pairing to take place, though only here and there clearly manifest and often shown by only a small number of the chromosomes. Little is known as yet regarding the time at which the pairing takes place. In *Drosophila* Metz found the

[1] This condition, so interesting for all the problems of chromosome-individuality, seems first to have been seen by Montgomery ('04) in the urodeles (*Plethodon*), and in Hemiptera ('06); and by Strasburger ('05, '07, '08), in certain seed-plants. It was afterwards found in various other animals and plants. See Geerts ('07), Janssens and Willems ('08), Sykes (09), Müller ('09, '12), Gates ('12), Stomps ('11), Metz ('14, '16, etc.).

[2] Stevens ('08), Metz ('14, '16, '20); see also M. Taylor ('15, '16), Whiting ('17), Hance ('17), Holt ('17).

[3] *E.g.*, Strasburger ('09, p. 90).

pairing already in early embryonic stages; and more recently Huettner ('22) has found it even before completion of the first cleavage of the ovum. A similar pairing was described by Hutchinson ('15) in the first cleavage of *Abies*.[1]

The important bearing of the side-by-side pairing of the chromosomes in these cases on the theory of synapsis in general and of parasynapsis in

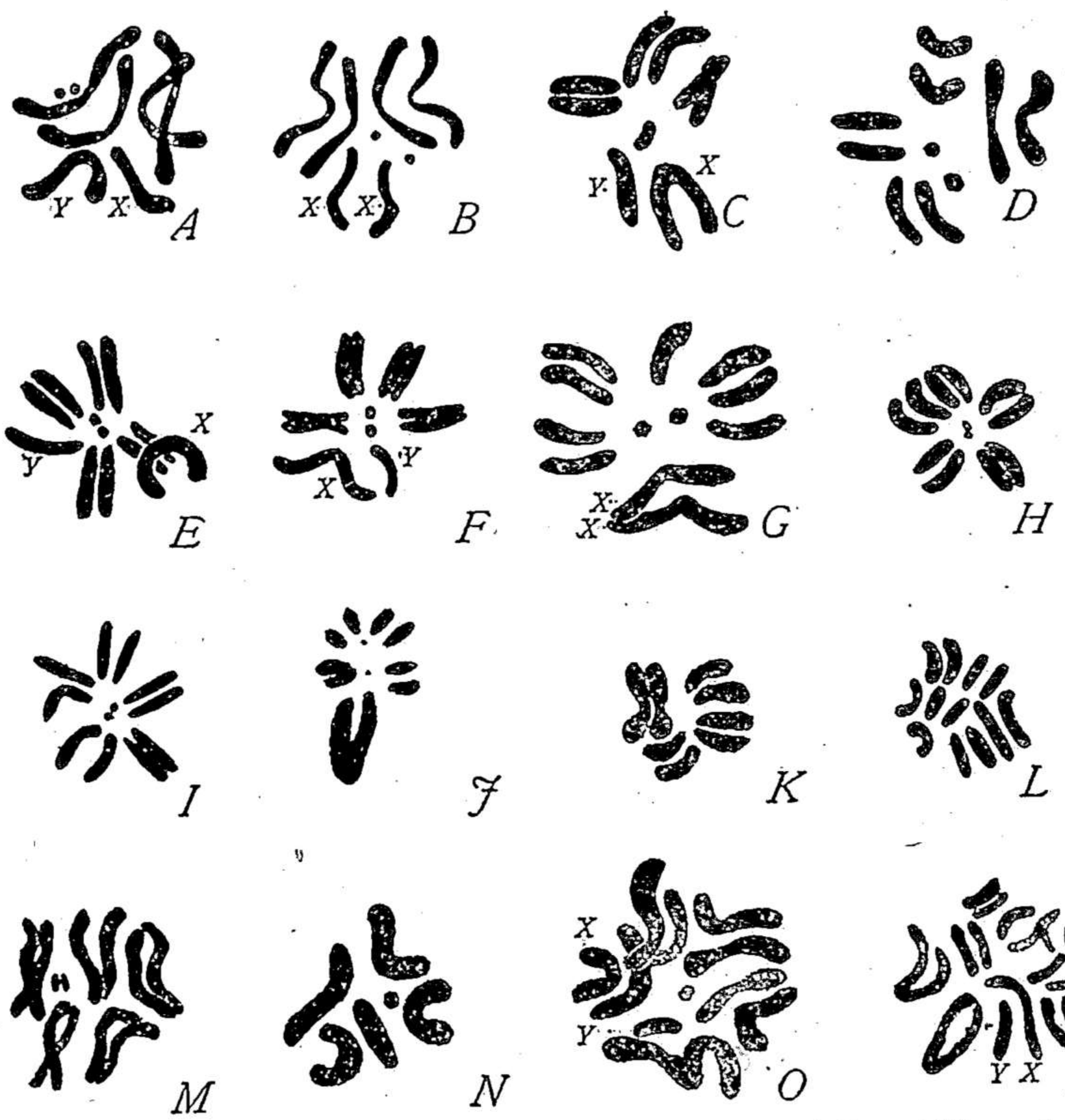

Fig. 396.—The diploid chromosome-groups in various species of *Drosophila* and other Diptera, not schematized. (*A*, *B*, from BRIDGES, the rest from METZ.)

A, *Drosophila melanogaster* ♂; *B*, *the same* ♀; *C*, *obscura* ♀; *D*, *melanica* ♀; *E*, *F*, *Mulleri* ♂; *G*, the same ♀; *H*, *virilis* ♀; *I*, *ramsdeni* ♀; *J*, *funebris* ♀; *K*, *immigrans* ♀; *L*, *Spogostylum simsoni* ♀; *M*, *Calliphora erythrocephala* ♀; *N*, same, first spermatocyte metaphase; *O*, *Sarcophaga tuber sarraceniæ* ♂; *P*, *Anthrax sinuosa* ♂.

particular, has earlier been indicated (p. 575). That the synaptic mates should thus pair in definite order, each with its parental homologue, is indeed an astonishing fact, and one that unmistakably indicates the existence of perfectly ordered qualitative differences among the chromosomes of which their different sizes and forms are outward expressions (p. 927).

[1] The pairs thus formed were said to divide *transversely* during the ensuing cleavage; and a similar account was offered by Chamberlain ('16) for *Stangeria* and by Weninger ('18) for *Lilium*. This account was, however, contradicted by Nothnagel ('18) in *Trillium* and by Sax ('18) in *Fritillaria*.

3. Differences in Behavior. Autosomes (Euchromosomes) and Heterochromosomes (Allosomes)

Certain special peculiarities of behavior on the part of particular chromosomes during mitosis and meiosis have been noted in the preceding pages, in particular those due to different modes of attachment to the spindle-fibers, to the lagging of particular chromosomes on the spindle, and the like. There are certain types of chromosomes which differ so widely in behavior from the others as to have received the special name of *heterochromosomes* or *allosomes* in contradistinction to the *autosomes* or *euchromosomes*, which include those of the more usual type.[1]

As first defined by Montgomery, the "heterochromosomes" were characterized by their tendency to undergo "heteropycnosis" during the growth-period of the spermatocytes (p. 758), and sometimes also in the spermatogonia, and hence classed by Montgomery ('98, '01) as "chromatin-nucleoli." Subsequently ('06) the term "allosome" was substituted for "heterochromosome" but has never come into general use. Many recent writers have used the term "heterochromosome" as a synonym of "sex-chromosome"; but this is inaccurate. Montgomery also distinguished between paired and unpaired heterochromosomes, the former being called *diplosomes*, the latter *monosomies*. Later researches showed, however, that the "diplosomes" included two wholly unrelated types, namely, the sex-chromosomes (XY-pair) and the microchromosomes or m-chromosomes which have no relation to sex and are alike in both sexes; while the "monosome" is the unpaired X-chromosome or accessory chromosome as it appears in the digametic sex.[2]

The special behavior of the sex-chromosomes has earlier been indicated. The m-chromosomes are a pair of small and sometimes very minute chromosomes at present known only in the coreid Hemiptera, where they were first described by Paulmier ('99) in *Anasa tristis* and have since been found in all the other Coreidæ thus far examined. They differ widely in size in different species (Fig. 397); in *Pachylis* and *Archimerus* they are excessively minute, in the former case hardly larger than centrioles; in *Anasa*, *Alydus* or *Syromastes* considerably larger; in *Leptoglossus* only just distinguishable from the smaller autosomes; in *Protenor* usually indistinguishable from the latter save in behavior (Wilson, '11).

Their most noteworthy feature is a marked tendency to delayed synapsis (p. 563) as first noted by Gross ('04) in *Syromastes* and afterwards found to be characteristic of them in many other forms (Wilson, '05, '09, '11). These chromosomes often remain separate, during the whole of the growth-period

[1] The first three of these terms are due to Montgomery ('04, '06), the fourth to McClung ('12).
[2] Wilson ('05, '06, etc.).

and only unite to form a bivalent in the final prophases after the nuclear wall has broken down and the chromosomes are passing upon the spindle. Nothing is yet known concerning their physiological significance. Their

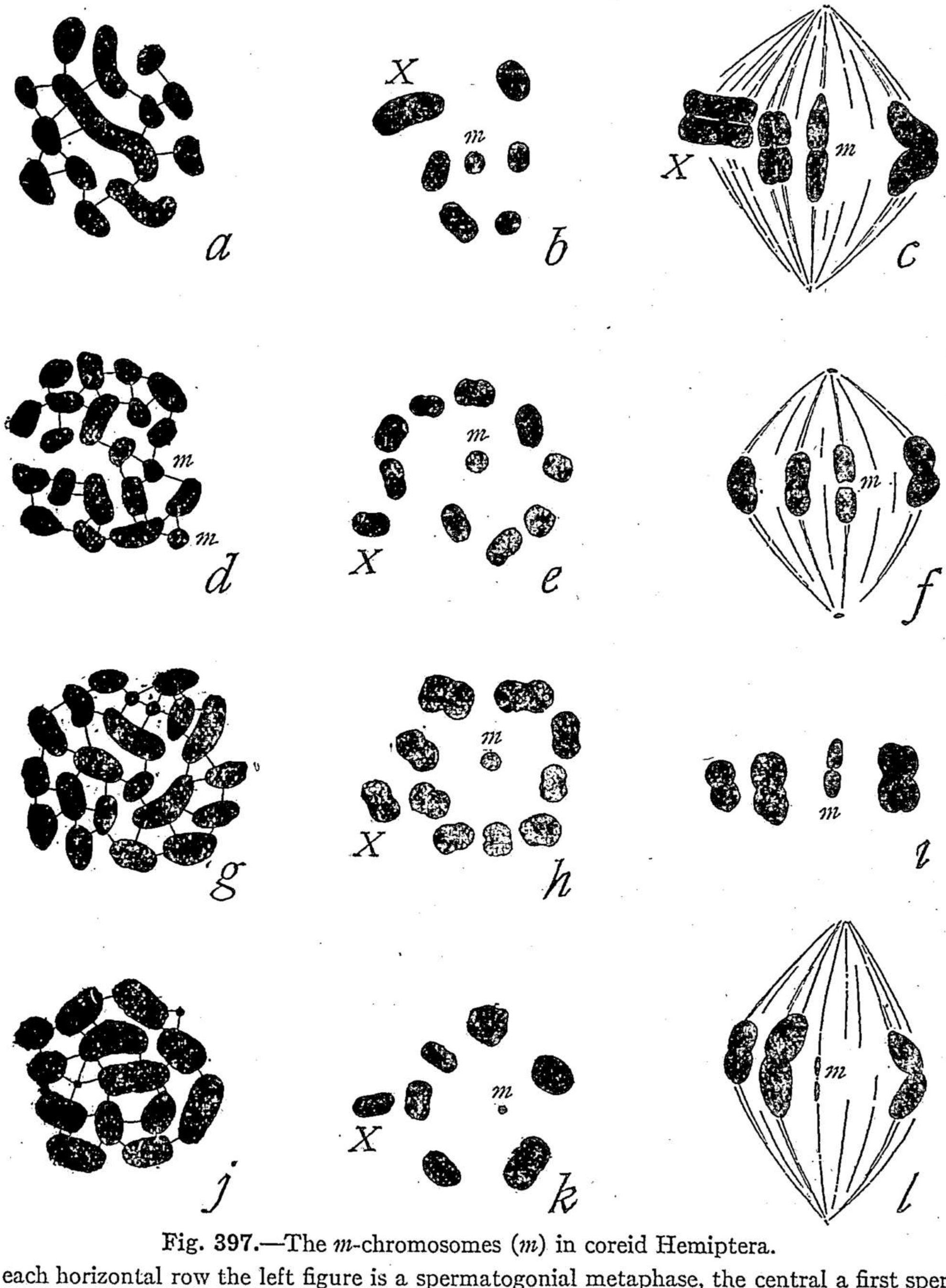

Fig. 397.—The *m*-chromosomes (*m*) in coreid Hemiptera.

In each horizontal row the left figure is a spermatogonial metaphase, the central a first spermatocyte-metaphase, and the right a first spermatocyte-metaphase in side view; *a–c*, in *Protenor; d–f* in *Leptoglossus; g–i*, in *Anasa; j–l* in *Pachylis*.

main present interest lies in the extreme clearness with which they show the processes of conjugation and disjunction (p. 507); in the demonstration which they offer of definite differences of behavior among the chromosomes:

and in their suggestions concerning one possible mode by which the chromosome-number may change from species to species.

III. THE CHROMOSOMES OF HYBRIDS

1. Relation of the Haploid and Diploid Groups

The parental chromosome-groups of hybrids may be alike in respect to both the number and size-relations; such hybrids may be quite fertile and

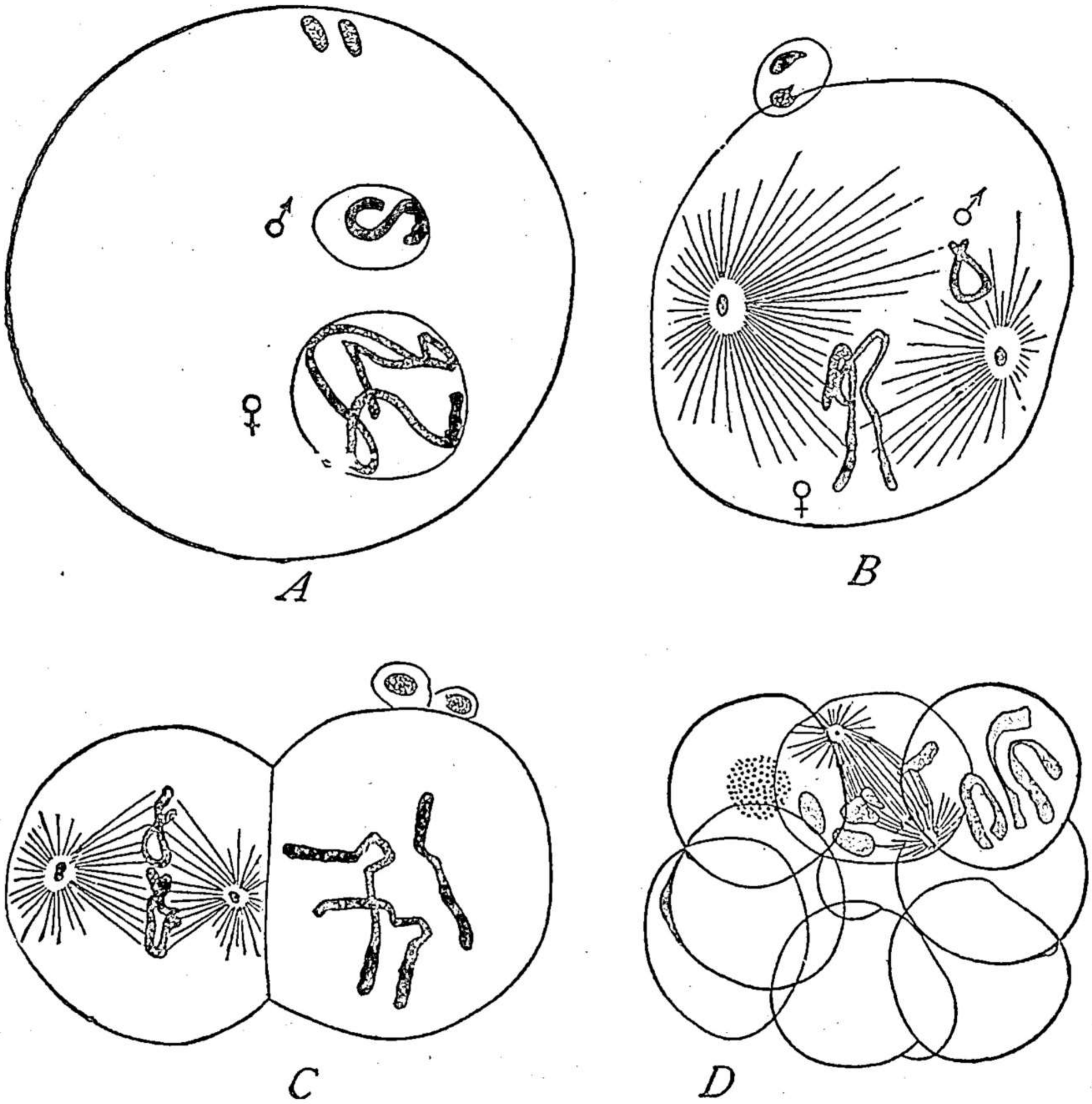

Fig. 398.—Hybrid fertilization of the egg of *Ascaris megalocephala*, var. *bivalens*, by the sperm of var. *univalens* (HERLA).

A, the gamete-nuclei shortly before union; *B*, the cleavage-figure forming; the sperm-nucleus has given rise to one chromosome (♂), the egg-nucleus to two (♀); *C*, two-cell stage dividing; *D*, twelve-cell stage, with the three distinct chromosomes still shown in the primordial germ-cell or stem-cell.

show a normal behavior in meiosis. Of greater interest are those not infrequent cases in which the parental chromosomes differ in number, size, or both, which offer a valuable means of experimental analysis.

With certain definite exceptions the somatic number of the hybrid, as might be expected, is typically equal to the sum of the parental gametic or haploid numbers. The classical case (Fig. 398) is shown in *Ascaris mega-*

locephala (var. bivalens 2 × var. *univalens* 1=hybrid 3). In the sun-dew *Drosera rotundifolia* the gametic number, is 10, in *D. longifolia*, 20, the diploid number in the hybrid 30 (Rosenberg, '04, '09). *Triticum durum* (n=14) × *T. vulgare* (n=21), and two other similar crosses gave hybrids with 2n = 35.[1] In the moth, *Biston hirtarius* the haploid number is 14, in the nearly related *Nyssia zonaria* 56, while the hybrid diploid number is about 70 (Doncaster and Harrison, '14) (p. 851). In the Moth, *Pygæra curtula* (Federley, '13), the haploid number is 29, in *P. anchoreta* 30, and the

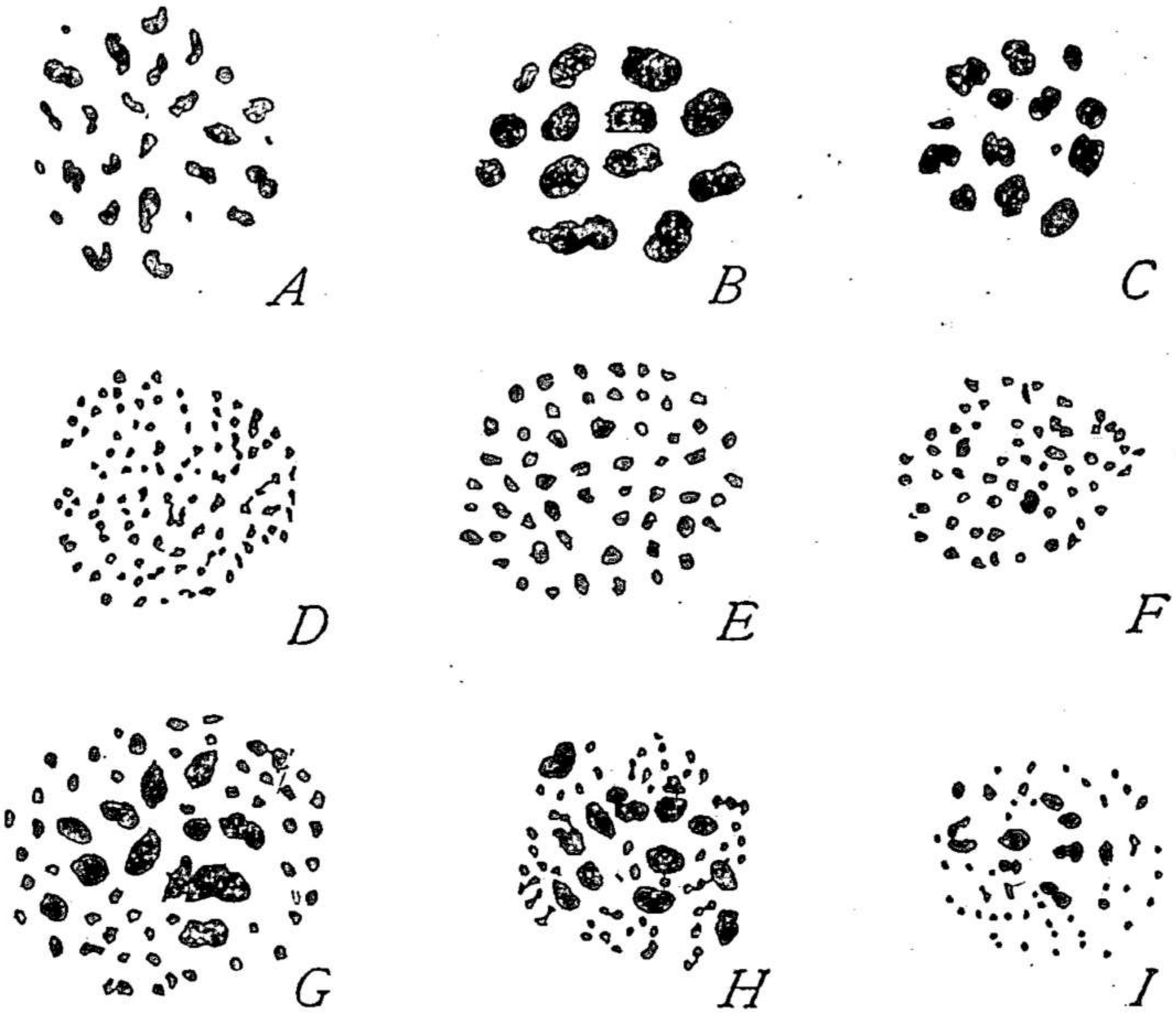

Fig. 399.—Chromosomes of hybrid moths (HARRISON and DONCASTER).

A, *Biston hirtarius*, oögonial metaphase, 28 chromosomes; *B*, first spermatocyte-metaphase; *C*, second spermatocyte-metaphase; *D*, *E*, *F*, corresponding stages in *Nyssia zonaria*, showing respectively 100–120 (spermatogonial) chromosomes, 56 tetrads, and 56 dyads; *G*, *H*, hybrid *zonaria* ♀ × *hirtaria* ♂; *G*, spermatogonial metaphase; *H*, first spermatocyte-metaphase; *I*, second spermatocyte-metaphase.

hybrid number is 59 (p. 851). In the hybrid between *Œnothera gigas* (n=14) and *Œ. lata* (n usually=7 or 8, but occasionally 6 or 9), most of the hybrids according to Lutz ('09) have, as is to be expected, either 21 chromosomes (14 + 7) or 22 (14 + 8). Interesting exceptions to this rule arise from the fact that in certain crosses some or even all of the paternal chromosomes are unable to sustain themselves in the maternal cytoplasm. The most important of these cases have been observed in the sea-urchins (Baltzer, '09, '10). In *Sphærechinus granularis* the haploid number is 20, in *Paracentrotus* (*Strongylocentrotus*) *lividus* 18, from which we should expect the diploid number of the hybrid to be 38. In point of fact this expectation is realized

[1] Kihara ('19). See also Sax ('22).

only in the cross *Sphærechinus* ♀ × *Paracentrotus* ♂. In the reverse cross, *Paracentrotus* ♀ × *Sphærechinus* ♂, the hybrid diploid number varies from 19 to 24, most often 21 or 22. This difference results from the fact that in the first case all of the *Paracentrotus* chromosomes are able to survive and divide normally in the *Sphærechinus* cytoplasm, while in the reverse cross only 3 or 4 of the *Sphærechinus* chromosomes can thus adapt themselves to the foreign environment. The remaining 16 or 17 are eliminated during the first cleavage of the egg (Fig. 455). The cells of these larvæ thus receive the complete complement of maternal *Paracentrotus* chromosomes, but only three or four of the paternal *Sphærechinus;* hence their usual diploid number 21 or 22 (18 + 3 or 4). An elimination of chromosomes more or less similar in type, though varying in the details, has been found in several other sea-urchin crosses, both by Baltzer and by other observers [1] and also by Pinney ('18) in certain teleost hybrids, for example in *Fundulus heteroclitus* ♀ and *Stenotomus chrysops* ♀ fertilized by the sperm of *Ctenolabrus adspersus*. Here again the reverse cross, *Ctenolabrus* ♀ × *Fundulus* ♂ shows but slight disturbance of the paternal chromosomes, the early mitotic behavior being prevailingly normal. Extreme cases of this type are offered by heterogeneous crosses, such as the fertilization of sea-urchin eggs by the sperm of an annelid or mollusk, in which the sperm serves merely to activate the egg, the nucleus being usually unable to undergo the mitotic transformation, and soon degenerating (p. 970). In these cases the hybrid (if it can so be called) develops with only the maternal chromosomes (*i. e.*, by gynogenesis, p. 460) and with the haploid number (Kupelwieser).

The case for the theory of genetic continuity as applied to the chromosomes becomes still stronger when we consider hybrids in which the gametic groups differ in respect to the size or shape as well as (in some cases) the number of the chromosomes; here, indeed, we find a crucial experimental demonstration of the theory. The classical case of this kind is afforded by the fish-hybrids, described by Mœnkhaus ('04) in the cross *Menidia* × *Fundulus* and by Morris ('14) in the cross *Fundulus* × *Ctenolabrus*. The haploid number is here 18 in each case, but the chromosomes of *Fundulus* are much larger than those of *Menidia*. Both kinds of chromosomes appear in the hybrids, 18 of each as nearly as can be determined, and of characteristic size (Fig. 400) and retain their characteristics throughout the cleavage at least up to the formation of the young embryo. In the moth-hybrids *Biston hirtarius* × *Nyssia zonaria* (Fig. 399), the two types of parental chromosomes, much larger and fewer in one parent than in the other, persist as such during the whole life-cycle up to the time of sexual maturity. Again, in *Datura stramonium* (2n = 24) the haploid group contains six recognizable sizes

[1] See Doncaster and Gray ('12), Tennent ('12).

of chromosomes, including one largest, one smallest and ten of intermediate sizes. Normal (diploid) plants show 12 pairs of corresponding sizes, tetraploid mutants 24 pairs, while the hybrid shows three of each size

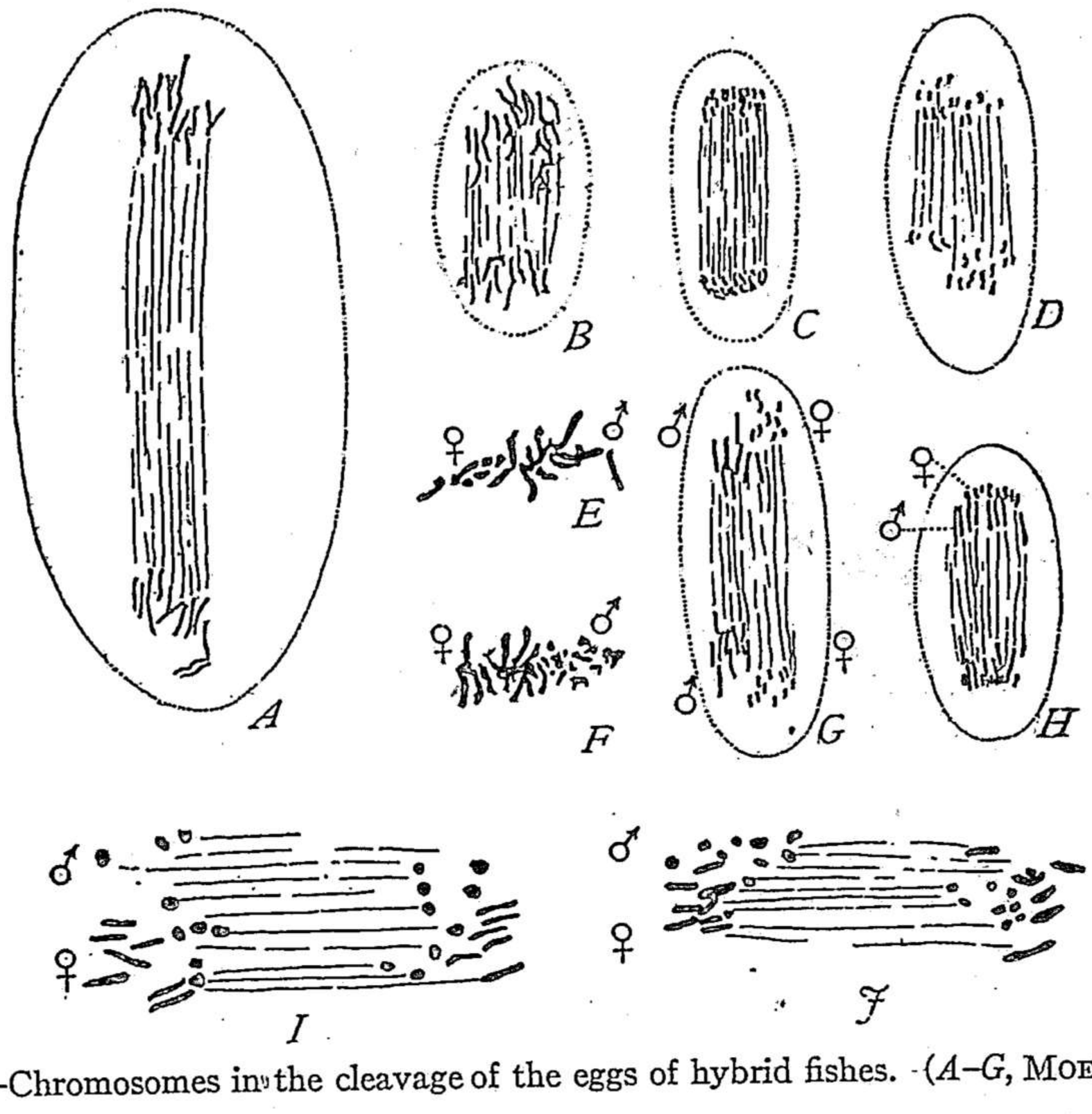

Fig. 400.—Chromosomes in the cleavage of the eggs of hybrid fishes. (*A–G*, MOENKHAUS; *H*, *I*, MORRIS).

A, first cleavage, *Fundulus; B*, *C*, later cleavage of same; *D*, first cleavage of *Menidia; E*, first cleavage-metaphase, hybrid *Menidia* ♀ × *Fundulus* ♂; *F*, similar group from the reverse cross, *Fundulus* ♀ × *Menidia* ♂; *G*, anaphase of same hybrid as *E; H*, from same hybrid, later cleavage after loss of the gonomery; *I*, *J*, anaphases of first cleavage, *Fundulus* ♀ × *Ctenolabrus* ♂.

(p. 567).[1] All such cases offer an irresistible demonstration, indirect though the evidence is, of the genetic continuity of the chromosomes.

2. Meiosis in Hybrids

Many hybrids live through only the earlier stages of development; [2] others cannot be reared to full maturity; still others may attain to sexual maturity but show various degrees of abnormality in the meiotic processes which are certainly in part responsible for the partial or complete sterility so often observed in hybrids. Such abnormalities have been observed by many investigators [3] and are of many kinds and degrees. They may involve irregu-

[1] Belling and Blakeslee ('22).

[2] See Newman ('08, '10, '18), G. and P. Hertwig ('14), Pinney ('18).

[3] *E. g.*, Juel, '00 (*Syringa*), Guyer, '00, '02 (pigeons), Cannon, '03 (cotton), Smith, '13 (pigeons), Smith and Thomas, '13 (pheasants), Cutler, '18 (pheasant × fowl), Wodsedalek, '16 (horse × ass), Rosenberg, '04, '09, '17 (*Drosera, Hieracium*), Täckholm, '20, '22 (roses).

larities in synapsis, spireme formation, and chromosome distribution; in the occurrence of multipolar mitoses; abnormal formation and degeneration of the gametes, and even a complete failure to form them, as is commonly the case in the mule (Wodsedalek). Meiosis may, however, take place quite normally and produce fertile offspring; but such cases seem to be possible only when the parental chromosome-groups are alike in number and other respects.

Hybrids between parental forms differing in respect to the gametic chromosome-groups show three main types of behavior, namely: (1) When more than two synaptic mates are present (as in triploids) all may conjugate in synapsis to form plurivalent instead of bivalent elements. (2) The synaptic mates may conjugate in pairs as far as possible, to form bivalents, while the others remain unmated and enter the heterotypic division as univalents. (3) Synapsis may fail in greater or less degree—in a few cases almost completely—so that many univalents may enter the heterotypic division. Each of these cases shows many variants, some of them of most instructive character.

(1) The first and rarest case is illustrated by certain triploid hybrids between tetraploid and diploid mutants in plants. In certain such hybrids [1] the heterotypic division shows the haploid number (in *Datura* 12) of *triads* (or, if the equation-division be taken into account, hexads), the synaptic mates having united in threes. During the division the elements of each triad break up and separate in such a manner that two components pass to one pole and one to the other. Since the triads show a random or chance orientation on the spindle, various numbers are found in the second division, ranging in *Datura* from 12 to 24, the sum of the numbers in each pair of sister-cells being 36, the triploid number (12 + 24, 13 + 23 . . . . . 18 + 18)—a remarkable example of random assortment in chromosome-distribution (p. 944).

(2) In the second and more frequent case the chromosomes of the smaller gametic group commonly conjugate with a corresponding number from the larger group to form bivalents, leaving the unmated ones as univalents. The heterotypic division therefore shows both bivalents and univalents on the same spindle, the former showing the usual behavior (*i. e.*, as in pure-bred forms) while the latter show numerous irregularities.[2]

The classical case of this type is that of the sun-dew *Drosera* in which,

[1] *E. g.*, in *Morus* (Osawa, '20), *Canna* (Belling, '21) and *Datura* (Belling and Blakeslee, '22).

[2] Attention may here again be called to the interesting fact that in this respect the meiosis of apogamous plants often shows irregularities closely similar to those of hybrids (p. 848); and this, taken in connection with the chromosome-numbers, gives strong reason to conclude that such plants, originally arose as hybrids. See especially the works of Juel, Murbeck, Rosenberg ('17), Osawa, Strasburger, Tischler, Holmgren, Winkler, Blackman and Harrison, and Täckholm ('22). Only a few examples of these facts can here be referred to.

as above mentioned, the diploid number in *D. longifolia* is 40, in *rotundifolia* 20, and in the hybrid (unfortunately sterile) 30 (20 + 10). The heterotypic division shows 20 chromosomes (Fig. 401) of which 10 are obviously double and 10 apparently single.[1] The 10 double (bivalent) chromosomes undergo a regular division and distribution to the poles, while the 10 single univalents fail to divide wander irregularly towards one pole or the other, and often fail to enter the daughter-nuclei. The natural interpretation of this, as indicated by Rosenberg, is that the ten *rotundifolia* chromosomes conjugate with ten of the *longifolia* to form bivalents, leaving ten univalent *longifolia* chromosomes without synaptic mates.[2] In the reduction-division (here the first) the bivalents disjoin as usual while the univalents pass towards one pole like other unpaired chromosomes (supernumeraries, or accessory chromosomes, etc.). The lagging and scattered univalents later vary in behavior. Some seem to enter the daughter-nuclei; others fail to reach the poles and give rise to dwarf nuclei, but apparently some of them may finally fuse with the main nuclei. In any case some, but not all, of them pass upon the second spindle and there (presumably) divide, the observed metaphase-numbers varying from 12 to 18.

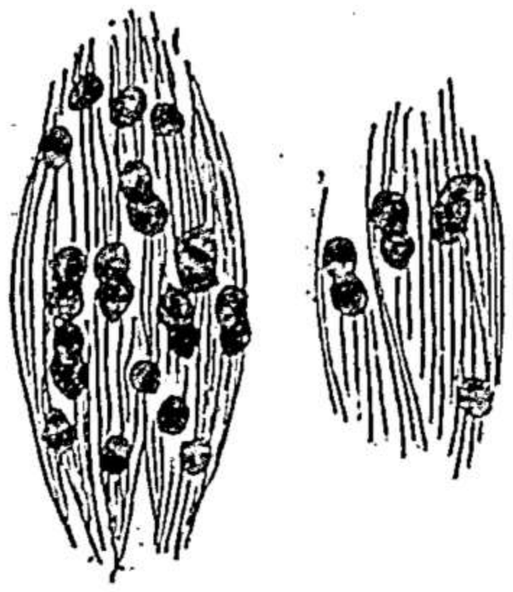

Fig. 401.—Heterotypic mitosis in the hybrid between *Drosera rotundifolia* (20 chromosomes) and *longifolia* (40 chromosomes) (ROSENBERG).

The chromosome-group (from two sections) shows 10 (hybrid) bivalents and 10 single (*longifolia*) chromosomes.

Many interesting cases more or less similar in principle have more recently been observed in various plants and a few animals; and we may here include both known hybrids and certain apomictic triploid or other heteroploid forms, which may have originated as hybrids (p. 848). In most cases the unmated chromosomes pass as univalents upon the heterotypic spindle; and further complications not infrequently arise through a partial or even complete failure of synapsis and through varying behavior on the part of the univalents. In Kihara's *Triticum* hybrids (p. 842) with 35 chromosomes, (14 + 21) the heterotypic division showed 14 bivalents and 7 univalents. The former divide equally in both divisions, the latter only in the first, and in the second pass irregularly and undivided towards the poles. A similar result was reached also by Sax ('21, '22). *Papaver somniferum* (n=11) × *orientale* (n=21) gives hybrids with 32 chromosomes, the heterotypic division showing 11 bivalents and 10 univalents which have a behavior like that of *Triticum* (Yasui, '21, Ljungdahl, '22). The 21-chro-

[1] Rosenberg, '04, '09.

[2] It is possible that the 20 *longifolia* chromosomes conjugate two-by-two, with each other, leaving the 10 rotundifolia unmated; but this is improbable in view of the facts of meiosis in other hybrids.

mosome hybrids between *Œnothera gigas* (n=14) and *Œ. lata* (n=7 or 8) gives hybrids with 21 chromosomes. In the heterotypic division Geerts

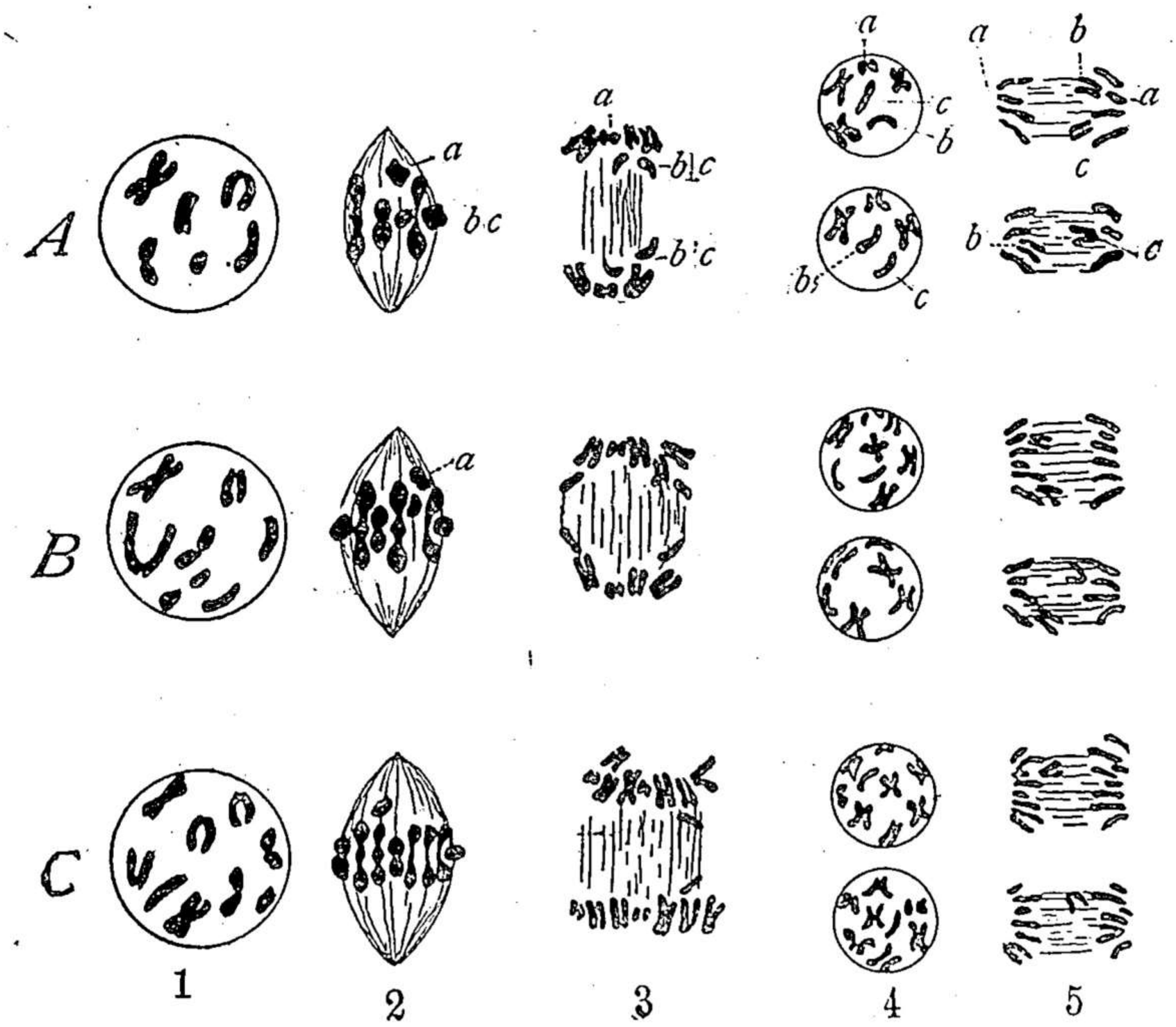

Fig. 402.—Diagrams of meiosis in *Hieracium* (*Pilosella*) hybrids (ROSENBERG)

(The number of chromosomes represented is one-third the actual number.)

First vertical line, (1) diakinesis; second, heterotypic metaphase; third, anaphase; fourth, interkinesis; fifth, homeotypic anaphase.

A, of the type *H. auricula* (n=9) × *aurantiaca* (n=18), 3 (9) bivalents and 3 (9) univalents. All of these divide excepting one univalent (*a*) which passes double to one pole. In the homeotypic division the latter divides, while the two other univalents *b*, *c*, are delayed, again split, and pass double to one or both poles. Gametes may thus arise having 4, 5, or 8 chromosomes.

B, partial failure of synapsis in a pure-bred form with 2n=12 (36) chromosomes, giving 4 bivalents and 4 univalents, and irregularities resulting in the formation of gametes with 6 or 9 chromosomes.

C, hybrid with 2n=16 (48), showing both defective synapsis and irregularities of distribution. In 1 and 2, 7 bivalents and 2 univalents. Gamete numbers, 7, 8, 9, and 10.

('11) found 7 bivalents and 7 univalents, the former dividing regularly, the latter passing without division irregularly to the poles.[1]

A behavior of the univalents similar in principle to the foregoing but often differing more or less in detail, is described in the interesting work of Rosenberg ('17) on hybrids and apogamous species of *Hieracium* (commonly sterile), and those of Blackman and Harrison ('21) and of Täckholm ('20, '22) on the corresponding phenomena in roses. The most important of the deviations appears in the fact, that some of the univalents are said to *split equationally in both mitoses*. In some cases all the univalents, like the

[1] Studies on this hybrid by other observers (Lutz, '12, Gates, '09, '13a) gave somewhat different results.

bivalents, divide in the heterotypic division (Fig. 404). In other cases some divide (*b*, *c*, in Fig. 402, A) while others (*a*) pass without division to one pole, becoming double in the anaphase. In the latter case univalents are divided in the homeotypic division; but it is also said that those which have divided in the heterotypic mitosis may *again split lengthwise in the homeotypic mitosis*. In this case, however, the products often fail to separate, passing as double bodies to one pole, and thus causing an increase in the normal gametic number (*b*, *c*, in Fig. 402, A).

In general agreement with the foregoing are the remarkable results of Täckholm ('20, '22) and of Blackburn and Harrison ('21) on many forms of roses, especially of the section *Caninæ*, which are highly polymorphic, some of the so-called species being hybrids, while many others (sterile forms) are believed to have arisen as hybrids and are held constant to type because of their exclusively asexual reproduction (vegetative apogamy, or the like), which is of widespread occurrence in this group.

These investigators revealed a remarkable series of chromosome-numbers in the group, most of the diploid numbers being multiples of 7, namely, 14,

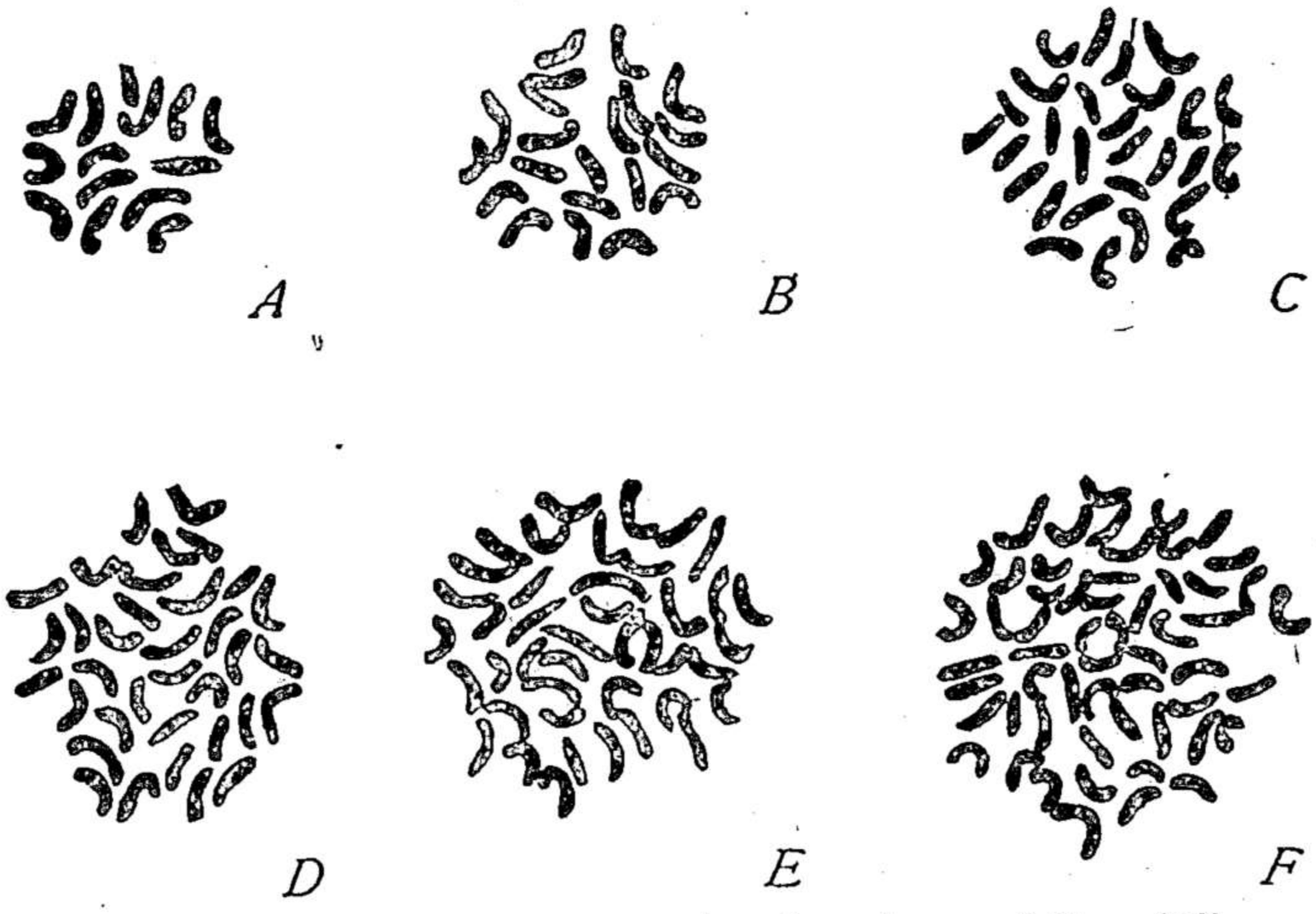

Fig. 403.—Diploid chromosome-groups of various forms of *Rosa* (TÄCKHOLM).

A, *R. webbiana*, 14 chromosomes; *B*, *R. chinensis*, 21 ch.; *C*, "Konrad Meyer," 28 ch.; *D*, *Fomentosa cuspidatoides*, 35 ch.; *E*, *R. nutkana*, 42 ch.; *F*, octoploid hybrid, 56 ch.

21, 28, 35, and 42, and in one hybrid form 56 (Fig. 403). Intermediate numbers were rarely found. Forms having 14 chromosomes and some with 28 or 42 undergo a typical meiosis, with reduction to the corresponding haploid numbers, 7, 14, or 21; and these are believed to reproduce only by sexual reproduction and for the most part to be pure bred stable forms. Those with 21 or 35 (and some with 28 or 42) show a behavior analogous to that of the *Drosera* or *Hieracium* hybrids and are maintained exclusively by apogamy. As in the preceding cases the heterotypic divisions show both

bivalents and univalents, the former dividing symmetrically in typical fashion and in advance of the univalents which are at first scattered on the spindle and later show varying behavior (Fig. 404). As will appear from the following table the numbers of bivalents and of univalents in each case added together (counting each bivalent as two) equal the diploid number.

Type No.	Somatic No.	No. of Bivalents in Heterotypic Division	No. of Univalents	Constitution
1	14	7	0	diploid
2	28	14	0	tetraploid
3	42	21	0	hexaploid
4	21	7	7	triploid
5	28	7	14	tetraploid
6	35	7	21	pentaploid
7	42	7	28	hexaploid
8	35	14	7	pentaploid
9	42	14	14	hexaploid
10	32–36	Variable	Variable	anorthoploid

All cases in which unmated univalents appear in the heterotypic division fall into line under the assumption that they are hybrids or the descendants of hybrids (some of them are known to be such) between forms having different numbers of chromosomes. As in *Drosera* or *Hieracium* the chromosomes of the smaller parental haploid group (7 or 14 in the above examples) unite in synapsis with an equal number of synaptic mates from the larger group to form bivalents while the remaining univalents are left unmated. In this case, as before, the behavior of the bivalents is typical. That of the univalents shows many variations. In the heterotypic mitosis (pollen-mother-cells) they are as a rule scattered during the division of the bivalents, but later take up a position at the equator and divide equationally (Fig. 404); their distribution to the poles is, however, often irregular. In the second mitosis they usually pass irregularly to the poles, but are said in some cases to undergo a second equational division, as in *Hieracium;* the proof of this latter conclusion seems, however, inadequate.

Except for the supposed occasional second equational division of the univalents the foregoing cases are in the main similar to the *Drosera* hybrids; and in all, the presence of univalents in the heterotypic division is due, obviously, to their failure to find suitable synaptic mates owing to the original difference of gametic number.

(3) Complications due to a partial, or in extreme cases a complete, failure of synapsis are less frequent. An example is offered by fern-hybrids examined by Farmer and Digby ('10). In *Polypodium aureum* the haploid number is

34–36, in *P. vulgare* about 90. In the hybrid the number of chromosomes in the heterotypic division is commonly 95–105 and sometimes as high as 125; and the chromosomes are of two sizes, large and small. This indicates that while many of the *aureum* chromosomes find *vulgare* mates with which they

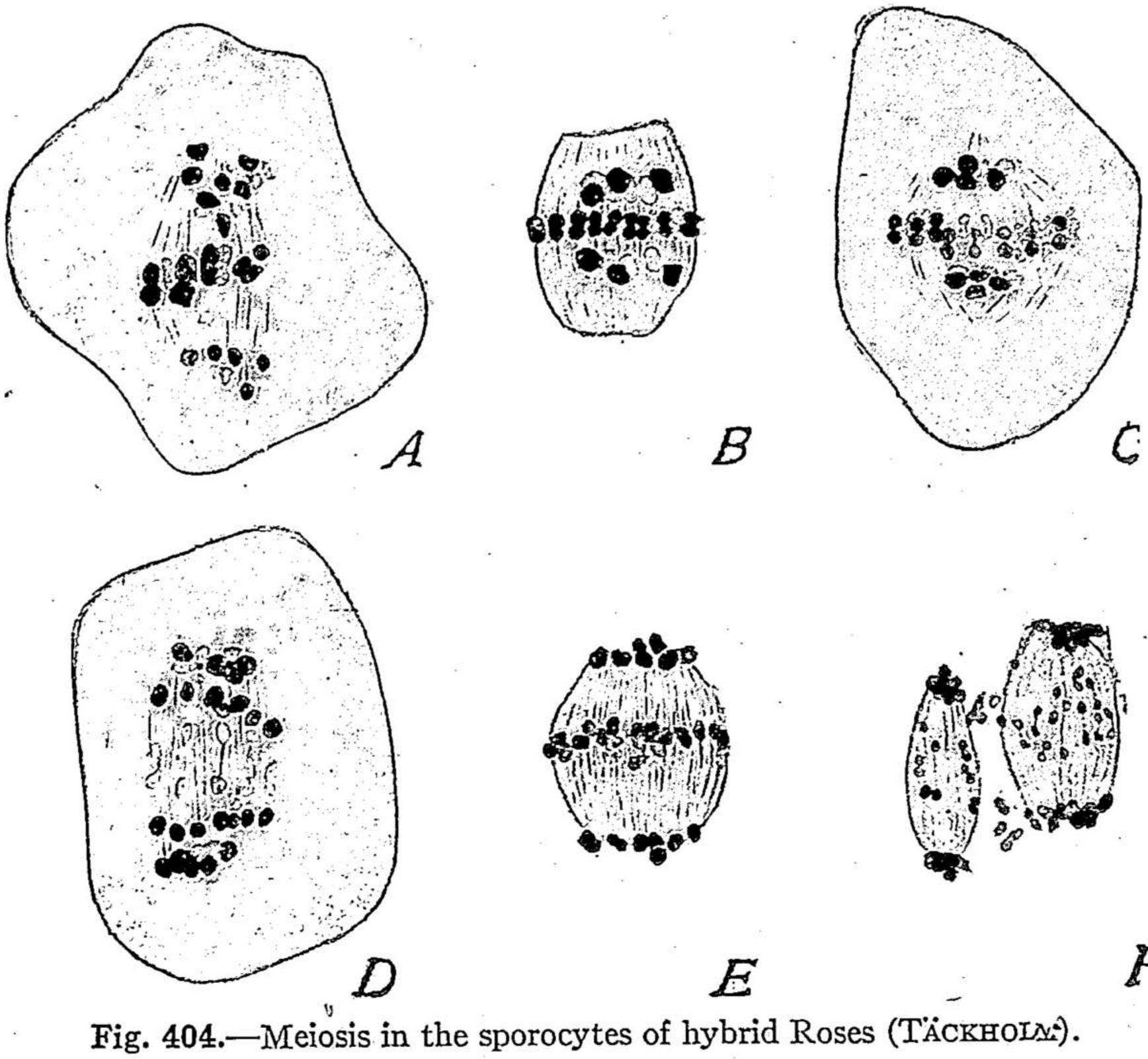

Fig. 404.—Meiosis in the sporocytes of hybrid Roses (TÄCKHOLM).

A, heterotypic metaphase (*R. sicula*) with 7 bivalents at equator and 21 scattered univalents; *B*, later stage (*R. glauca-plebeia*), bivalents in anaphase, univalents dividing in metaphase; *C*, slightly later (*R. Jebei*); *D*, univalents in anaphase (*R. contracta*); *E*, homeotypic division (*R. Desvausii*), univalents at equator; *F*, *recondita*, homeotypic anaphase, with dividing univalents.

pair, certain of them fail to do so; the expected number of bivalents is thus decreased and of univalents increased.

Rosenberg ('17) has more recently described an interesting series of gradations in respect to synapsis in the pollen-formation of triploid apomictic species of *Hieracium* with 27 chromosomes (9 + 9 + 9). *H. boreale* (Fig. 405, A) shows a considerable but not complete failure of synapsis, the heterotypic division having only 4 to 6 bivalents (instead of 9) and correspondingly larger numbers of univalents (19 to 13). In *H. lacerum* and *lævigatum* synapsis fails wholly and the first division shows 27 univalents which *without division* pass to the poles in two groups, often different in number, which divide equationally in the homeotypic mitosis. This type is by Rosenberg called "half-heterotypic" (Fig. 405, B). By a modification of this arise cases in which the chromosomes split lengthwise without separating into two groups on the spindle but become inclosed in a single membrane

(Fig. 405, C) and undergo an equation-division in the homeotypic mitosis. Finally, in *H. pseudoillyricum* (Fig. 405, D), the reduction-division is wholly suppressed and the primary sporocyte undergoes but one division, equational, and with the full diploid number of chromosomes. This indicates,

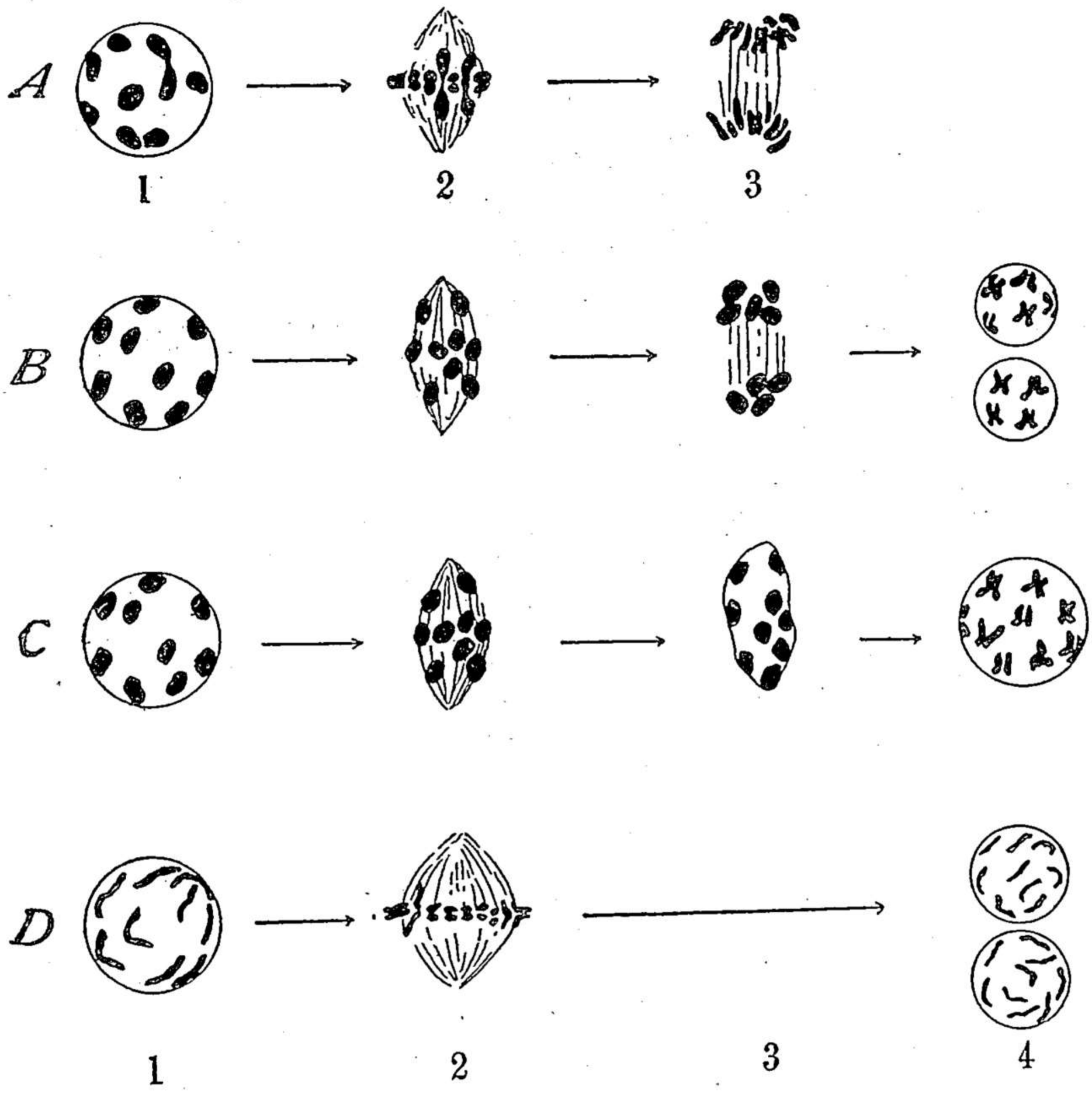

Fig. 405.—Diagram of types of heterotypic divisions in pollen-forming mitoses of apogamous species of *Hieracium* having 18+9 chromosomes (ROSENBERG).

(The number of chromosomes is one-third the actual number.) First vertical row (1) the diakinesis; second and third, heterotypic division; fourth, its products.

A, *H. boreale* type with 2 bivalents (instead of the expected 3) and 5 univalents (instead of 3) (2n=9, actually 27), all dividing symmetrically.

B, *C*, *H. lævigatum* type, half-heterotypic division, with total failure of synapsis, 9 univalents, either passing undivided to the poles (*B*) or producing a single nucleus (*C*).

D, *H. pseudo-illyricum* type, complete failure of synapsis with one equational division. No heterotypic division.

perhaps, how diploid parthenogenesis may have arisen by a similar suppression of the reduction-division in case of the macrosporocytes.

Among animals remarkable phenomena of the same general type have been observed in hybrid Lepidoptera by Doncaster and Harrison ('14) and by Federley ('13, '14). The first-named observers found in *Biston* 14 pairs of chromosomes (11 large and 3 small), in *Nyssia zonaria* approxi-

mately 56 pairs of very small ones. The hybrids (sterile) clearly show both types of chromosomes (Fig. 399), approximately in the expected numbers (14 + 56 = 70). If all the *Biston* chromosomes that persist up to the time of meiosis paired with *Nyssia* chromosomes, the heterotypic division should show approximately 56 chromosomes (14 bivalents + 42 small univalents), but the actual number is 60–65. Not more than 5–10 of the *Lycia* chromo-

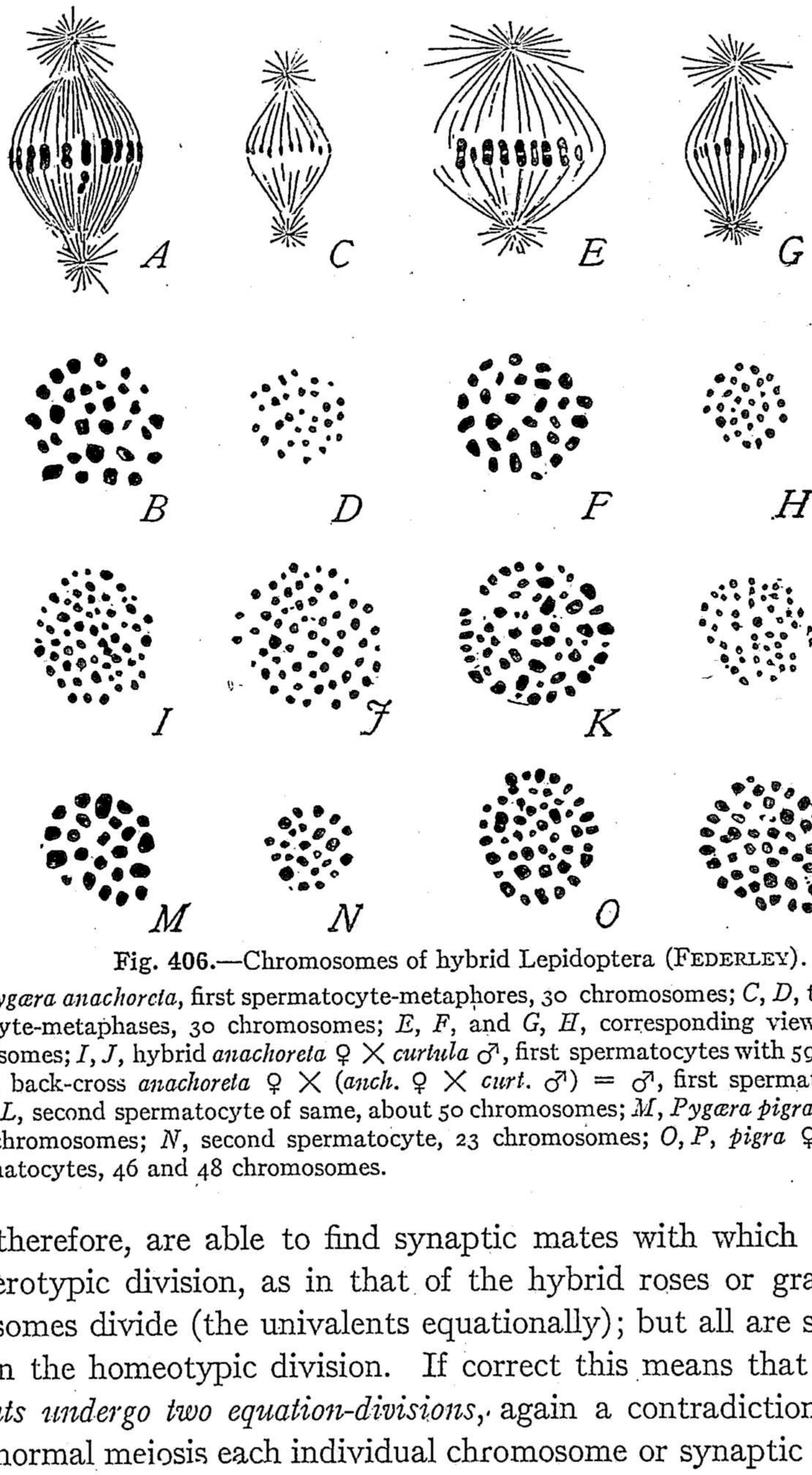

Fig. 406.—Chromosomes of hybrid Lepidoptera (FEDERLEY).

A, *B*, *Pygæra anachoreta*, first spermatocyte-metaphores, 30 chromosomes; *C*, *D*, the same, second spermatocyte-metaphases, 30 chromosomes; *E*, *F*, and *G*, *H*, corresponding views of *P. curtula*, 29 chromosomes; *I*, *J*, hybrid *anachoreta* ♀ × *curtula* ♂, first spermatocytes with 59 and 58 chromosomes; *K*, back-cross *anachoreta* ♀ × (*anch.* ♀ × *curt.* ♂) = ♂, first spermatocyte, 56 chromosomes; *L*, second spermatocyte of same, about 50 chromosomes; *M*, *Pygæra pigra*, first spermatocyte, 23 chromosomes; *N*, second spermatocyte, 23 chromosomes; *O*, *P*, *pigra* ♀ × *curtula* ♂, first spermatocytes, 46 and 48 chromosomes.

somes, therefore, are able to find synaptic mates with which to pair. In the heterotypic division, as in that of the hybrid roses or grasses, all the chromosomes divide (the univalents equationally); but all are said again to divide in the homeotypic division. If correct this means that *the unmated univalents undergo two equation-divisions*, again a contradiction of the rule that in normal meiosis each individual chromosome or synaptic mate divides

but once (p. 505). This result receives a very circumstantial confirmation in the extensive work of Federley on moth-hybrids of the genus *Pygæra* which are partially fertile, and also by some of the plant hybrids already considered (p. 848).

In this case the haploid parental numbers are in *P. curtula* 29, in *P. anachoreta* 30, while the hybrids have 59 chromosomes. The heterotypic division often shows nearly the full diploid number, 59 (Fig. 406); *i. e.*, synapsis or pseudo-reduction nearly fails, so that nearly all the chromosomes must be univalent. Nevertheless all the univalents divide *in both mitoses*, so that the gametes (sperms) also receive nearly or quite the full diploid number. This result is borne out by the results of crossing this hybrid (♂) back with the pure *anachoreta* ♀. The resulting secondary hybrids should be triploid or nearly so (59 + 30=89), and do in fact approach this condition, though the number could not be counted precisely. The heterotypic division, however, again shows approximately the *diploid* number (59±), about half the chromosomes being large and double, and half smaller and single (Fig. 406). This means, that the two *anachoreta* chromosome-sets conjugate two-by-two in synapsis, to form bivalents, while the *curtula* chromosomes remain univalent. Federley ('14) reached substantially similar results with crosses of *Smerinthus* and *Dilina*.

The double division of the univalents in these moth-hybrids seems very anomalous; nevertheless Federley's evidence seems conclusive, not only cytologically, but also on its genetic side (p. 929). The questions that it raises relate, however, especially to the mechanism of synapsis and disjunction (p. 505) and do not weaken the strong support obviously given by the chromosomes of hybrids to the theory of genetic continuity.

IV. NORMAL CHROMOSOME NUMBERS

1. Introductory

To speak of the number of chromosomes as a specific constant does not mean that the number is absolutely fixed. Deviations from the typical number are often observed within the species and even in different cells of the same individual; and this fact has led some writers to a premature denial of the constancy of the chromosome-number and even of the genetic continuity of the chromosomes. Such a conclusion, however, could only result from lack of critical consideration of the facts.

It would seem to be a very simple matter to count chromosomes correctly; but the history of the subject abundantly demonstrates the contrary. The fundamental chromosome-number can only be determined with com-

plete certainty *when the whole cycle of the chromosomes is taken into account*, including comparison of the gametic with the zygotic number as shown in the formation of the gametes, their union in syngamy, and the number seen in the diploid or somatic divisions, particularly during the early stages of development. When these give consistent results, the fundamental number may be established with a high degree of probability, which becomes a practical certainty in all cases where the size-differences of the chromosomes are sufficiently marked to make identification of the individual chromosome-pairs of the diploid groups possible (p. 837). It must be confessed that only a comparatively small number of cases have been thus completely determined. In practice, however, the numbers may often be determined with sufficient accuracy by a less exacting standard.

The chromosome-number has been counted, with varying degrees of accuracy, in representatives of all the larger groups of plants and animals and in a very large number of species—according to E. B. Harvey ('16, '20) in nearly 1000 species of animals, while Tischler ('17) lists them for more than 700 species of plants; but the number of thoroughly established cases is very much smaller than these figures indicate. The limited list which follows is confined almost exclusively to multicellular forms, and excludes many groups concerning which uncertainty still exists. The selection has been made rather arbitrarily, to illustrate by a few examples the general range and distribution of chromosome-numbers in different groups, in a few cases their relations within single or nearly allied genera in order to indicate the possible modes in which chromosome-numbers may have changed from species to species, and certain other problems discussed in the text.[1]

Supplementary lists are given also at pp. 753, 766, 773, in connection with the subject of the sex-chromosomes. In order to simplify the lists we shall for the moment lay aside most of the observed deviations from the fundamental numbers, however caused; but an exception is made in certain cases of reduplication (p. 870). The lists include both haploid and diploid numbers so far as both are known; when only one of these has been directly observed the other (as inferred) is inclosed in parentheses.

[1] Its compilation has been much facilitated by several important general reviews, in which will be found fuller data and more detailed references to the literature. See especially those of Tischler ('17), with an excellent critical discussion, and Mrs. E. B. Harvey (Miss E. N. Browne) ('16, '20); also those of Gates ('15), Ishikawa ('16) and Winge ('17). Earlier and less complete lists in Wilson ('00), Enriques ('05), Montgomery ('06) and Haecker ('07). The first accurate counts of chromosome-numbers seem to have been made by Flemming ('82) in the salamander, and by Strasburger ('82) in several species of plants.

Examples of Chromosome-Numbers in Animals

Porifera

Species	Group	Haploid	Diploid	Authority
Sycandra raphanus	Porifera	8	16	Jörgenssen, '09
" "	"			

Cœlenterata

Tiara sp.	Hydrozoa	14	28	Boveri, '90
Hydra fusca and viridis	"	6	12	Downing, '05, '09
Campanularia flexuosa	"	10	20	Hargitt, '13
Aglantha digitalis	"	8	16	" '17
Clava leptostyla	"	12	24	Haecker, '92

Chætognatha

Sagitta bipunctata	Chætognatha	9	18	Boveri, '90, Stevens, Buchner, etc.

Nemathelminthes

Gordius tolsunus	Nematoda	2	4	Vejdovský, '12
Paragordius varius	"	7	14	Montgomery, '04
Ascaris megalocephala univalens	"	1 (compound) 1=27 or 36	2 (compound) 2=63 or 72	Boveri, '87, Hertwig, '90, etc. Kautzsch, '13
	"	1=22 or 30	2=52 or 60	Geinitz, '15 See pp. 323, 869
A. bivalens	"	2 (compound)	4 (compound)	Van Beneden, '83–'84, Nussbaum, '84, Boveri, Hertwig, etc.
Heterakis vesicularis	"	4, 5	9, 10	Gulick, '11
Ancyracanthus cystidicola	"	5, 6	11, 12	Mulsow, '11, '12
Ascaris canis	"	12, 18	30, 36	Walton, '16, '18
A. incurva	"	14, 21	35, 42	Goodrich, '14
A. lumbricoides	"	19, 24	43, (48)	Edwards, '10

Platoda

Vortex viridis	Rhabdocæla	2	4	Lepeschkin, '10
Paravortex,	"	4	8	Patterson, '12
Procerodes gerlachei	"	6	12	Böhmig, '07
Dendrocœlum lacteum	Triclada	7	14	Gelei, '13
Leptoplana tremellaris	Polyclada	8	16	Francotte, '97
Thysanozoön ellipticus	"	9	18	Van der Stricht, '97, '98
Eustylochus ellipticus	"	10	20	Van Name, '99

EXAMPLES OF CHROMOSOME-NUMBERS IN ANIMALS—*Continued*

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Trematoda				
Polystomum integerrimum	Trematoda	4	8	Goldschmidt, '02
Gyrodactylus elegans	"	6	12	Gille, '14
Brachycœlium lanceatum	"	10	20	Goldschmidt, '08
Nemertinea				
Lineus ruber	Nemertinea	8	16	Nussbaum and Oxner, '13
Cerebratulus marginatus	"	16	32	Coe, '99
Rotifera				
Hydatina senta		10–14	20–30	Whitney, '09
" "		(6)	12	Shull, '21
Annelida				
Dinophilus gyrociliatus	Archiannelida	10	20	Shearer, '11, '12
Allolophora fœtida	Oligochæta	11	22	Foot and Strobell, '98, etc.
Enchytræus adriaticus	"		24	Vejdovský, '07
" humicultor	"	16	32	"
Lumbricus herculeus	"	16	32	Calkins, '95
Rhynchelmis limosella	"	32	64	Vejdovský, '07
Saccocirrus major	Archichætopoda	4	8	Hempelmann, '13
" "	"	9	18	Baehr, '13
Ophryotrocha puerilis	Polychæta	2	4	Korschelt, '95
" "	"	4	8	Schreiners, '06
Tomopteris elegans	"	5	10	Senna, '11
" onisciformis	"	9	18	Schreiners, '06
Chætopterus pergamentaceous	"	9	18	Mead, '98
Phascolosoma gouldii	Gephyrea	10	20	Gerould, '04
Thalassema mellita	"	12	24	Griffin, '99, Lefevre, '06
Nephelis vulgaris	Hirudinea	8	16	Jörgenssen, '08
Mollusca				
Paludina vivipara	Gasteropoda	7	14	Meves, '01
Helix pomatia univalens	"	12	24	Von Rath, '92; Godlewsky, '97; Prowazek, '02
" " bivalens	"	24	48	Bolles-Lee, '96, '11; Murray, '98; Ancel, '02, etc.
Arion sp.	"	16	32	Lams, '10
Carinaria mediterranea	"	16	32	Boveri, '90
Enteroxenus ostergreni	"	17	34	Bonnevie, '05
" "	"	21	42	Schreiner, '07
Crepidula plana	"	30	60	Conklin, '02
Mactra sp.	Pelecypoda	12	24	Kostanecki, '04, '11
Unio. sp.	"	16	(32)	"

EXAMPLES OF CHROMOSOME-NUMBERS IN ANIMALS—*Continued*

Crustacea

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Cyclops viridis, var. brevispinosus	Copepoda	2	4	Chambers, '12
Cyclops gracilis	"	3	6	Matschek, '09, '10
" signatus	"	4	8	Haecker, '90
" viridis var. americanus	"	5	10	Chambers, '12
Cyclops diaphanus	"	6	12	Braun, '09
" albidus	"	8	16	" "
" dybowskii	"	9	18	" "
" strenuus	"	11	22	Braun, '09, Matschek, '10, Amma, '11
Canthocamptus staphylinus	"	12	24	Haecker, '92, Matschek, Krüger
Diaptomus cœruleus	"	14	28	Krimmel, '10, Amma, '11
" castor	"	17	34	Amma, '11
Branchipus grubii	Phyllopoda	12	24	Brauer, '92, Fries, '09
Artemia salina	"	84	168 or 84	Brauer, '93, '94
" " var. bivalens, parthenogenetic, of Capo d'Istria, etc.	"		84	Artom, '08, '11, '12, etc.
Id., var. univalens, sexual form, Cagliari, etc.	"	21	42	"
Oniscus asellus	Isopoda	16	(32)	Nichols, '09
Idotea irrorata	"	28	(56)	"
Talorchestia longicornis	Amphipoda	18	(36)	"
Eupagurus prideauxii	Macrura	12	(24)	Weismann and Ishikawa, '88
Hippa talpoidea	"	60	(120)	Nichols, '09
Astacus sp.	"	58	(116)	Prowazek, '02
Cambarus virilis	"	100	200	Fasten, '14
C. immunis?	"	104	208	" "
Cancer magister	Brachyura	60	100	" '18

Arachnida

Pediculopsis gramimum	Acarida	2	4	Reuter, '09
Ixodes reduvius	"	14	28	Nordenskiöld, 09
Epeira scolopetaria	Arancida	11, 12	23, (24)	Berry, '06
Agalena nævia	"	25, 27 ±	(52–54) ±	Wallace, '05, '09
Buthus eupeus	Scorpionida	(11)	22	Sokolow, '13
Centrurus exilicauda	"	13	26	Wilson, '16
Euscorpius carpathicus	"	28–40	70–84	Sokolow, '13
Opisthacanthus, sp.	"		80–100 ±	Wilson
Macrobiotus lacustris	Tardigrada	5	10	von Wenck, '14

EXAMPLES OF CHROMOSOME-NUMBERS IN ANIMALS—*Continued*

Tracheata

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Peripatus, sp.	Prototracheata	14	28	Montgomery, '00
Geophilus linearis	Myriapoda	8	(16)	Bouin and Collin, '01
Scolopendra heros	"	16, 17	33, (34)	Blackman, '03, '05, '10
Scutigera forceps	"	18, 19	37, (38)	Medes, 05
Anurida maritima	Aptera		8	Claypole, '98
Podura aquatica	"		8	Willem, '00
Cerastipsocus venosus	Corrodentia	8, 9	17, (18)	Boring, '13
Thysanura domestica	Thysanura	16, 18	34, (36)	Charlton, '21
Termopsis angusticollis	Isoptera	26	52	Stevens, '05
Libellula basalis	Odonata	12, 13	25, (26)	Smith, '16
Anax junius	"	13, 14	27, 28	Lefevre and McGill, '08
Platyplax designatus	Trichoptera	30	55–60	Lutman, '10
Blatta germanica	Orthoptera (Blattidæ)	11, 12	23, 24	Wassilieff, '07
Periplaneta americana	"	16, 17	33, 34	Morse, '09
Anisolabis maritima	(Forficulidæ)	12	24	Randolph, '08
Forficula auricularia	"	12	24	Sinéty, '01 Stevens, '10
Tenodera superstitiosa, Paratenodera aridifolia	" (Mantidæ)	13, 14	26, 27	Oguma, '21
Aplopus mayeri	" (Phasmidæ)	17, 18	35, 36	Jordan, '08
Gryllus domesticus	" (Gryllidæ)	10, 11	21, 22	Baumgartner, '04, Gutherz, '07–'09
" assimilis	" "	14, 15	29, (30)	Baumgartner, '04
Gryllotalpa vulgaris	" "	6	12	Payne, '16
" borealis	" "	11, 12	23, 24	" '12
Decticus verrucivorus	" (Locustidæ	11, 12	23, (24)	Vejdovský, '12
Steiroxys trilineata	" "	14, 15	29, (30)	Davis, '08, Meek, '13
Locusta viridissima	" "	14, 15	29, 30	Mohr, '14
Orphania denticauda	" "	15, 16	31, (32)	Sinéty, '01
Xiphidium, sp.	" "	16, 17	33, (34)	McClung, '02, '14
Jamaicana flava	" "	17, 18	35, (36)	Woolsey, '15
Diastremmena marmorata	" "	28, 29	57, (58)	Schellenberg '13
Brachystola magna				Sutton '01, '02
Hippiscus tuberculatus				Davis, '08
Arphia tenebrosa	" "			" "
Chortophaga iridifasciata				" "
Dissosteira carolina				" "
Mecosthethus sp.				McClung, '14
Melanoplus (7 species)				" and others
Rhomaleum micropterum				"
Trimerotropis fallax	Orthoptera (Acrididæ)	11, 12	23, 24	"
Phrynotettix magnus				Pinney, '08, McClung, Wenrich
Syrbula admirabilis and nearly fifty additional species of this family.				Robertson, '08 Meek, '13, Carothers, '13, Nowlin, '08, 12
Stenobothrus biguttulus	" "	8, 9	17, (18)	Gérard, '09 Meek

EXAMPLES OF CHROMOSOME NUMBERS IN ANIMALS—*Continued*

Tracheata—Continued

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Chorthippus curtipennis	Orthoptera (Acrididæ)	8, 9	17, (18)	Davis, '08, Robertson, '16
Circotettix lobatus	" "	10, 11	21, 22	Carothers, '17
" radula				
Paratettix leuconotus-leucothorax	" "			Harman, '15
Acridium granulatus and other species	" Tettigidea	6, 7	13, (14)	Robertson, '08, '15, 16, '17
Paratettix, sp.	"			
Tettigidea parvipennis				
Alydus pilosulus	Heteroptera (Coreidæ)	6, 7	13, 14	Wilson, '05, Montgomery, '06
Harmostes reflexulus				
Protenor belfragei				
Anasa tristis	" "	10. 11	21, 22	Wilson, '05, '06, McClung, etc.
Chelinidea vittigera				
Euthoctha galeator				
Leptoglossus phyllopus, and others				
Margus inconspicuus	" "	(11, 12)	23, 24	Wilson, '09, etc.
Chariesterus antennator	" "	(12, 13)	25, 26	"
Syromastes marginatus	" "	10, 12	22, 24	" " Gross
Largus cinctus	" (Pyrrhorcoridæ)	5, 6	11, 12	" '07, '09
" succinctus		6, 7	13, 14	" "
Pyrrhocoris apterus	" "	11, 12	23, 24	" "
				(*cf.* Henking '90)
Pentatoma senilis	" (Pentatomidæ)	3	6	Wilson '13
" juniperina	" "	(7)	14	" "
Œbalus pugnax	Heteroptera (Pentatomidæ)	(5)	10	Wilson, '09
Euschistus crassus	" "	6	12	Foot and Strobell, '12
" fissilis, servus	"	7	14	Montgomery, '01,
" variolarius				'06, Wilson, '05
" etc.				
Podisus bractatus	Heteroptera (Pentatomidæ)	(7)	14	Wilson, '09
" placidus	" "	8	16	" "
Thyanta custator	" "	8	16	" '11
" calceata	" "	13, 14	27, 28	" "
Banasa dimidiata	" "	8	16	" '07
" calva	" "	13	26	" "
Aphis saliceti	Homoptera (Aphidæ)	2, 3	5, 6	Baehr, '09, '12
Phyllapis coweni	" "	2, 3	5, 6	Morgan, '15
Aphis ("milkweed, black")	" "	3, 4	(7), 8	Stevens, '09
" œnotheræ	" "	4, 5	9, 10	" '05, '06, '10
" ("golden-rod")	" "	(5, 6)	(11), 12	" '09

EXAMPLES OF CHROMOSOME-NUMBERS IN ANIMALS—*Continued*

Tracheata—Continued

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Aphis ("rose aphid, green")	Homoptera (Aphi-	6, 7	(13, 14)	Stevens, '06, '09
" ("rose, migratory")	" " [dæ)	(8), 9	(17), 18	" '06
Pamphigus pyriformis spirotheca	" "	(9, 10)	(19), 20	Baehr, '08, '09
Icerya purchasi	" (Coccidæ)	2	4	Pierantoni, '12, '14
Apis mellifica	Hymenoptera	16	32	Nachtsheim, '13
Osmia cornuta	"	16	(32)	Armbruster, '13
Xylocopa violacea	"	16	(32)	Granata, '09, '13
Paracopidosomopsis sp.	" (Cynipidæ)	8	16	Patterson, '17
Rhodites rosæ	" "	9	18	Henking, '92, Hogben, '20
Neuroterus lenticularis	" "	10	20	Doncaster, '09, '11
Nematus ribesii	" (Tenthredinidæ)	8	16	" '04–'10
Lasius niger	" (Formicidæ)	10	20	Henking, '92
Formica sanguinea	" "	24	48	Schleip, '08
Phyllosamia cynthia	Lepidoptera	13	26	Dederer, '07, '15
Pieris brassicæ	"	14	28	Henking, '90
" "	"	15	30	Doncaster, '12
Callosamia promethea	"	19	38	Cook, '10
Pygæra pigra	"	23	46	Federley, '13
" curtula	"	29	(58)	" "
" anchoreta	"	30	(60)	" "
Lymantria dispar	"	31	62	Seiler, '14
Talæoporia tubulosa	"	30, 29	60, 59	" '17, 19
Fumea casta	"	31, 30	62, 61	" " "
Theophila mandriana	"	27	(54)	Yatsu, '13
Bombyx mori (17 varieties)	"	28	60–50	" "
Nyssia zonaria	"	56±	112±	Doncaster, '14
Necrophorus sagi	Coleoptera	6, 7	13, (14)	Stevens, '09
Odontola dorsalis	"	8	16	" '06
Coptocycla guttata	"	9	18	Nowlin, '06
Photinus consanguineus	"	9, 10	19, 20	Stevens, '09
Diabrotica vittata	"	10, 11	21, 22	" '08, Hoy, '14
Coptocycla aurichalcea	"	11	22	Nowlin, '06
Chrysomela similis	"	11, 12	23, 24	Stevens, '09
Lestotrophus cingulatus	"	13	26	" '09
Trirhabda virgata	"	14	28	" '06
" Canadense	"	15	30	" "
Lena trilineata	"	16	32	" '09
Doryphora cliricollis	"	17	(34)	" "
" decemlineata	"	18	36	" '06
Dytiscus marginalis	"	19	38	Schafer, '07
Anopheles punctipennis	Diptera	3	6	Stevens, '11
Culex pipiens	"	3	6	" "
Drosophila earli	"	(3)	6	Metz, '16
" melanogaster (=ampelophila)	"	4	8	Stevens, '08
" amœna and 7 other species	"	(4)	8	Metz, '16
" obscura and 3 other species	"	(5)	10	" "
" funebris and 2 other species	"	(6)	12	" "

EXAMPLES OF CHROMOSOME-NUMBERS IN ANIMALS—*Continued*

Tracheata—Continued

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Musca domestica	Diptera	6	12	Metz, '16
Asilus notatus	"	7	14	"
Anthrax sinuosa	"	9	18	"
Miastor americana	"	20–24	(40–48)	Hegner, '14

Echinodermata

Parechinus microtuberculatus univalens	(Echinoidea)	9	18	Boveri, '90, '05 Stevens, '02
Parechinus microtuberoulatus bivalens	"	18	36	Boveri, '90, '05, Stevens, '02, Baltzer, '09–'13
Paracentrotus lividus	"	18	36	Boveri, '02, Baltzer, '13
Echinus acutus	"	[19]	38	Doncaster and Gray, '13
" esculentus	"	["]	38	
Sphærechinus granularis	"	20	40	Baltzer, '10
Moira atropus	"	(23)	46	Pinney, '11
Asterias vulgaris	(Asteroidea)	9	18	Tennent, '07
" forbesii	" "	18	36	" " Jordan, '07, '08

Protochordata

Amphioxus lanceolatus	Cephalochorda	12	24	Cerfontaine, '05
Stylopsis grossularia	Tunicata	2	4	Julin, '93
Phallusia mammilata	"	8	16	Hill, '95
Ciona intestinalis	"	9	18	Boveri, '90

Vertebrata

Myxine glutinosa	Pisces (Cyclostomata)	26	52	Schreiner, '04
Lepidosiren paradoxa	Pisces (Dipnoi)	19	38	Agar, '11, '12
Torpedo, sp.	" (Elasmobranchii)	12	24	Moore, '95
Scyllium canicula	" "	12	24	" "
Pristiurus, sp.	" "	18 ±	36 ±	Rückert '92
Spinax niger	" "		60–70	Schreiner, '07
Fundulus heteroclitus	" (Teleostei)	(18)	36	Mœnkhaus, '04
Menidia notata	" "	(18)	36	" "
Salamandra maculosa	Amphibia (urodela)	12	24	Flemming, '82
Plethodon cinereas				Montgomery, '03
Triton alpestris				Janssens, '00, '01
" cristatus				" "
Batrachoseps attenuatus				" "
Desmognathus fuscus and others				Eisen, '00, Janssens, '05, etc. Kingsbury, '99 Montgomery '03
Aneides lugubris	" "	14	28	Snook and Long, '14
Amblystoma tigrinum	" "	(14)	28	Parmenter, '19
Pelodytes punctatus	Amphibia (Anura)	6	(12)	Bataillon, '10

EXAMPLES OF CHROMOSOME-NUMBERS IN ANIMALS—*Continued*

Vertebrata—Continued

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Bufo vulgaris	Amphibia (Anura)	8–9		Lebrun, '01, Bataillon, '10
Bufo lentiginosus	" "	12	24	King, '02, '07
Alytes obstetricans	" "	16	32	Janssens and Willems, '09
Rana fusca (?)	" "	12	24	Von Rath, 95 Bataillon, '10
" catesbiana	" "	13	26	Swingle
Columba livia domestica	Aves	8	16	Harper, '04
Gallus domesticus	"	9	18	Guyer, '09, '16 (See p. 786)
Phasianus, sp.	"	10–11	20–22	Cutler, '18
Felis catus	Mammalia	17, 18	35, 36	Winiwarter and Saintmont, '09
Canis familiaris	"	10, 11	21, 22	Malone, '18
Didelphys virginiana	"	11	22	Painter, '21
Mus norvegicus albinus	"	18, 19	37 (38)	Allen, '18
Sus scrofa	"	(20)	40	Hance, '17, '18
Bos taurus	"	18, 19	37, 38	Wodsedalek, '20
Homo sapiens [1]	"		47, 48	Winiwater, '12, '21
" "	"	24	48	Painter '21, '22

EXAMPLES OF CHROMOSOME-NUMBERS IN PLANTS

Thallophytia

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Ceratiomyxa, sp.	Myxomycetes	8	16	Jahn, '08
Rhopalodia gibba	Diatomeæ	4	8	Klebahn, '96
Surirella saxonica	"	64–65	128–130	Karsten, '12
Closterium Ehrenbergii	Conjugatæ	60 +		Van Wisselingh, '13
Spirogyra neglecta	"	12	24	Tröndle, '11
" calospora	"	8–10	16–20	"
Zygnema stellinum	"	12–14	25–28	Kurssanow, '11
Hæmatococcus pluvialis	Chlorophyceæ	32		Reichenow, '09
Chlamydomonas Dilli	"	10 ±		Dangeard, '98
" monadina	"	30		"
Hydrodictyon uniculatum	"	10		Timberlake, '01
" africanum	"	18		Yamanouchi, '13
Coleochæte sculata	"	32		Allen, '05
Œdogonium cynthigerum	"	19		Van Wisselingh, '08
Chara crinita	"	12	24	Ernst, '18
Cutleria multifida	Phæophyceæ	24	48	Yamanouchi, '12
Fucus vesiculosus	"	32	64	" '09
Dictyota dichotoma	Rhodophyceæ	16	32	Mottier, '00, Williams, '04
Griffithsia bornetiana	"	7	14	Lewis, '09
Nemalion multifidum	"	8 ±	16 ±	Wolfe, '04
Scinaia furcellata	"	10	20	Svedelius, '15
Delesseria sanguinea	"	20	40	" "
Pyronema confluens	Ascomycetes	12	24	Claussen, '12
Humaria rutilans	"	16	32	Fraser, '08, Guilliermond, '11

[1] See note at p 766.

EXAMPLES OF CHROMOSOME-NUMBERS IN PLANTS—*Continued*

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Cormophyta				
Riccia lutescens	Hepaticæ	4	8	Lewis, '06
" frostii	"	8	16	Black, '13
Pellia eliphylla	"	8	16	Farmer, '95, Davis, '01
Bryum capillare	Musci	10	(20)	É. and É. Marchal, '11
Sphagnum squarrosum	"	20	(40)	Melin, '15
Mnium hornum	"	6	12	M. Wilson, '08, Arens, '08
Polytrichum juniperinum	"	6	(12)	Arens, '08, Allen, '12
Pteris aquilina	Pteridophyta	32	64	Stevens, '98
Nephrodium molle	"	64–66	128–132	Yamanouchi, '08
Dryopteris (Nephrodium) pseudo-mas	"	72	144	Farmer and Digby, '07
Ceratopteris thalictroides	"	120–130		Gabe and Gasni, '13
Marsilia, 5 sp.	"	16	32	Strasburger, '07
Equisetum limosum	"	45–50		Bönicke, '11
" arvense	"	115		Beer, '13
Gymnospermæ				
Cycas revoluta	Cycadales	(12)	24	Ishikawa, '16
Dioön edule	"	12	(24)	Chamberlain, '09
Callitis cupressoides	Coniferales	6	(12)	Saxton, '10
Taxus baccata	"	8	16	Overton, '93, Strasburger, '04
Cephalotaxus drupacea	"	10	(20)	Lawson, '07, Ishakawa, '16
Pinus, 8 sp.	"	12	24	Dixon, '94 Chamberlain, '99 Ferguson, '01
Larix, 5 sp.	"	12	(24)	Strasburger, '92 Juel, '00, Belajeff, '94
Abies balsamea	"	16	32	Hutchinson, '15
Sequoia sempervirens	"	16	32	Lawson, '04
Angiospermæ (Dicotyledoneæ)				
Crepis virens	Compositæ	3	6	Rosenberg, '09, Digby, '14
" tectorum	"	4	8	Juel, '05
" lanceolata, var.	"	5	(10)	Tahara and Ishikawa, '11
" japonica	"	8	16	Tahara, '10
" biennis	"		very many	Digby, '14
Lactuca denticulata	"	5	(10)	Ishikawa, '16
" stolonifera	"	8	(16)	" '11
" laciniata	"	9	(18)	" '16
" thunbergiana	"	11 or 12	(24)	" '11
" debilis	"	24	(48)	" '16
Hieracium venosum	"	7	14	Rosenberg, '07, '17
" auricula	"	9	18	" "

EXAMPLES OF CHROMOSOME-NUMBERS IN PLANTS—*Continued*

Angiospermæ (Dicotyledoneæ)—Continued

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Hieracium aurantiacum	Compositæ	18	36	Rosenberg '17
" flagellare (apog.)	"	21	42	" "
Chrysanthemum coronarium and others	"	9	16	Tahara, '15, '21
C. leucanthemum, indicum	"	18	(36)	" "
" morifolium	"	27	(54)	" "
" decaisneanum	"	36	(72)	" "
" arcticum, marginatum	"	45	(90)	" "
Spinacia oleracca	Chenopodiaceæ	6	12	Stomps, '10
Chenopodium album	"	9	(18)	Winge, '16
" bonus henricus	"	18	(36)	" "
Viola glabella	Violaceæ	6	(12)	Miyaki, '13
" grypoceras + 5 species	"	10	(20)	"
" okuboi + 2 species	"	12	(24)	"
" diffusa	"	(13)	(26)	"
" japonica	"	24	(48)	"
Vicia faba	Leguminosæ	6	12	Nemec, '04, Strasburger, '11, Sharp, '13, '14
Pisum sativum	"	7	(14)	Cannon, '03, Sakamura, '16
Œnothera lamarckiana (also grandiflora, rubinerois, biennis, etc.)	Œnotheraceæ	7	14	Lutz, '07, Gates, '07, Geerts, '07
Œnothera lata (various forms)	"	7, 8±	15	Lutz, '12 / Gates, '12
Œnothera semigigas	"		21	Lutz, '12, Stomps, '12, etc.
" gigas	"		28	Lutz, '07, Gates, '08, etc.
			(27, 29)	
Ribes, 2 sp.	Saxifragaceæ	8	16	Tischler, '06
Solanum lycopersicum	Solanaceæ	12	24	Winkler, '09
" nigrum	"	36	72±	"
Drosera rotundifolia	Droseraceæ	10	20	Rosenberg, '04
" longifolia	"	20	40	" '09
Primula sinensis	Primulaceæ	9	18	Gregory, '09
" verticillata	"	12	24	Digby, '12
" kewensis	"	18	36	" "
Thalictrum minus	"	12	(24)	Overton, '09
" purpurascens (apog.)	Rosaceæ	24	48	" "
Rosa; various forms (races, species?)	"	7	14	Täckholm, '20 (see p. 848)
Many apogamous		14	21	
			28	
			32–36	
			35	
			42	
			56	
Alchemilla arvensis	"	16	32	Murbeck, '01
" grossidens and others	"	32	64	"
Potentilla rupestris	"	8	16	Forenbacher, '14
Potentilla sylvestris and others	"	16	32	Forenbacher, '14

EXAMPLES OF CHROMOSOME-NUMBERS IN PLANTS—*Continued*

Angiospermæ (*Monocotyledoneæ*)

SPECIES	GROUP	HAPLOID	DIPLOID	AUTHORITY
Naias marina	Naiadaceæ	6	12	Guignard, '99, Müller, '12
Triticum monococcum	Gramineæ	7	14	Sakamura, '18, Sax, '21
" durum	"	14	28	" "
" vulgare	"	21	42	" "
Avena strigosa	"	7	14	Kihara, '19
" barbata	"	14	28	"
" byzantina	"	21	42	"
Zea mays	"	10—	20—	Kuwada, '15
Carex pilulifera	Cyperaceæ	9		Heilborn, '22
" ericetorum	"	15		"
" vaginata	"	16		"
" montana	"	19		"
" dicœca	"	26		"
" atrafa	"	27		"
" Helleri	"	28		"
" caryophyllea	"	31		"
" pallescens	"	32		"
" vulpina	"	34		"
" flava	"	35		"
" riparia	"	36		"
" aquatilis	"	37	74	Stout, '13
" rostrata	"	38		Heilborn, '22
" cœspitosa	"	40		"
" vesicaria	"	41		"
Musa sapientina var. "Dole"	Musaceæ	8	16	Tischler, '10
" sapientina var. "Raja Siam"	"	16	(32)	"
" sapientina var. "Kladi"	"	24	(48)	"
Disporum Hookeri	Liliaceæ	5	(10)	Lawson, '11
Trillium grandiflorum	"	6	12	Atkinson, '99
Medeola virginiana	"	7	(14)	Ishikawa, '16
Allium cepa	"	8	16	Schaffner, '98, Miyake, '05
Hyacinthus orientalis	"	8	16	Hyde, '09 Müller, '12
Galtonia candicans	"	8	16	Schniewind-Thies, '01, etc.
Lilium martagon and 9 other species	"	12	24	Guignard, '84, '91, Strasburger, '82, '88, etc.
Iris squalens and 3 other species	"	12	(24)	Strasburger, '00, Miyaki, '05
Smilacina racemosa	"	24	(48)	McAlister, '13, Woolery, '15
Calopogon pulchellus	Orchidaceæ	13	26±	Pace, '09
Gyrostachys (Spiranthes) gracilis	"	15	(30)	" '14
Gyrostachys cernua	"	30	(60)	"
Listera ovata	"	16	32	Rosenberg, '05

The foregoing list makes evident the fact that the number of chromosomes varies within very wide limits but in far the greater number of cases is relatively small, commonly not more than 36 (diploid) and often less. Among the most frequent diploid numbers in both plants and animals are 16, 18 and 24.[1] The smallest observed diploid number, at the theoretical limit 2, occurs in *Ascaris megalocephala univalens*, but these "chromosomes" represent assemblages of much smaller ones linked together in linear series (p. 879). The next smallest number 4, though rather rare, has been described here and there in several groups of plants, from the fungi (and possibly in the algæ) up to the seed-plants, and among animals in certain platodes (*Vortex*), nematodes (*Gordius*), copepods (*Cyclops*), arachnids (*Pediculopsis*), insects (*Icerya*) and tunicates (*Stylopsis*). Diploid numbers 6, 8, and 10 are also not very frequent; those from 12 to 36 are most frequent, and higher ones rare. The highest numbers have been recorded in some of the radiolarian rhizopods, ranging from 1000 to 1500 (*Aulacantha*, *Castanidium*); but these undoubtedly represent compound groups formed by many synchronously dividing nuclei in a syncytium.[2] In higher organisms the largest numbers seem to be found in the Filicales (up to 200), the decapod Crustacea (200 or more), and the Lepidoptera (up to 100 or more).

Closer study of the numbers brings out many points of interest. Of these, perhaps the most important is that the chromosome-numbers may differ widely within the limits even of the smaller groups (genus or family) and sometimes even between closely related species. An interesting case is that of the hemipteran species *Thyanta custator* in which were found two "races" previously confused under the same name and morphologically almost indistinguishable, in external appearance, one constantly having the diploid number 16 in both sexes, the other 27–28 (Wilson, '11). Later studies proved the two "races" to be distinct species, the former being the original *custator* of Fabricus, the latter the *calceata* of Say, which had long been buried in the literature as a synonym of *custator* (Barber, '11).

Such cases demonstrate clearly that *the number of chromosomes is per se a matter of secondary significance.* Both cytological and genetic evidence prove that the chromosomes are compound bodies, containing many different components. So long as the sum-total of these remains the same, or nearly so, it seems to be immaterial whether they be grouped to form few or many larger aggregates (p. 903). It is not surprising, therefore, to find no more than a slight degree of correlation between chromosome-numbers and systematic relationships—the numbers 16 and 24, for instance, are found in nearly

[1] *Cf.* Winge ('17).

[2] See Borgert ('01), Haecker (07).

all the main groups of plants and animals. As far as the larger groups are concerned, therefore, there is little to favor the hope of finding a satisfactory basis of classification in the chromosome-numbers. Nevertheless the fact is not to be overlooked that some groups show on the whole characteristic peculiarities in this respect, and in some cases a number of greatest frequency or "type-number" may be distinguished. Among higher plants, as Tischler emphasizes, the bryophytes are in general characterized by low numbers, pteridophytes by high, and seed-plants by intermediate ones. Among Crustacea low numbers occur in Copepods, high in decapods; among insects relatively low numbers appear in Diptera, much higher ones in Lepidoptera, etc. In the Amphibia the greatest frequency or type-number may be taken as $2n=24$; in the Acrididæ as 23, 24; in the Pentatomidæ as 14, and so on.[1] So many exceptions exist, however, that figures of this kind do not seem very significant, especially when we consider how small a fraction of the existing species have yet been examined.

It is a striking fact that *higher numbers are often exact multiples of lower ones*. In the simplest of these cases the higher number is double the lower; such cases occur in many genera of animals and plants, for instance in *Cyclops*, *Gryllotalpa*, *Aphis*, *Drosophila*, *Crepis*, *Hieracium*, or *Chrysanthemum;* and differences of the same type often appear between species of different genera. The significance of this is, however, made doubtful by the fact that in most such cases intermediate numbers also occur and the problem here raised is more complicated than would first appear. Many attempts have been made to arrange chromosome-numbers in some kind of significant system; but these have not as yet been very successful.

Some writers have assumed that within the limits of particular groups the haploid numbers are either multiples of 2, *e. g.*, 2, 4, 8, 16, or of 3, *e. g.*, 6, 12, 18, etc.; and it has been shown that many of the recorded chromosome-numbers fall into one or the other of these two systems; [2] but many of the series are incomplete or disturbed by the existence of intermediate numbers that cannot be fitted into the system, or by the existence of irreconcilable fundamental haploid numbers such as 5, 7 or 11. Of greater significance, perhaps, is the fact, conspicuously shown by recent investigation especially on the higher plants, that the diploid numbers not infrequently are progressive multiples of a fundamental *haploid* number by 2, 3, 4, and so on in arithmetical progression, sometimes with few or no intermediate numbers,

[1] E. B. Harvey ('20) assigns type-numbers to several of the larger groups, *e. g.*, for the Nemathelminthes $n=6$, Echinoderms $n=18$, Platyelminthes $n=8$, Mollusca $n=16$, etc.

[2] See Haecker ('04), Enriques ('05), Strasburger ('10), Gates ('15), and especially Tischler ('15) and Winge ('17).

so that they are often spoken of as diploid, triploid, tetraploid, etc.[1] The most remarkable examples of this have been found among plants, *e. g.*, in *Chrysanthemum*, *Triticum*, *Avena*, *Musa*, or *Rosa*. Here it may be pointed out that the exceptions in most of these various systems are so numerous as largely to deprive them of significance; for instance in the Copepod genus *Cyclops* and its allies *Diaptomus* and *Canthocamptus*, or in the Coleoptera, where the lowest known haploid number is 3, the second lowest 6, while beyond this point appear all numbers in continuous series from 7 up to 19.[2] Other examples of nearly continuous series are offered by the aphids, the pentatomids, and the seed-plants (*e. g.*, in *Carex*) and further observation seems likely to render many of the existing partial series more complete.

Without further multiplying instances, and with due allowance for incompleteness of the existing data, we must therefore admit the present inadequacy of attempts to reduce the chromosome-numbers to any simple or consistent arithmetical rules. This conclusion, as will presently be seen, forms part of the evidence which indicates that the evolution of chromosome-numbers has not followed a single or consistent course but has taken place on the whole fitfully, irregularly and in various ways.

V. DEVIATIONS FROM THE FUNDAMENTAL CHROMOSOME-NUMBERS

Many of the supposed variations and contradictions of chromosome-numbers as recorded in the literature have been a product of erroneous observation or of theoretic preconception; but apart from these the fact of variation in number, both in the individual and in the species, has been conclusively demonstrated. Some writers have considered this as a disproof of the specific constancy of chromosome-number and have concluded that "not constancy but variability in number of chromosomes is the general rule in all organisms," (Della Valle, '09). Verbally, perhaps, this is not incorrect, though a palpable exaggeration; in substance it is highly mis'eading.[3]

In general it may be said that variations in the chromosome-number are much more frequent in somatic cells than in those of the germ-line, and are also more frequent in old, highly specialized or degenerating cells. Such variations may be either definite or indefinite. The former are of more fixed type, and may affect not merely one or a few cells of the indi-

[1] The use of these terms, though convenient from a phyletic point of view, is somewhat confusing since they were originally applied to reduplication of the haploid groups due to pathological processes, such as polyspermy, fusion of eggs, and the like.

[2] For these cases see preceding lists.

[3] For specific criticisms of Della Valle's conclusions see Wilson ('10), Enriques ('11), McClung ('14, '17), Tischler ('17), Hance ('17, '18), Parmenter ('19), etc.

vidual but often large groups of them, or even all of them, in the same way. In such cases different individuals of the same species may differ definitely in apparent chromosome-number, but the number is constant in each particular individual. Variations of this type take their origin in linkage or in disturbances of mitosis, meiosis or fertilization, giving rise to new combinations which, once established, are thereafter maintained by normal mitosis. Indefinite fluctuations are not ordinarily thus produced but arise in the prophases by a fragmentation or transverse division of one or more of the chromosomes. They are in general inconstant, varying in different cells of the same individual or tissue; and, as will be seen later, some of them differ essentially from definite variations. *Both types, when critically examined, bring strong support to both the theory of genetic continuity and that of the specific constancy of the chromosomes.*

1. Somatic Cells and Germ-Cells

As a rule the chromosomes-groups of somatic mitoses agree closely with those of the germ-line though often with certain minor differences of form.[1] In some cases, however, definite differences of chromosome-number exist between them. The classical example of this is offered by *Ascaris megalocephala* in which cells of the germ-line divide with either two large chromosomes (variety *univalens*), or four (var. *bivalens*), while in all the somatic cells these larger chromosomes break up into much greater numbers of very small ones (Figs. 144, 145).[2] Again, in the honey-bee the fundamental haploid number is 16, as found by all observers. The male-producing (parthenogenetic) egg segments with this number, which is also retained in the spermatogonia, while the female-producing (fertilized) egg divides with the diploid number 32 (p. 797). In later stages the somatic divisions may show multiples of these basic numbers, namely, 32 or even 64; but the oögonial divisions, like the spermatogonial, show 16 chromosomes, probably as a result of coupling.[3]

In the same category, perhaps, we should place the apparent reduction to one-half the *haploid* number in the spermatocytes or spermatids described in certain Hymenoptera and some other animals. The best known example of this is offered by the honey-bee *Apis*. The haploid number (16) appears in the first (abortive) spermatocyte-division and may appear also in the second.[4] In many cases, however, the second division seems to show

[1] Morrill, '10, Hoy, '16, etc.

[2] In var. *univalens* this number is about 52 in the male and 60 in the female (Geinitz, '15), somewhat larger according to Kautzsch, '14. *Cf.* p. 855.

[3] Petrunkewitsch ('01), Doncaster ('06, '07), Meves ('07), Granata ('09, '13), Nachtsheim ('12), Armbruster ('13), etc.

[4] Meves ('07), Mark and Copeland ('06).

but 8 chromosomes (Fig. 383); but, as shown by Doncaster ('07) and especially by Nachtsheim ('13), the eight chromosomes are often seen to be double during the anaphases. This is evidently due to a coupling of the chromosomes, two by two, since the metaphase, according to Nachtsheim, shows 16 double chromosomes. A similar coupling seems to take place also in the oögenesis, where Petrunkewitsch ('01) found but 8 tetrads and was thus led to the erroneous conclusion that 8 is the haploid number. Meves, Nachtsheim and others have, however, proved that 16 is the haploid number as shown by the numbers in the gamete-nuclei and in the parthenogenetic development of the males (p. 797). A similar apparent reduction to the semi-haploid condition was found by Armbruster ('13) in the solitary bee *Osmia*, and in several of the vertebrates.[1] There is some reason to suspect that in some of these cases the appearance is due to an artificial clumping by the fixative; but such an interpretation can hardly be generally applicable.

2. Reduplication. Polyploidy

By this term may be designated a rather common form of definite variation in which either the whole diploid chromosome-group, or one of the haploid groups is doubled, or multiplied to give triploid, tetraploid, or polyploid groups. Attention has earlier been directed to the existence in various animals of the so-called "bivalent" (more properly tetraploid) individuals or races in which the normal chromosome-number is doubled but which do not otherwise differ visibly from the usual type (*Ascaris*, *Echinus*, *Artemia*, pp. 231, 869). More commonly the doubling (or higher multiplication) of the chromosomes appears only here and there in certain somatic cells, particularly those that are old, highly specialized or degenerating. Such groups are, for instance, common in the connective tissue-cells, fat-cells, investing-cells of the gonads and follicle-cells of insects (Fig. 407) and in the tapetal or investing cells of the sporangia in plants. As above mentioned reduplication is of common occurrence in the somatic divisions of Hymenoptera. It is highly probable that this condition arises from nuclear fusion or from some form of incomplete mitosis, such as monocentric mitosis (p. 168), incomplete separation of daughter chromosome-groups, or a fusion of daughter-nuclei after mitosis. Processes of this type have often been induced experimentally, *e. g.*, in sea-urchin eggs, *Spirogyra* filaments, or growing root-tips of plants that are exposed to the action of cold, CO_2, narcotics, or other poisons during mitosis.[2]

[1] In the opossum (Jordan, '11), man (Guyer, '10), pig, horse and bull (Wodsedalek, '13, '14, '20), and in some species of birds (Guyer, '00, '02, '09, '16, Cutler, '18).

[2] See p. 729, O. and R. Hertwig ('87), Demoor ('95), Wilson ('01b), Gerassimoff ('01), Boveri ('05) Nemec ('10), Herbst ('12, '14), etc.

Such cases of reduplication in certain cells of the individual are exactly parallel to those in which the normal diploid numbers of related races or species show constant differences of the same type (p. 867); and are no doubt due to similar causes. Even more interesting are cases in which the aberrant somatic numbers, again as in case of different races or species, do not form a simple geometrical series but are multiples of the fundamental hap-

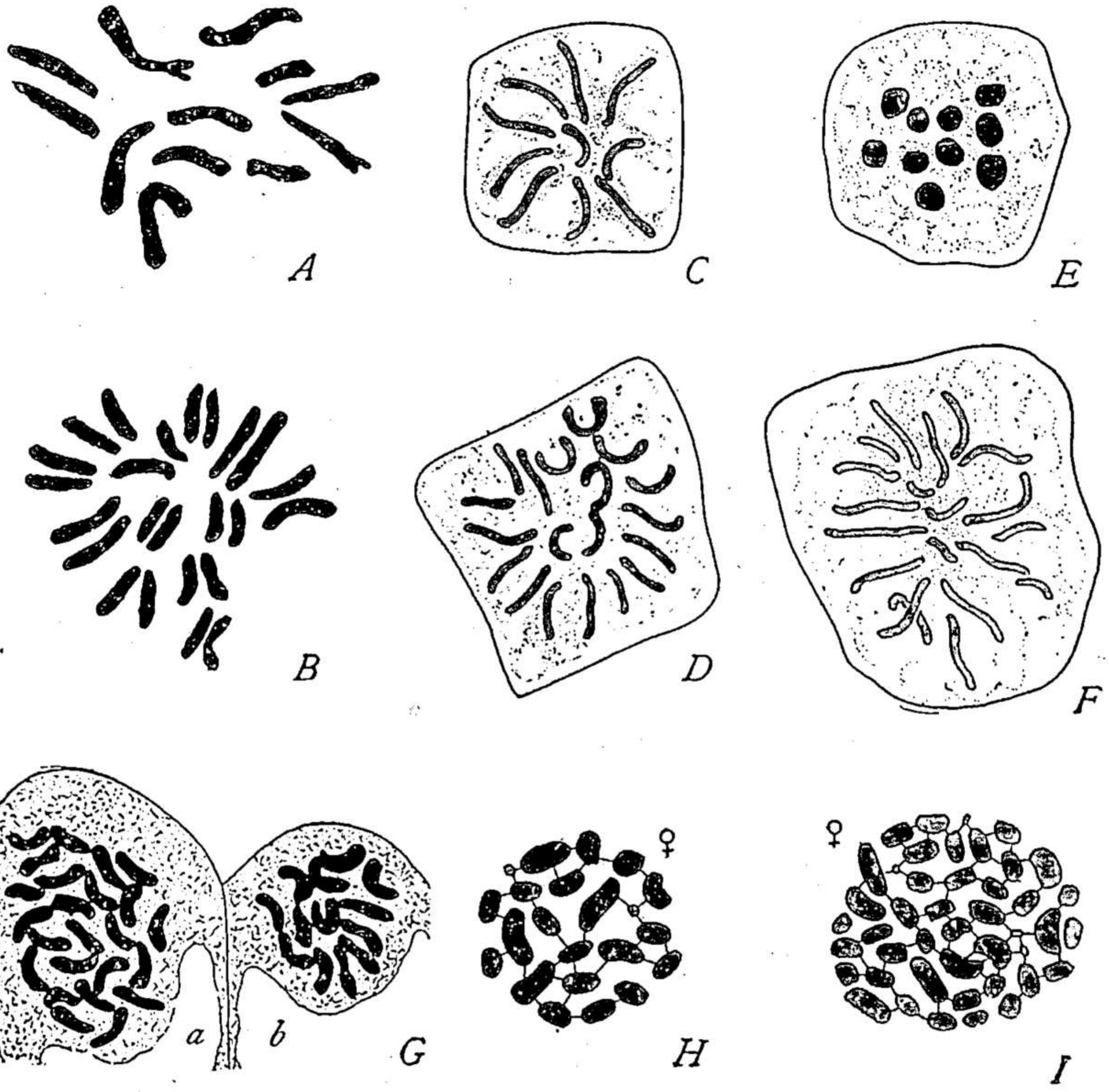

Fig. 407.—Haploid, diploid and tetraploid chromosome-groups in plants and animals (*A*, *B*, from STOMPS; *C–F* from MARCHAL; *G* from NEMEC; *H*, *I*, from WILSON).

A, diploid group from *Spinacea; B*, tetraploid group of same, chromosomes paired; *C*, haploid group from gametophyte of moss *Bryum capillare*, 10 chromosomes; *D*, normal diploid groups of the same species from the sporophyte; *E*, heterotypic division of same, 10 bivalents; *F*, diploid group from artificially produced gametophyte regenerated from the sporogonial tissue; *G*, from slightly chloralized root-tip of *Pisum*, *a* with tetraploid group (24 chromosomes), *b*, diploid group (one chromosome missing); *H*, normal diploid group (follicle cell) in the hemipter *Anasa tristis*, showing 22 chromosomes; including 2 small *m*-chromosomes and 4 large ones; *I*, tetraploid group of same, 44 chromosomes, 4 small and 8 large.

loid number in more or less regular arithmetical progression (*cf.* p. 867). Such a case is offered by the mosquito *Culex pipiens* (Holt, '17) in degenerating intestinal pupal cells during the metamorphosis. The normal diploid number is here 6 (often apparently 3, owing to the close paired association of the somatic mates, p. 837). In these cells were found mitoses with 6, 9, 12, 18, 24, 36, and even 72 chromosomes, the most frequent being 12, 24,

and 48. These latter numbers ("6-series") may be taken as a result of simple doubling; but those with 9 or its multiples 9, 18, 36, and 72 ("9-series") apparently must have involved, at least in the production of its first term, a reduplication of one of the gametic groups independently of the other. Numbers thus arising are very similar to those seen in highly hybridized groups, such as the roses (p. 848). This might have arisen from an original difference between the division-rhythm of the paternal and maternal haploid groups (Holt, *op. cit.*),[1] or possibly by multipolar mitosis following a bi-nucleate or syncytial condition which might produce many irregularities of number afterwards held constant by bipolar division (p. 917).

3. Supernumerary Chromosomes and Missing Chromosomes. Non-Disjunction. Fragmentation

A frequent source of definite variation in chromosome-number is shown by the appearance of one or more *supernumerary chromosomes*, in addition to the normal chromosome-group.[2] Such chromosomes are of two kinds, differing entirely in nature and mode of origin, and producing certain types of definite and indefinite variation respectively. The first of these result from an abnormality of mitosis known as:

a. Non-disjunction. This process is a failure of two synaptic mates to separate in the reduction-division and their passage together to one pole of the spindle (Wilson, '09, Bridges, '16, etc.) and it may appropriately be applied also to a failure of sister-chromosomes to separate in an ordinary equation-division. In such cases one daughter-nucleus receives an extra chromosome (thereafter a supernumerary) which is correspondingly missing in the sister-nucleus. If it occurs in a meiotic or haploid division this chromosome will be diploid in one nucleus and absent in the other; if in a diploid division it will be correspondingly either triploid or single. In either case the initial modification may be handed on to later descendants of these cells; and when the gametes have been affected may reappear in one or more following generations as a constant character of the individual. Supernumeraries thus arising may therefore lead a kind of wandering life in the species (hence Painter's term *planosome*), passing from one individual to another in successive generations,[3] but forming no necessary part of the chromosome-group as a whole and often

[1] This surmise is based on the fact that the "6=series" and "9=series" never appear in the same individual.

[2] These were first recognized in certain species of Hemiptera, viz. *Banasa calva* (Wilson, '05, '07a); several species of *Metapodius* (Wilson, '07b, '09) and in the beetle *Diabrotica* (Stevens, '08). They have since been found in Diptera (Bridges) in Orthoptera (Stevens, Carothers, McClung and others), spiders (Painter) and in many plants (Lutz, Hance, etc.).

[3] This has been proved conclusively by the breeding experiments of Bridges ('16) on the supernumerary X- and Y-chromosomes in *Drosophila* (p. 947).

being absent. Their inconstancy in the species was the source of confusion in the earlier literature and gave rise to some ill-considered criticism. In point of fact, however, their behavior is tantamount to an experimental demonstration of the genetic continuity of the chromosomes; and the cytological phenomena also find genetic expression in modified forms of heredity which give an equally cogent demonstration of the determinative action of the chromosomes in heredity (p. 944).

The process of non-disjunction has been directly observed in very few cases;[1] but indirectly both the cytological and the genetic evidence indicate

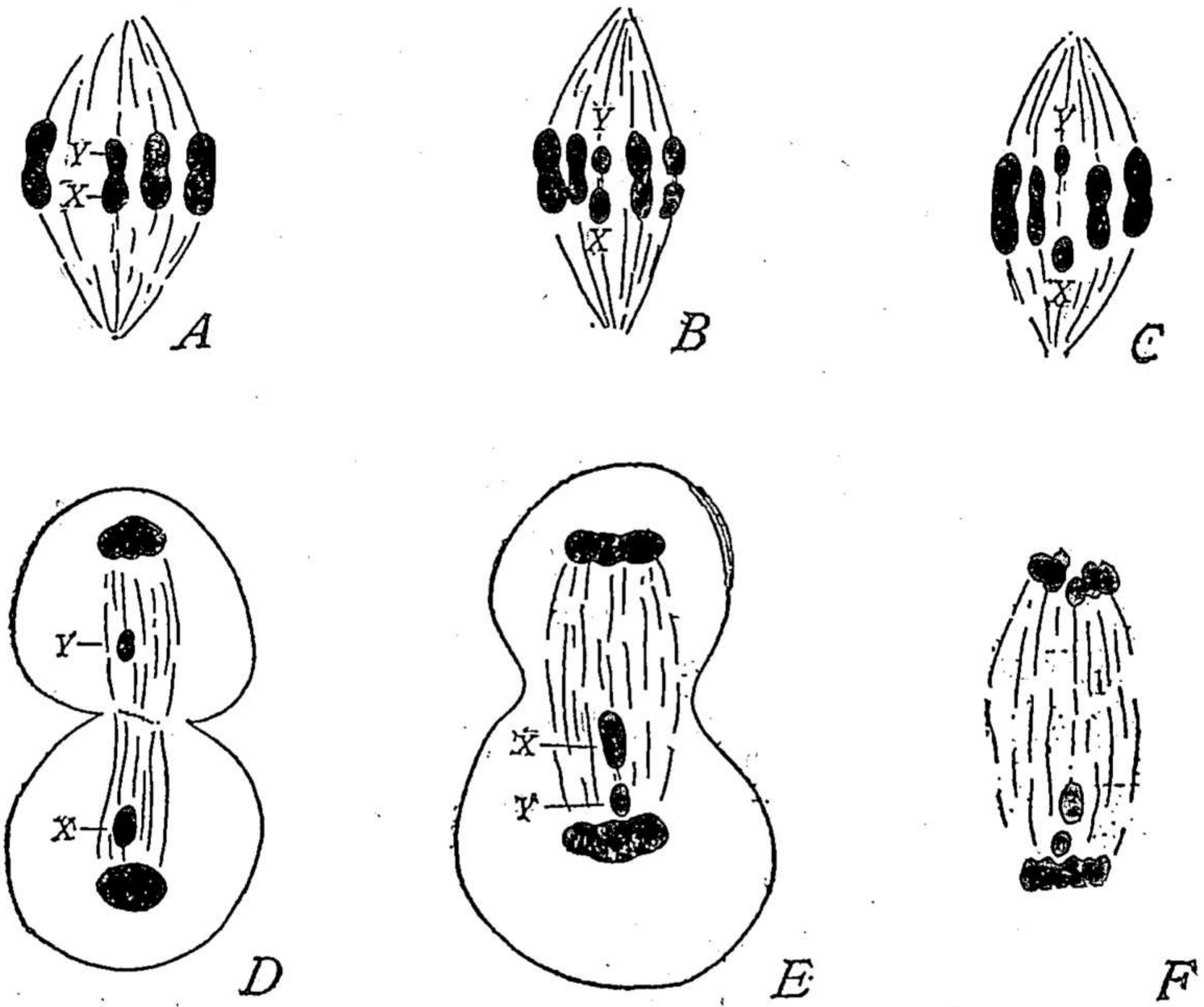

Fig. 408.—Non-disjunction of the *XY*-pair in *Metapodius*.

A–D, normal disjunction of *X* and *Y*, second spermatocyte division (*A–C*, *M. femoratus; D*, *M. granulosus*); *E*, non-disjunction, *M. femoratus; F*, *M. terminalis*.

its occurrence much oftener.[2] In *Œnothera* (diploid 14) it results in the production of spore-nuclei having respectively 6 and 8 chromosomes instead of the usual 7. In this case the minus or 6-chromosome class is believed to be non-viable but the 8-chromosome class is believed to survive and ultimately to give rise to an 8-chromosome gamete-nucleus. Union of such a nucleus with the normal 7-chromosome type will produce a 15-chromosome zygote, diploid in respect to 6 chromosome-pairs but triploid

[1] By Gates ('08) in the heterotypic division of the pollen-mother-cells of *Œnothera*, confirmed by Davis ('10, '11); independently by Wilson ('09) in case of the XY-pair of sex-chromosomes in the hemipter *Metapodius;* more recently by Seiler ('21) in the polar divisions of the moth *Talæporia*.

[2] Mavor ('21, '23) has reported the experimental production of non-disjunction in Drosophila by X-rays.

in respect to one pair (*i. e.*, with one supernumerary). This condition exists in a considerable group of mutants, of which *Œ. lata* is the type, known to have arisen from 14-chromosome forms such as *Œ. lamarckiana*, *biennis* or *rubricalyx*.[1] Blakeslee ('20) has recently found similar conditions in the

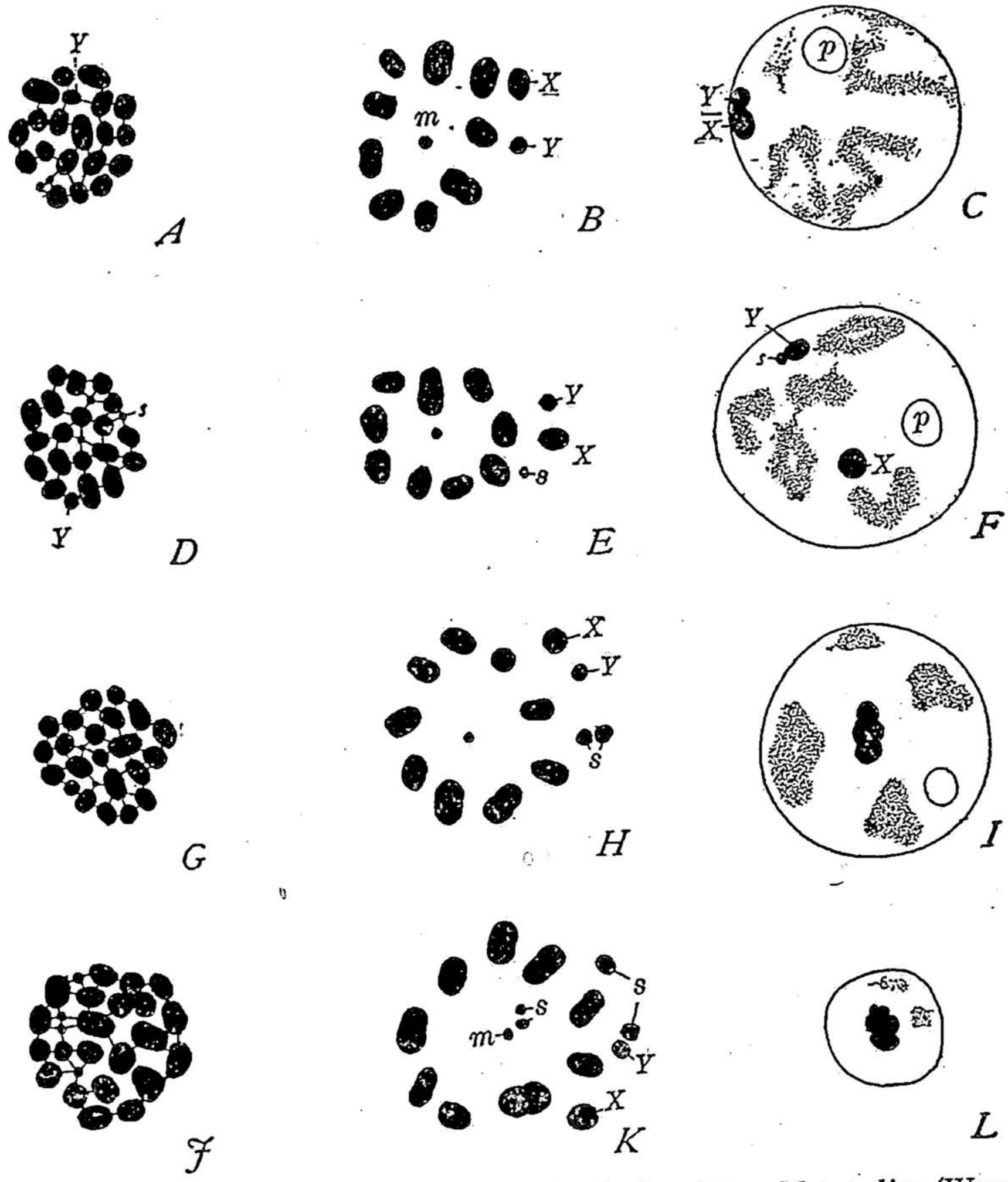

Fig. 409.—Supernumerary *Y*-chromosomes in the hemipter, *Metapodius* (WILSON).

In each horizontal row the left figure is a spermatogonial metaphase, the middle one a first spermatocyte, the right one a spermatocyte nucleus with chromosome-nucleoli (*X*, *Y*, *s*) and plasmosome (*p*); *X*, *Y*, the sex-chromosomes, *s* the supernumeraries, and *m* the *m*-chromosomes. *A–C*, *M. terminalis*, 22 chromosomes, no supernumerary; *D–F*, the same, 23 chromosomes, one small supernumerary (*s*); *G–I*, the same, two large supernumeraries; *J–L*, *M. femoratus*, 26 chromosomes, 2 large supernumeraries and 2 small.

jimson-weed (*Datura*). There the diploid number is normally 24 but it is 25 in a series of forms that are comparable with the *lata-group* (p. 945).

In *Metapodius*, likewise, non-disjunction was observed in the meiotic division (spermatogenesis), and the particular chromosome-pair concerned could here be positively identified as the unequal sex-chromosomes or XY-pair (Fig. 408). The supernumeraries thus produced retain all the charac-

[1] See Gates, '15.

teristics of Y-chromosomes, and have been found in varying numbers in different individuals of three species. Some individuals have 22 chromosomes (the normal diploid number) including one Y, others but 21 (Y being missing); still others 23, 24, 25, 26 or (in a single case) 27, both the number and the size-relations being constant in each individual.

In synapsis these supernumeraries usually couple with the normal XY-pair to form compound groups (Fig. 409). During this mitosis they disso-

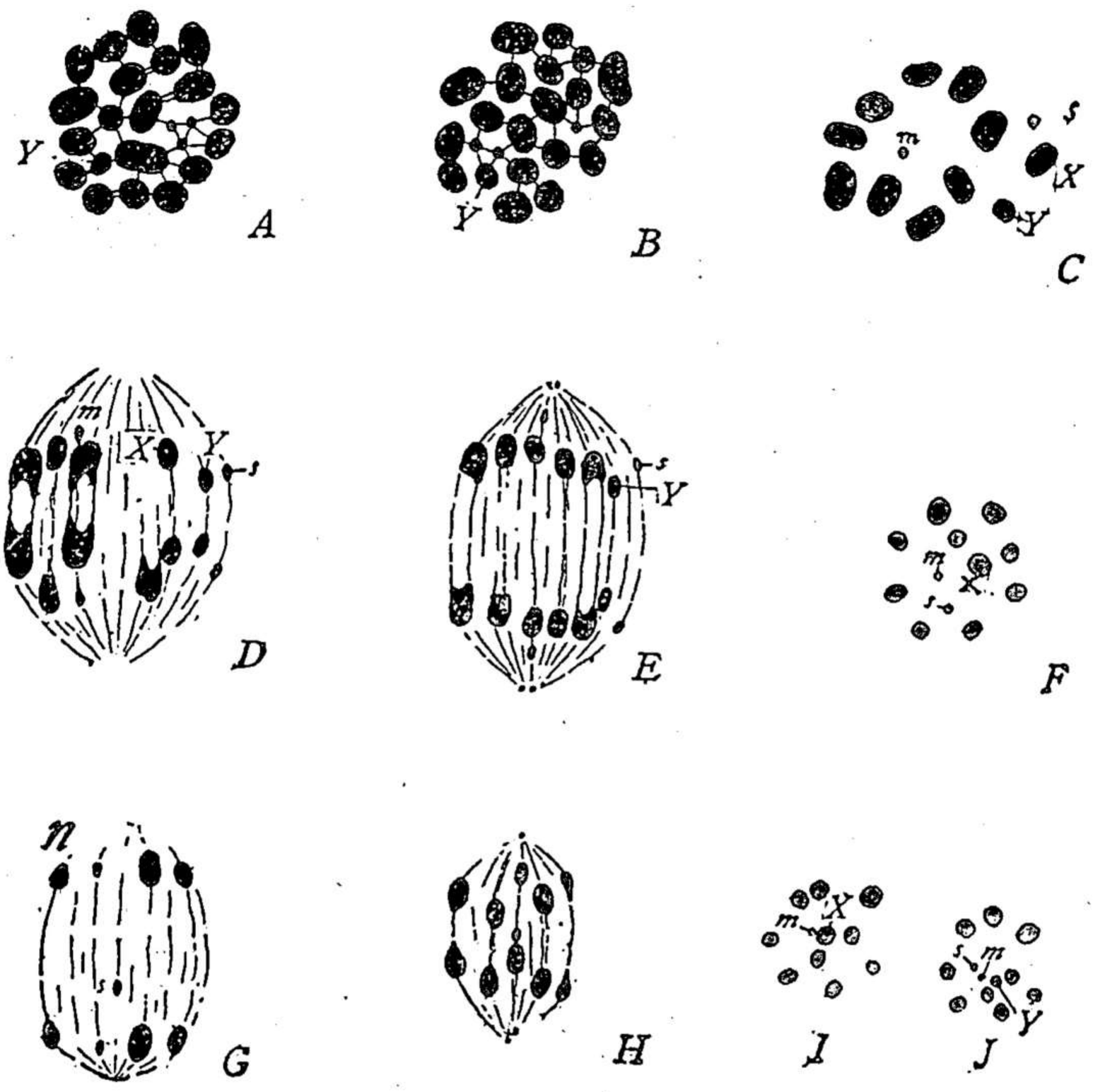

Fig. 410.—Chromosomes of *Metapodius terminalis*, with one small supernumerary *Y*-chromosome (*s*) (WILSON).

A, *B*, diploid (spermatogonial) metaphases, 23 chromosomes (2 small *m*'s, 1 small supernumerary); *C*, corresponding first spermatocyte-metaphase; *D*, *E*, 1st (heterotypic) spermatocyte division in side-view, division of *X*, *Y* and *s*; *F*, second spermatocyte-metaphase; *G*, *H*, anaphases, *s* undivided; *I*, *J*, sister groups of same, polar view, one with *s* and one without it.

ciate in various ways, X and at least one Y always separating, while the supernumeraries may accompany either X or Y, apparently at random (Fig. 410) so that various combinations therefore appear in the sperm-nuclei. Since those of the X-class (female-producing) may contain also Y the possibility thus exists of introducing supernumerary Y-chromosomes into both sexes at the next fertilization.

By further recombinations the number of supernumeraries might theoretically increase indefinitely; but in point of fact not more than 5 or 6 have yet been found in *Metapodius;* and they are often smaller than Y in

various degrees. Probably, therefore, the supernumeraries sooner or later degenerate and disappear.

Metapodius also afforded the proof that supernumeraries may be of more than one definite type; for a single individual of *M. femoratus* was found having one supernumerary showing none of the peculiarities of a Y-chromosome but all those of an *m*-chromosome (Wilson, '10). These peculiarities are of such marked type (p. 839) as to preclude all error in the identification and the case is further remarkable because this individual lacks a Y-chromosome (*cf.* p. 815) yet the small *m* does not take its place but behaves

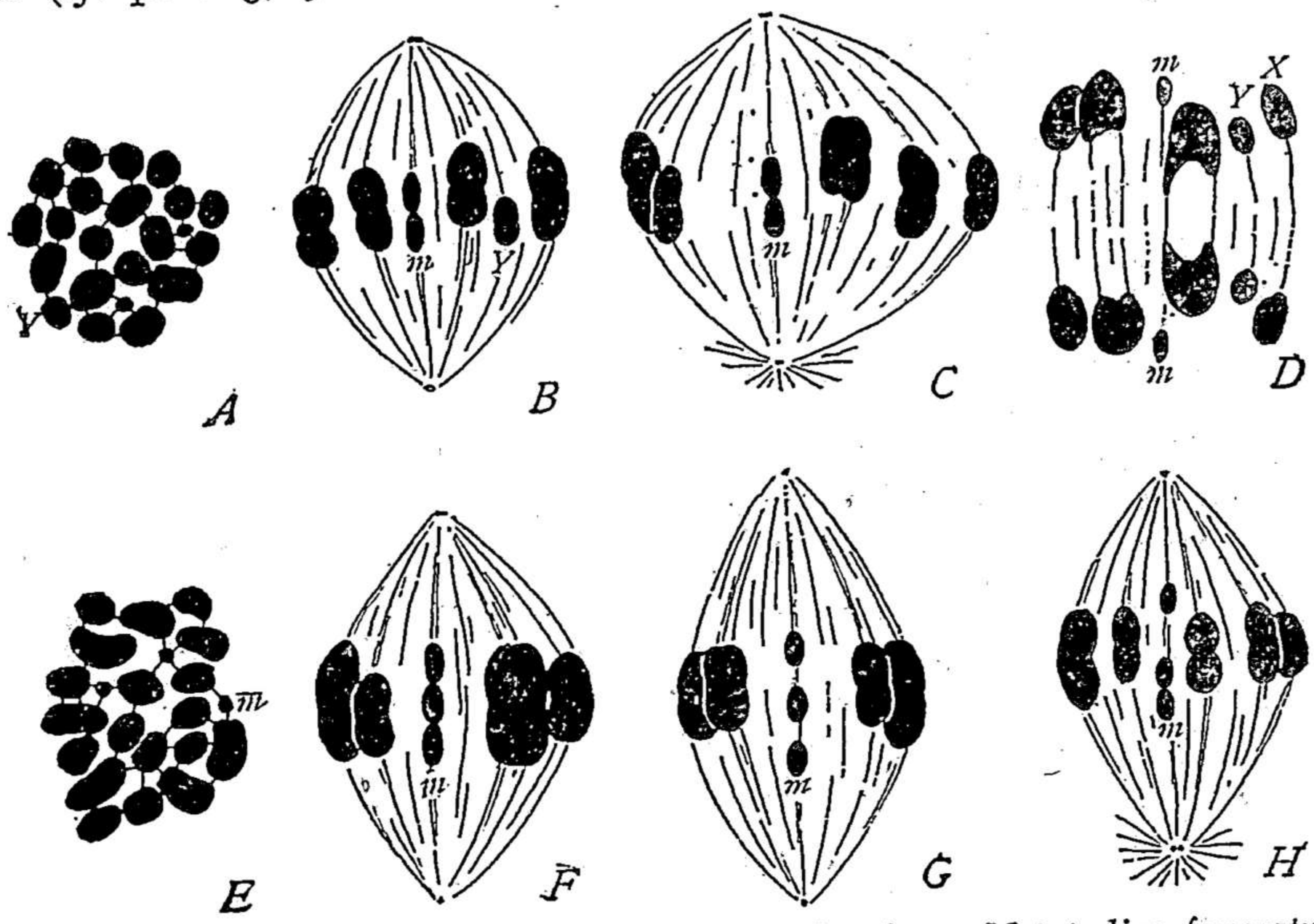

Fig. 411.—Supernumerary *m*-chromosomes in the hemipter *Metapodius femoratus*.

A–D, normal form, for comparison with modified from (*E–H*).

A, spermatogonial metaphase, 22 chromosomes; 2 *m*'s; *B*, *C*, normal metaphases of first spermatocyte, with *m*-bivalent, in side-view; *D*, anaphase, *m*'s and the *X*- and *Y*-chromosomes dividing separately. The *m*-chromosomes are here disjoining (reduction-division) the *X*- and *Y*-chromosomes dividing equationally.

E, spermatogonial group with 23 chromosomes (3 *m*'s); *F*, *G*, *H*, side-views of first spermatocyte-metaphases, *m*-trivalent.

after its own kind and in meiosis couples with the other *m*-chromosomes to form a trivalent element (Fig. 411). It thus offers a striking example of characteristic differences of behavior between chromosomes which in other respects appear exactly alike to the eye (p. 839). These cases demonstrate with the utmost clearness the fact that univalent chromosomes typically divide but once in the course of the meiotic divisions, passing undivided to one pole in the other division. In *Metapodius* it is the first division in which the supernumeraries divide (Fig. 410); in *Banasa*, the second; in *Diabrotica*, according to Stevens, in either division but not in both.[1]

[1] More recently Seiler ('21, '23) has been able to observe non-disjunction directly in the first spermatocyte-division of *Talæporia tubulosa*.

Analogous to the foregoing case is that discovered by Bridges ('13, '14, '16) in *Drosophila*, remarkable because it was purely genetic study that first led him to predict the existence of an extra or supernumerary chromosome in this particular race; and this was fully confirmed by cytological examination. The non-disjunction itself has not yet actually been seen, but the behavior of the sex-linked factors (p. 947) leaves no doubt that it takes place in the meiosis of the egg, and affects the XX-pair. A primary disjunction of this type would give eggs containing either XX or no-X; and fertilization of such eggs by normal sperm would give XXX, XO, XXY and YO. The first and fourth of these classes have not been found in this race and are believed to be non-viable. The XO-class is composed of males, of normal appearance but absolutely sterile, thus demonstrating a connection between the Y-chromosome and fertility (p. 815). From the XXY females (having 9 chromosomes) Bridges raised a race in which the phenomena of "secondary non-disjunction" of the XX-pair is continued in about 4% of cases. Bridges explains this as due to the presence of Y, since in the maturation of eggs containing XXY, Y is always disjoined from one X, while the second X may pass to either pole. Thus may arise four classes of mature eggs, namely: (1) XX, (2) XY, (3) XO and (4) YO; and fertilization of these by normal sperms (X or Y) might give as zygotes the six classes (1) XXX, (2) XXY, (3) XX, (4) XY, (5) XYY and (6) YY. Of these, XXX, XYY and YY are unknown (though the class XYY probably exists); XX and XY are ordinary males and females; while XXY may serve as a starting-point for repetition of the process. The genetic aspect of this interesting case is further considered at p. 947.

More recently Bridges has found in *Drosophila* a supernumerary autosome of the very small fourth pair, which offers a close parallel to the supernumerary *m*-chromosome of *Metapodius* (p. 876). Blakeslee's recent observations on 25-chromosome mutants of *Datura*, make it probable that in that form non-disjunction is of rather frequent occurrence and may effect any one of the twelve chromosome-pairs (see p. 945).

b. Fragmentation. "Deficient" Chromosomes. Fluctuations. In the foregoing cases the normal chromatin-content of the nucleus is increased (or correspondingly decreased) in a definite and constant manner. In a second type supernumeraries arise by a cross-division or fragmentation of one or more of the chromosomes—a process which does not alter the total chromatin-mass but only breaks it up into a larger number of pieces than the normal. The variations thus produced are inconstant, varying in different cells of the same individual and thus having the character of indefinite variations or fluctuations. This is clearly demonstrated by the studies of Hance on the somatic mitoses of the pig ('17) and of *Œnothera scintil-*

lans ('18) in which the typical diploid numbers are respectively 40 and 15. No deviations from these numbers were found in the germ-line; but in the somatic mitoses, along with the typical numbers occur also numbers ranging in the pig from 40 to 58, and in *Œnothera* from 15 to 21, owing to the presence of supernumeraries (Fig. 412).

This seems at first sight a flat contradiction of the specific constancy of chromosome-number; but Hance's careful studies place the matter in a very

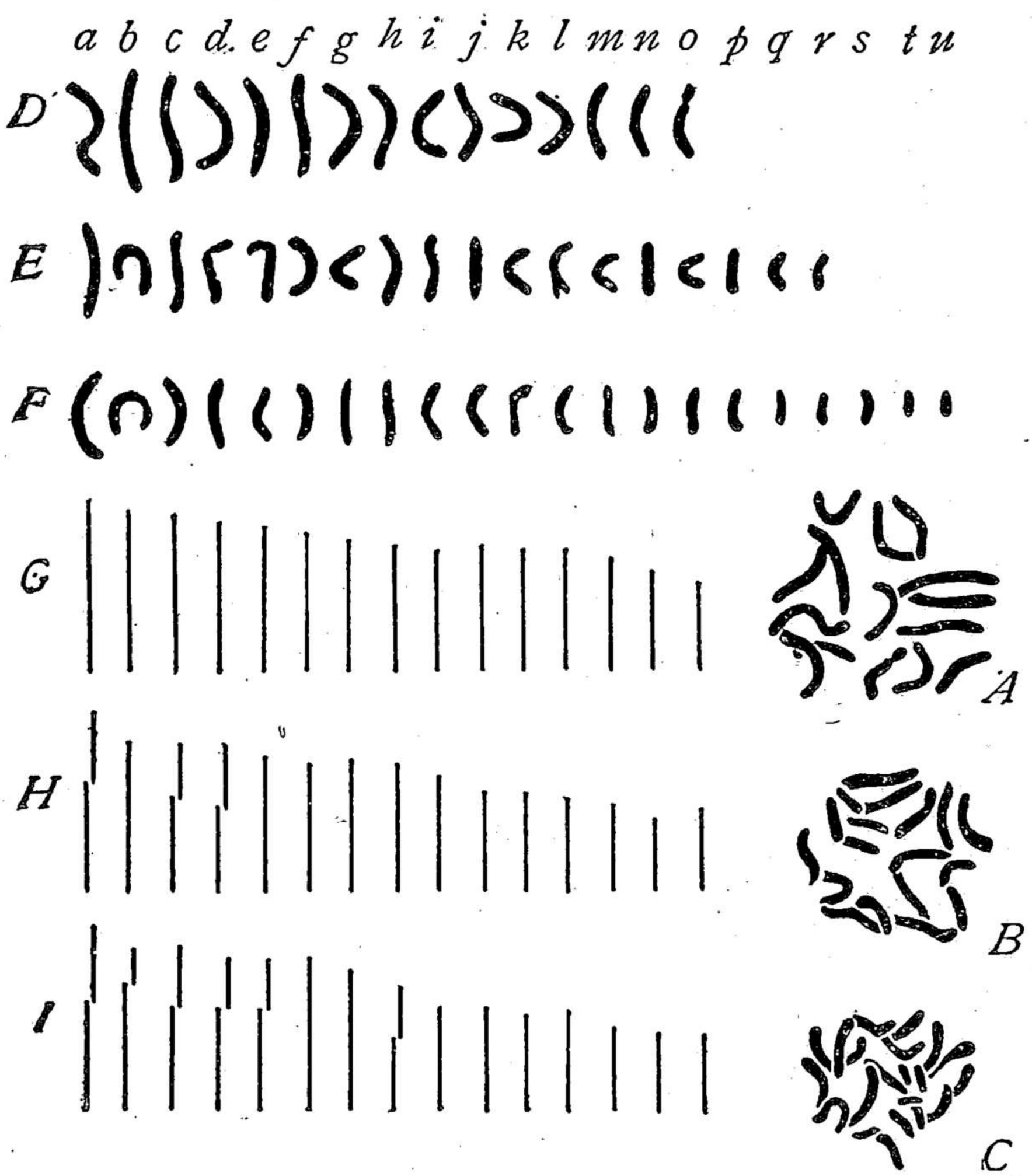

Fig. 412.—Variations of chromosome-number in *Œnothera scintillans* (HANCE).

At the right, *A*, typical somatic group, with 15 chromosome; *B*, one with 19 chromosomes; *C*, one with 21. Above, *D*, *E*, *F*, the chromosomes of such groups arranged in the order of their size, from *a* to *u*. Below, *G*, *H*, *I*, the corresponding chromosome-lengths, similarly graded, so arranged as to bring together the chromosome-fragments and to show the constant total length.

different light. The supernumeraries are always smaller than the normal chromosomes and both their number and size are exactly correlated with corresponding deficiences in the lengths of particular chromosomes; so that when the former are artificially fitted upon the latter the normal size-relations are restored (Fig. 412). *The total length of the chromosomes is*

thus a specific constant irrespective of their number. In respect to their mode of origin, therefore, these supernumeraries are evidently not whole chromosomes but pieces, though in behavior they are not to be distinguished from true chromosomes, dividing lengthwise in mitosis, so as to be handed on from cell to cell without loss of their identity.

This conclusion is sustained by many other observations. Carothers ('13, '17) and Robertson ('15) showed that the unequal or heteromorphic chromosome-pairs observed in certain grasshoppers arise in certain cases by the cross-division of one member of the pair; and Carothers shows further that the break takes place at a particular point marked by two large chromosome-vesicles at which the spindle fibers are attached (Fig. 438). This, again, is in harmony with numerous observations which demonstrate the presence of cross-sutures at certain points in the chromosomes, which in some species at least are constant in position. The conclusion that chromosomes may occasionally fragment across the transverse sutures and thus increase the number of chromosomes becomes still more plausible when taken in connection with other evidence concerning the compound nature of the chromosomes (p. 903) and the possible modes by which chromosome-numbers may have permanently changed. The evidence indicates that the position of these cross-sutures is constant for any given chromosome; and hence that if supernumeraries be produced in the supposed manner they probably have a quite definite value.

6. Chromosome-linkage

This subject has already been touched on in case of the sex-chromosomes, the X-chromosome, and possibly also the Y-chromosome, being in some cases attached to one of the autosomes (p. 779). Such linkage constitutes a source of definite variation in number that is the reverse of that caused by the presence of supernumeraries. A similar linkage of autosomes with one another is known to take place in some species, especially among insects; and the evidence indicates that it has probably played an important part in the permanent change of number from species to species.

The classical case is offered by *Ascaris megalocephala*, where the chromosomes of the somatic cells, which are small and numerous, are in the cells of the germ-line united in linear aggregates to form larger and fewer chromosomes (p. 323). We might, it is true, reverse this terminology, designating the breaking up of the long chromosomes into smaller bodies in the primordial somatic cells as a process of fragmentation. This, however, is a mere question of terminology which leaves the fact unaltered, and it is rendered improbable by the numbers in related species of *Ascaris* (p. 855).

Most frequently linkage takes place between the chromosomes two by

two to produce so-called "bivalent" elements, each such linkage reducing the apparent chromosome-number by one. Some of the best examples of this are found among the acridian grasshoppers, in which the typical diploid number is 23 or 24, with all the chromosomes rod-shaped and having terminal attachments. This relation is typically shown in *Chortophaga viridifasciata* (Fig. 413, A); but McClung found one male of this species in which

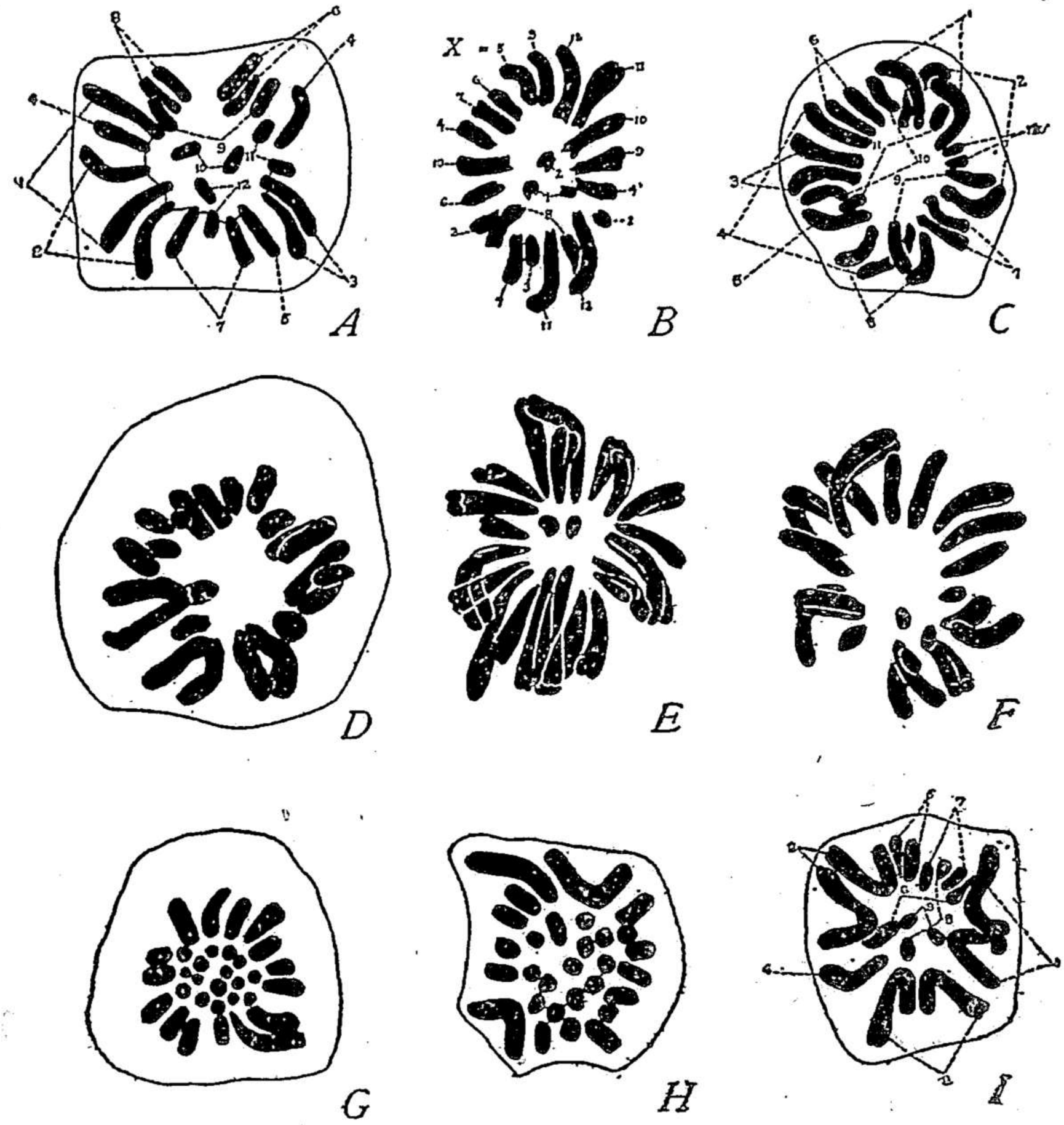

Fig. 413.—Spermatogonial metaphase chromosome-groups in Orthoptera. (*A*, *D*, *E*, *F*, McClung; *B*, Robertson; *C*, *H*, *I*, Davis; *G*, Buchner).

The chromosomes in *A–C* numbered according to their size. In *A–C*, *F*, *G*, all the chromosomes telomitic with no linkage; in *D*, three atelomitic V's, in *H* two, and in *I* six.

A, *Chortophaga*, *B*, *Syrbula*, *C*, *Arphia*, each with 23 rod-shaped telomitic chromosomes; *D*, *Chortophaga* with 20 chromosomes (3 pairs linked); *E*, *Mecostethus; F*, *Tropidolophus* (23 chromosomes); *G*, *Decticus;* (31 chromosomes); *H*, *Steiroxys* (29 chromosomes); *I*, *Stenobothrus* (17 chromosomes).

the number of separate chromosomes was reduced to 19, four of the chromosomes being V-shaped with attachment at the apex of the V (Fig. 413, D). Here, obviously, the apparent reduction in number is due to the linkage of four pairs of the rod-shaped chromosomes, two by two at their inner ends, to form bivalent V's. This condition was found in every visible spermatogonial chromosome-group of this individual. Quite analogous is the case found by L. V. Morgan ('22) in a certain strain of *Drosophila melanogaster*,

in the females of which the two X-chromosomes, normally rod-shaped, are linked together, end-to-end, to form a single V (Fig. 415). Such a chromosome is never found in the male, since all eggs receiving it develop into females (p. 947).

Still more remarkable are the facts in *Hesperotettix* and *Mermiria* (McClung, '05, '17). *H. brevipennis* and *festivus* thus far have shown only the typical acridian relations (23–24 rod-shaped chromosomes), and these likewise appear in certain individuals of *H. viridis*. In other individuals of the latter species, however, two or more of the rods were found to be linked by their central ends (points of attachment), to form V's (as in *Chortophaga*) attached to the spindle by their apices, thus producing an apparent corresponding reduction of number. The linkage may affect either the X-chromosome or the autosomes, X being rarely free and most commonly linked with the largest autosome (Fig. 414). Whatever be the character of the linkage *it is constant for the individual in all the cells of the germ-line* (spermatogonia, spermatocytes) though varying from one individual to another. Thus far six distinct kinds of classes of individuals have been found, as follows:

Class	Linkage	Apparent Spermatogonial Number	Apparent Number in 1st Spermatocytes
1.	No linkage. All the chromosomes free	23 rods	12
2.	X-linked with No. 12 (the largest)	21 rods; 1 V	11
3.	X-linked with No. 9; 11 and 12 linked	17 rods; 3 V's	10
4.	X-linked with No. 8; 11 and 12 linked; 9 and 10 linked.	15 rods; 4 V's	9
5.	X free; 11 and 12 linked; 9 and 10 linked	17 rods; 3 V's.	10
6.	X free; 11 and 12 linked	19 rods; 2 V's	11

The linked forms ("multiples" of McClung) are at once recognizable in the spermatogonia by their V-shaped or J-shaped form (Figs. 413, 414). In the first spermatocyte-division they are likewise distinguishable in size and form, the X-linkage producing the L-shaped type already described, while the autosome-linkage produces large tangential rings or V's of the "*Stenobothrus* or *Tomopteris* type" (p. 530). The second spermatocytes show corresponding relations.

In *Mermiria*, likewise, certain species show no linkage but in *M. bivittata* X is linked with one of the autosomes, producing a V-shaped multiple, the synaptic mate of which is in this case also V-shaped. In synapsis these two V's unite to form a trivalent element ("hexad") showing a complex appearance which formerly led McClung ('05) to conclude that in the first divi-

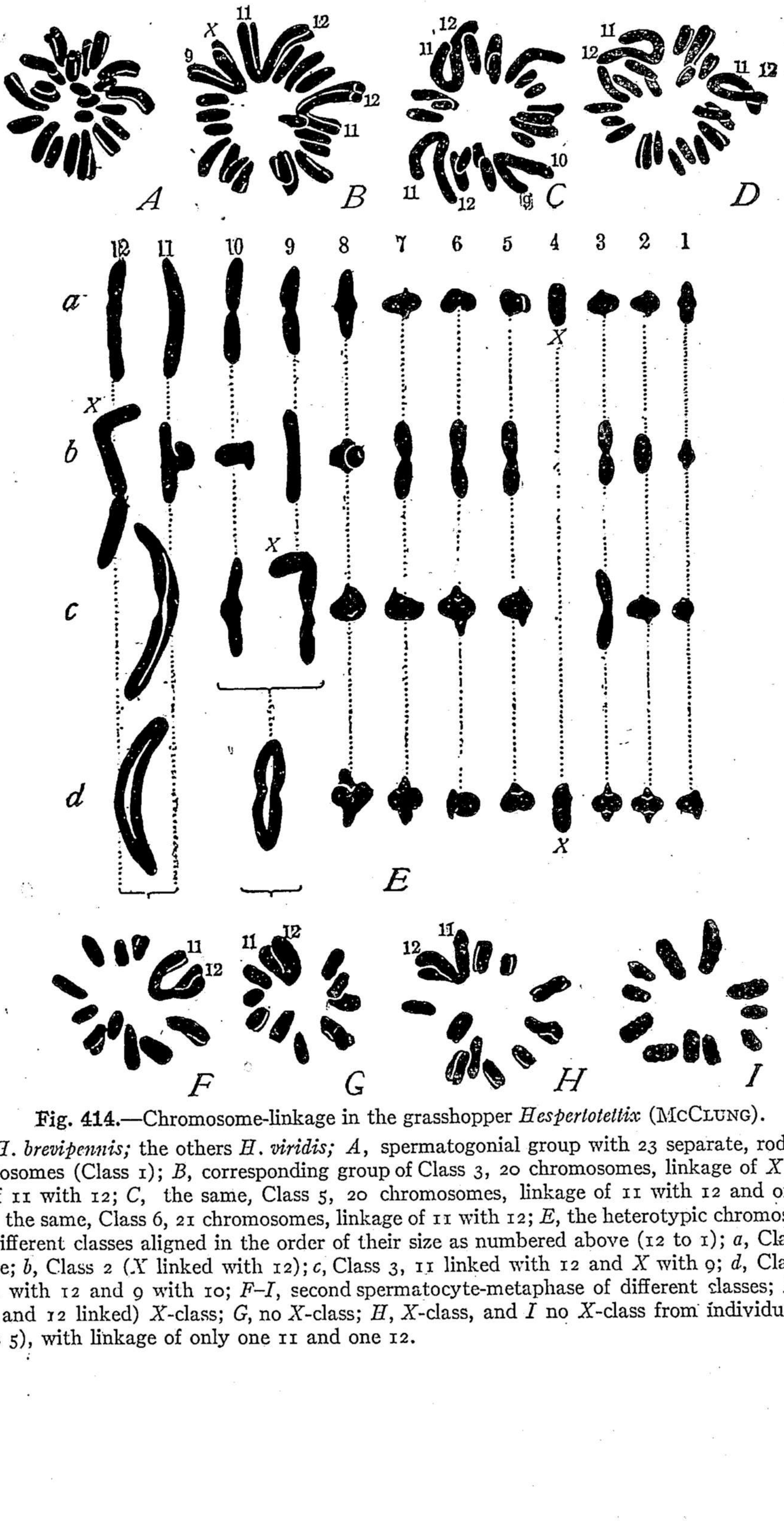

Fig. 414.—Chromosome-linkage in the grasshopper *Hespertotettix* (McClung).

A, *H. brevipennis;* the others *H. viridis; A*, spermatogonial group with 23 separate, rod-shaped chromosomes (Class 1); *B*, corresponding group of Class 3, 20 chromosomes, linkage of *X* with 9, and of 11 with 12; *C*, the same, Class 5, 20 chromosomes, linkage of 11 with 12 and of 9 with 10; *D*, the same, Class 6, 21 chromosomes, linkage of 11 with 12; *E*, the heterotypic chromosomes of four different classes aligned in the order of their size as numbered above (12 to 1); *a*, Class 1, no linkage; *b*, Class 2 (*X* linked with 12); *c*, Class 3, 11 linked with 12 and *X* with 9; *d*, Class 5, 11 linked with 12 and 9 with 10; *F–I*, second spermatocyte-metaphase of different classes; *F*, Class 6 (11 and 12 linked) *X*-class; *G*, no *X*-class; *H*, *X*-class, and *I* no *X*-class from individual like *c* (Class 5), with linkage of only one 11 and one 12.

sion whole bivalents (tetrads) passed to one pole. It is now clear that this trivalent differs from that of *Hesperotettix* only in the fact that both members of the trivalent are V-shaped or J-shaped (atelomitic).

Whether the linkage in these cases is permanent or temporary can only be determined by breeding experiments. In *Ascaris megalocephala* the linkage is clearly permanent from generation to generation in cells of the germline, but in each generation is broken up in all the somatic cells (pp. 323, 879). In the moth *Lymantria monacha* the linkage, as described by Seiler and Hanel ('21) is temporary. Here the diploid number in both sexes, including the gonia, is 62. We should expect the heterotypic division, accordingly, to show 31 bivalent chromosomes; but such is the case only in the female. In the male both divisions show but 28 chromosomes one of which is much larger than the others. The plain inference is that this chromosome represents not one pair but three pairs linked together. Since the diploid number,

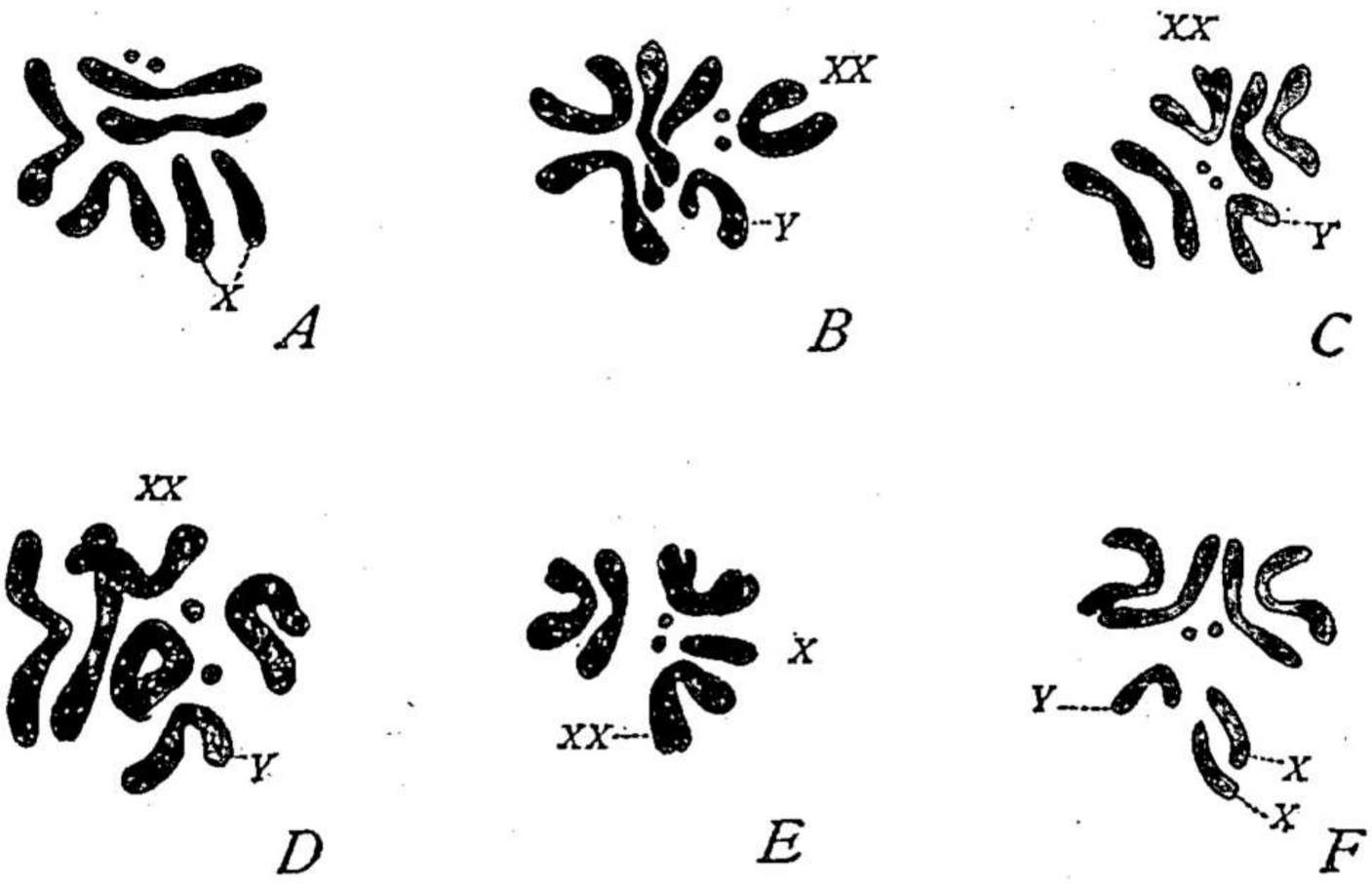

Fig. 415.—Linkage of the *X*-chromosomes in *Drosophila melanogaster* (L. V. MORGAN)

A, normal female diploid group, with two separate rod-shaped *X*'s (BRIDGES); *B*, *C*, *D*, from yellow (sex-linked) females with linked *X*-chromosomes (= *V*) and *Y*-chromosome; *E*, triploid-*X* (*V* + *X*); *F*, nondisjunctional female, with two free X's + Y (BRIDGES).

62, uniformly appears in the blastoderm cells, this linkage must be dissolved at some time, following the formation of the sperm, to be reëstablished at some time prior to the heterotypic division. The validity of this conclusion is established by the conditions seen in the meiosis of the female; for although the first division shows the haploid number (31) of bivalents, *with no large chromosome*, the second division agrees with those of the male in showing but 28, *including one large one*. This can only mean that in the female the linkage takes place after the first division and before the second, while in the male it occurs prior to the first division.[1]

It is evident that linkage, whether permanent or temporary, in no wise alters the nuclear content as a whole. The same nuclear materials are, as

[1] For the linkage in *Solenobia* see Seiler ('22).

it were, done up in packets of different number—in different individuals, or in different cells of one individual—but so distributed as always to ensure the same essential allotment to the daughter-cells and ultimately to the gametes. Genetically, such forms of chromosome-linkage might be expected to be expressed in a corresponding linkage of unit-factor groups; but except in the XX linkage of *Drosophila* (p. 880) this particular phenomenon has not yet been recognized.[1]

VI. PERMANENT CHANGES OF CHROMOSOME-NUMBER

We do not yet know with certainty, even in a single case, precisely how the chromosome-number has changed from species to species; but all points to the conclusion that many such changes first took place as variations of the same types as those above described within the species or individual. In respect to the general phylogeny of chromosomes we know still less. It is not even clear whether a large or a small number of chromosomes represents the more primitive condition. Both sides of this question have been supported by different writers. Montgomery ('01) accepted, rather doubtfully, the former alternative, Haecker ('04) the latter; but neither conclusion was sufficiently based. Both large and small numbers are found among Protista, and in higher forms it does not clearly appear that within the limits of particular groups the more primitive forms have smaller or larger numbers than the higher ones. A study of the facts leads, indeed, to the conclusion that specific changes of number have taken place in both directions, perhaps repeatedly and in many groups; linkage, for example, might cause a decrease, reduplication or fragmentation an increase, non-disjunction a change in both directions. It may, therefore, often be difficult or impossible to distinguish in any particular case between incipient linkage and fragmentation not yet fully fixed. With this in mind we may distinguish provisionally not less than six possible modes of change, as follows:

(1) By a gradual reduction in size and final disappearance of individual chromosomes, a process that may be connected with a corresponding dropping out of genetic factors, or a redistribution involving a transfer of their substance to other chromosomes. (Paulmier, '99.)

Very small chromosomes have been described in many forms, in some cases so minute as almost to suggest vestigial structures. The best known of these cases are the *m*-chromosomes (p. 839) and the Y-chromosomes, in both of which we may trace all gradations from chromosomes of ordinary size almost down to the vanishing point (pp. 768, 823). In case of the Y-

[1] For further remarks on linkage see pp. 887, 938.

chromosome it is almost certain that this process has in many cases culminated in total disappearance, since in a large series of forms the X-chromosome has been left without a synaptic mate. In case of the *m*-chromosomes the case is not so clear, since they seem always to be present in the *Coreidæ*, though in some cases so minute as to appear like vestigial structures (*Archimerus*, *Pachylis*).[1] In the nearly related family of *Pyrrhocoridæ* they are absent, so far as known. As shown especially by Metz ('14, '16) a somewhat similar series is shown in *Drosophila* and other Diptera by the two minute chromosomes that commonly lie near the center of the group. (Fig. 396).

(2) A second and probably widespread mode of change has no doubt been by the occurrence of abnormalities of mitosis, such as non-disjunction. Irregularities thus arising often produce combinations that are unstable (since they tend to break up in the next following meiosis). Nevertheless, a single such irregularity occurring during meiosis or at any other point in the germ-line, will if viable be multiplied many times by mitosis during the ensuing development. The chances of producing new and stable recombinations in the course of later processes of meiosis and syngamy are thus greatly increased; and we here see also how the result of an irregularity affecting even a single chromosome may ultimately appear in both gametic groups. In non-disjunction, for instance, the initial effect is to produce haploid groups of the types $n + 1$ and $n - 1$. Union of such groups with the normal will give respectively $2n + 1$ and $2n - 1$. Meiosis of the first of these may give as gametes $n + 1$ or n; and union of two gametes of the former type may give $2n + 2$, a stable combination having one more pair of synaptic mates. We can thus see how not alone non-disjunction but any other irregularity of distribution may readily become a source of permanent change of chromosome-number, provided the new combinations be viable, and above all if they involve new somatic characters of any value in survival. It is possible, as elsewhere indicated, that the 16-chromosome and 22-chromosome mutants of *Œnothera* may have had such an origin (p. 873), and the varying chromosome-numbers in *Metapodius* (p. 875) or *Datura* (p. 874) illustrate the condition of species now actually passing through such a state of transition.

(3) Analogous to the foregoing, but on a larger scale, is the occurrence of series of numbers of which the higher ones are exact multiples of the lower (polyploidy). Specific differences of this type are closely similar to the corresponding ones shown by different races or individuals such as have earlier been noted in the case of *Ascaris megalocephala*, *Parechinus microtuberculatus*, *Artemia salina* and other forms (p. 870); and they have probably

[1] Wilson ('11).

arisen in the same way. The most striking examples of this occur in plants, *e. g.*, in the species of *Chrysanthemum*, *Hieracium*, *Triticum* or *Musa;* but similar cases are not infrequent in animals, *e. g.*, in *Artemia*, *Asterias*, copepods or sea-urchins. In both cases the higher numbers are often associated with parthenogenesis or apogamy, which in many cases is the only known mode of reproduction, *e. g.*, in certain forms of *Artemia*, *Hieracium*, *Rosa*, or *Alchemilla* (p. 230). In some of these cases higher diploid numbers represent exact multiples of lower ones; but most usually intermediate numbers may also occur. In a considerable number of cases higher diploid numbers represent progressive arithmetical series of a fundamental haploid number; for example, in *Hieracium* (fundamental haploid 9) the specific diploid numbers include 18, 27, 36, and 54; in *Chrysanthemum* 18, 36, 54, 72 and 90; in *Rosa*, 14, 21, 28, 35, 42 and 56 (p. 848); in *Musa* 16, 24, 32 and 48. In many such cases, it is true, a certain number of intermediate numbers also occur; but in some of the series (*Rosa*) the progression is so remarkable as to make its origin by reduplication extremely probable.

The precise manner in which such reduplication has arisen is unknown; but there are many ways in which it may readily have occurred (*cf.* p. 870). One of the most probable is by an incomplete or "suspended" mitosis in the zygote, such as has been actually produced by the artificial induction of monaster-formation in sea-urchin eggs (Boveri, Herbst, and others).[1] This view has been adopted by many writers [2] but it is also possible that doubling may have arisen by the union of two diploid gametes (Stomps, '10), or by nuclear fusion. On the other hand, triploids and other forms that do not fall into the diploid series $2 \times 2 \times 2$, etc., must have arisen by a process involving only one of the gametic groups, such as the union of a diploid and haploid gamete, the union of three gamete-nuclei, or the like.[3] In any of these cases the total relative mass of chromatin is thus correspondingly increased; and, in general, cases of this type may be expected to produce larger cells (and often larger individuals) as is the case in *Œnothera gigas*, or in *Artemia;* but there are important exceptions to this (p. 101). It is however equally possible, as both DeVries and Strasburger have urged,[4] that double numbers may also arise by a *transverse* division or fragmentation which would produce chromosomes of double the number but of smaller size, without altering the sum total of chromatin. An example of this, emphasized by Strasburger, is offered by *Rumex acetosella*, which has 32 chromosomes of half the size of the 16 present in *R. acetosa* and several

[1] See p. 729.
[2] See Gates ('09, '13), Strasburger ('10), Artom ('11), Winkler ('09), etc.
[3] See Gates ('13, '15, '24).
[4] See Strasburger ('10).

other species (Roth, '06), the nuclei and cells being of the same size in the two cases (p. 101).[1]

(4, 5) A fourth and fifth mode of change, both probably important, are linkage and the opposite process of fragmentation, the former leading to a decrease of number, the latter to an increase. These can best be considered together owing to the practical difficulty in many cases of distinguishing between the two.

(a) That linkage is one important source of definite variations in the number and shape of chromosomes within the species is certain. Whether the same can be said of permanent changes of chromosome-number is less certain; nevertheless, there are some cases that find their most obvious explanation under such an assumption. The clearest of them are found among insects, the inter-specific conditions closely duplicating those produced by linkage within the species, as has been emphasized especially by Robertson ('16). Among the locustids, for example, one of the prevalent diploid numbers is 31 (♂), the chromosomes being rod-shaped with terminal attachments. In *Steiroxys trilineata* it is but 29, of which two are V-shaped (Fig. 413). If it be assumed that the latter have resulted from linkage, as in *Chortophaga*, the number becomes 31, as in the related form *Decticus*. Again, in the acridian genus *Chorthippus* (*Stenobothrus*), the male diploid number is but 17 but these include three pairs of V-shaped chromosomes (Fig. 413, I). If each of these be conceived as double, consisting of two rods permanently linked at their central ends (as in *Chortophaga*) the total number becomes 23, the type-number.

Facts of this type make it almost certain that linkage has played an important part in the change of chromosome-number in these animals by the union of rods to form V's, and suggest (as Robertson has especially urged) that the V-shaped chromosomes of other animals may have had such an origin in many cases. Robertson, however, seems to have carried this view too far by overemphasizing the constancy of the point of attachment to the spindle. This is conclusively shown by the recent studies of Carothers ('17) upon *Trimerotropis* and *Circotettix* which demonstrate that in the same species the point of attachment may shift from a terminal (*telomitic*) to a non-terminal (*atelomitic*) point, even in the same chromosome-pair. Thus arise V-shaped chromosomes, of which there may be in *Trimerotropis* from seven to seventeen (Figs. 439, 440), but the spermatogonial num-

[1] On the other hand, in the tetraploid mutant *Primula kewensis*, originally from a sterile diploid hybrid form, Farmer and Digby ('13) showed that the chromosomes, though twice as numerous, were but half as large as before, the original chromosomes having presumably fragmented transversely (as assumed by Strasburger). The total chromatin-mass thus remained unchanged; nevertheless the cells and nuclei were larger than in the diploid individuals in the approximate ratio 5:4. This result is ascribed by the authors to the increase of chromosome-surface.

ber remains 23, as in the type-forms. Again, *Circotettix* has but 21 chromosomes; but not merely one pair but from 4 to 7 pairs may be V-shaped. Here the V-shape of these chromosomes can at best be due to linkage in only two pairs. Clearly, therefore, the shape and mode of attachment is not in itself a safe guide in estimating the nature of V-shaped chromosomes in other animals.

(b) Whether fragmentation, like linkage, has been a cause of permanent change of chromosome-number is a question that will appear in a clearer light after considering the chromosomes as compound bodies. Here we only indicate the strong probability that such has been the case. The clearest evidence of this is offered by the X-element, which, as has been shown, may be either a single chromosome or a multiple group of components, ranging in number from two to eight, that behave as independent chromosomes during the diploid divisions but during meiosis are closely associated in a coherent group that behaves as a unit (p. 772). To regard this as a result of linkage involves great difficulties.

All becomes clear, however, if we assume the whole group to have been originally a simple XY-pair, the X-member of which has undergone a progressive segregation of different materials which, by a process of fragmentation, have finally emerged in the form of separate chromosomes.

In case of the autosomes the case is less convincing, owing to the difficulty of distinguishing between linkage and fragmentation. A good example of this is shown in the genus *Drosophila* and its near allies, in which, as shown by Metz ('14, '16), the number in different species ranges from six (*earlei*) to eight (*melanogaster*, *immigrans*, etc.), ten (*melanica*) or twelve (*funebris*). The diploid groups typically include one pair of very small chromosomes, the others being more or less elongate rods or V's, arranged in pairs, and showing not less than 12 different types in respect to number and shape. Some of these differences may plausibly be explained as a result either of a linkage of rods two by two to form V's or the fragmentation of V's at their apices to form pairs of rods (we know not which). Uncertainty arises, however, from the fact that V's or J's may have arisen from rods (or the reverse process) merely by a change of attachment to the spindle. Such a change certainly has occurred in some species in which the X-chromosome is a V instead of a rod (*Mulleri*, *obscura*, *affinis*, *caribbea* (Fig. 396). Again, *affinis* and *caribbea* are numerically alike in respect to the larger chromosomes; but while both have V-shaped X-chromosomes the former species has in addition three pairs of rods, the latter *three pairs of V's*.[1] The whole case concerning the change of number in *Drosophila* is thereby

[1] The difference of attachment in this case is analogous to that discovered by Carothers in *Trimerotropis* and *Circotettix* (p. 887).

rendered doubtful; and the same may be said of the pretty case of linkage (so-called) in the species of *Notonecta*, as reported by Browne ('10, '13, '16).

The same question arises in respect to the transverse sutures or constriction at certain points in the chromosomes, referred to beyond (pp. 904, 905). That these sutures may often represent points at which fragmentation may take place, has been made probable by Hance in the case of *Œnothera* (p. 878); but in many cases they may equally well be a consequence of linkage. Both linkage and fragmentation are nevertheless undoubted facts; and they facilitate our understanding of how changes of chromosome-number affecting only one or a few chromosomes have arisen. Here, perhaps, lies the explanation of the almost continuous series of numbers observed in some groups (*e. g.*, in copepods, beetles, or aphids) or the interpolation of intermediate or non-conformable numbers in other series which otherwise show a regular progression.

(6) It seems not improbable that chromosome-numbers may have changed by a sudden mutation. Such a process has already been considered under the head of reduplication (p. 870); and it seems probable that mutation may also have produced suddenly new numbers that are neither exact multiples nor fractions of the old. Such a change is suggested, for instance, by the very closely related two species of *Thyanta* (p. 866) in one of which the diploid number is 16, in the other 27, 28; but for the present such a mode of change is purely hypothetical.

(7) Lastly, it is not improbable that changed chromosome-numbers may have resulted from hybridization through irregularities of chromosome-distribution in the meiotic divisions, such as have earlier been indicated;[1] but little is yet positively known of this.

Conclusion. The evidence clearly indicates that specific changes of number may have been effected in several ways, involving sometimes an increase, sometimes a decrease, and that both processes may have taken place, perhaps many times, within the limits of the same groups, often accompanied with little morphological change. All this sustains the conclusion, that the number of chromosomes is of relatively minor importance. What is essential is the materials of which they are composed. Their number represents no more than a particular configuration assumed by these materials in the process of mitosis and meiosis; it is, in the phrase of Fick (though in a very different sense from his) a *tactical formation* of the nuclear constituents, and one that may change from species to species or even within certain limits from individual to individual, without necessarily producing any other visible disturbance of heredity or development. In view of all

[1] *Cf.* Rosenberg, '17, etc.

this, the surprising and significant fact is the fidelity with which within the species the number and relative sizes of the chromosomes adhere to the type.

VII. DIRECT EVIDENCES OF GENETIC CONTINUITY

Attempts to identify the individual chromosomes as such in the "resting" or vegetative nucleus have been completely successful only in exceptional cases. Among these may be recalled the fact that the chromosomes often visibly persist as such during the interphase between the meiotic divisions (p. 532), and during the growth-period of the auxocytes (p. 350); that the sex-chromosomes often persist in the form of chromosome-nucleoli in the spermatocytes (p. 758); and that the X-chromosome often gives rise to a separate and persistent nuclear vesicle in the spermatogonia of Orthoptera (p. 764). These, however, are special cases. We are here interested in the more general aspects of the question as offered by the nuclear cycle in ordinary forms of cells.

1. Relations of the Chromosomes in Telophase, Interphase and Prophase

Rabl ('85) assumed the chromosomes to retain their relative position in the vegetative nucleus (p. 829). Later observers have not succeeded in establishing this by direct observation, except in the case of very rapidly multiplying cells, such as plant root-tips, in which case several observers have concluded that the telophase-chromosomes, though much branched and vacuolated, may still be distinguished as individualized bodies during the interphase and pass over directly into the prophase-chromosomes without complete loss of their boundaries.[1] A parallel to this is found in the history of the chromosomes in the germinal vesicle of the oöcytes in many forms (p. 350).

One of the most successful attempts to attack the problem was made by Boveri ('88, '09) in his remarkable studies on the blastomere nuclei of *Ascaris megalocephala*. These nuclei commonly show a number of finger-shaped lobes, which are formed during the telophases by the free ends of the V-shaped chromosomes (Fig. 416),[2] thus giving landmarks in the resting nucleus to mark the position in which the chromosomes have entered into it. In the prophase the chromosomes (spireme-threads) always reappear *with their free ends lying in these lobes* and continue to occupy this position until the dissolution of the nuclear membrane.[3] In a general way therefore this fact confirms Rabl's assumption and the case was further strengthened

[1] Mano ('04), Strasburger ('07, '08), Grégoire ('06), Bonnevie ('08), Lundegårdh ('12), Schustow ('13), Sharpe ('13, '20), Litardière ('21), Overton ('22).

[2] Van Beneden and Neyt ('87), Boveri ('87, '88).

[3] This has since received repeated confirmation. See Bonnevie ('08, '13), Vejdovský ('12).

by the fact that both the number and the position of the nuclear lobes (and hence of the spireme-threads) vary widely in different cells, *but are alike in sister-cells*. This may readily be observed during the early cleavages of the ovum. In variety *univalens* there are two chromosomes (with four free ends); and the number of lobes varies from one to four, disposed in various ways. In respect to the number and position of these lobes sister-nuclei are mirror-pictures of each other, though with minor variations of

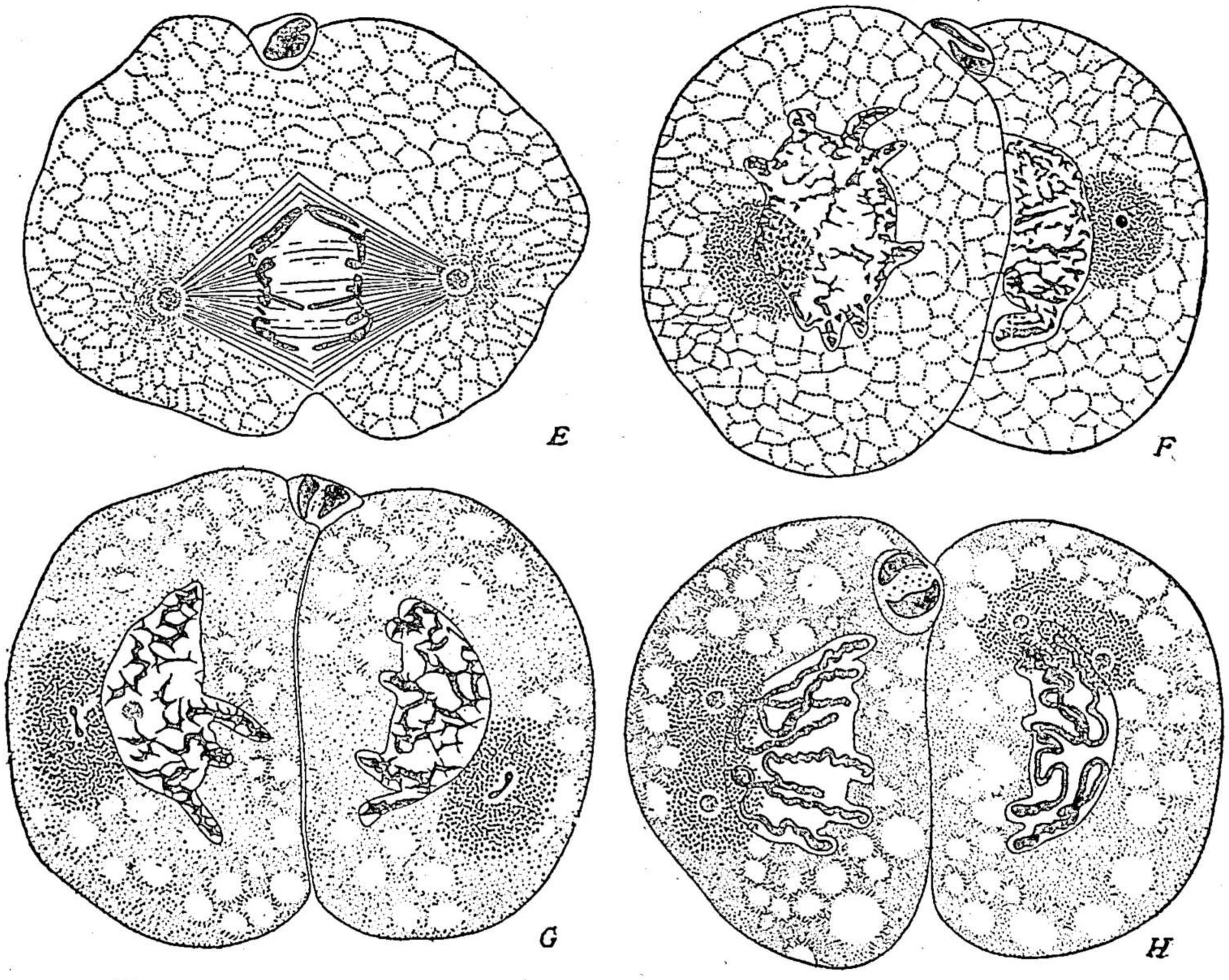

Fig. 416.—Individuality of the chromosomes in the eggs of *Ascaris* (BOVERI).

E, anaphase of the first cleavage; *F*, two-cell stage with lobed nuclei, the lobes formed by the ends of the chromosomes; *G*, early prophase of the ensuing division; chromosomes re-forming, centers dividing; *H*, later prophase, the chromosomes lying with their ends in the same position as before; centers divided.

detail (Figs. 417, 418). Boveri proved, in an elegant demonstration, that *the various observed groupings of telophase-chromosomes and nuclear lobes correspond closely to varying positions of the chromosomes during the prophases and metaphases*. The whole series of facts, therefore, is simply explained by the assumption that whatever be the chance grouping assumed by the chromosomes in the metaphase it is retained with only slight changes through all the subsequent stages, *including the interphase or "resting" nucleus*, until the ensuing prophases. When for example the four free ends are well

separated in the metaphase, four nuclear processes are formed, varying in grouping, but always more or less similar in sister-cells (Fig. 418, D). When two, three or even all four ends are very close together they become inclosed in a single process (418, C). Both the number and the grouping of the processes depend, therefore, on the grouping of the chromosomes, which varies continually from one mitosis to another owing to displacements in the later prophases.

Evidence of the same kind, but in some respects more direct, has been found in the spermatogonial divisions of grasshoppers where, as shown by Sutton ('00, '02), in *Brachystola*, the nucleus likewise often shows finger-shaped lobes corresponding to the telophase-chromosomes. In the telophases the chromosomes, without losing their polarized disposition, lose their homogeneous appearance, become granular or alveolized, and are finally transformed into elongate vesicles or karyomeres, which may give

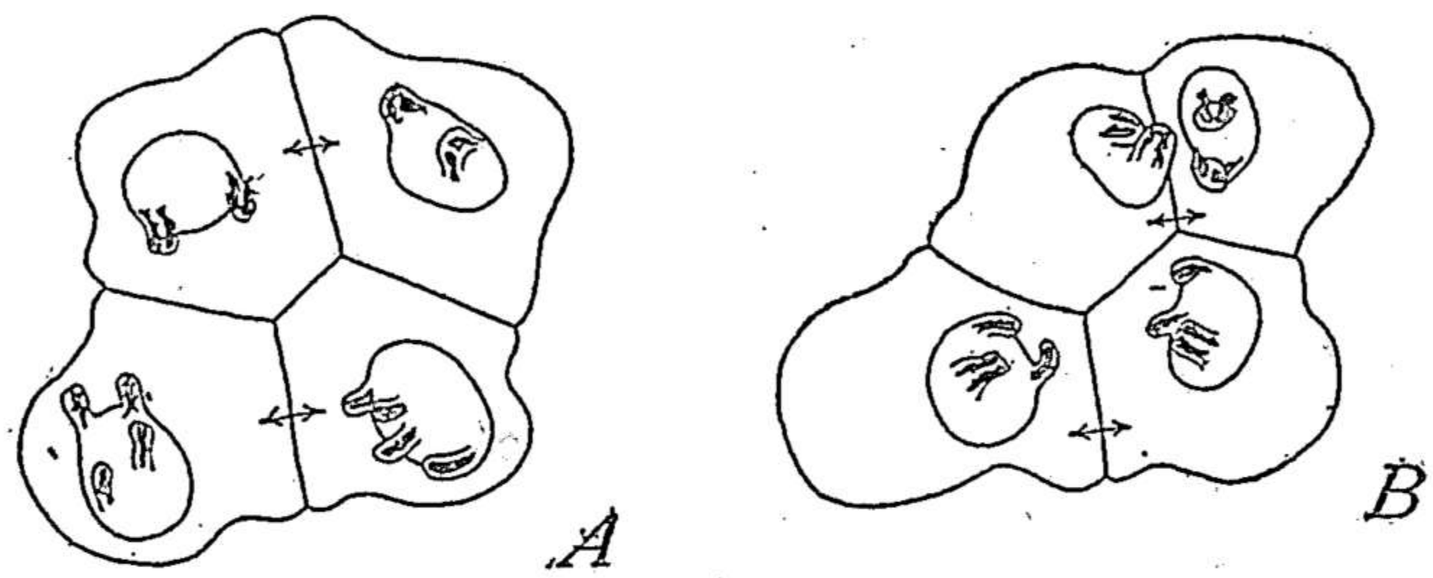

Fig. 417—Chromosome-grouping in sister-cells, 4-cell stages of *Ascaris megalocephala univalens* (Boveri.).

quite the appearance of small separate nuclei.[1] For a time, therefore, the nucleus appears to be composed of separate compartments; and this may persist more or less clearly during the whole interphase. As a rule the vesicles in later stages undergo partial fusion at their peripheral ends, leaving their opposite (central) ends free, in the form of lobes like the fingers of a glove, that are obviously comparable to those of *Ascaris*, as described above. These processes often persist during the whole resting-stage, and even in the main body of the nucleus distinct indications of the vesicles are often clearly visible at every stage (Fig. 361). *In the prophases a single spireme-thread is formed in each vesicle or process*, quite as in *Ascaris*, but the case is here even stronger owing to the partial persistence of the chromosome-boundaries throughout the resting-stage. (Figs. 265, 422.)

Still greater weight is given to this conclusion from the history of the X- or accessory chromosome which passes through essentially the same changes as the autosomes, with the important difference that the telophasic vesicle

[1] This account has been confirmed by many later observers (McClung, Davis, Pinney, Robertson, Wenrich).

to which it gives rise never fuses with the others but retains its identity at every stage, giving exactly the appearance of a small independent nucleus lying close beside the principal one and distinguished by its lightly

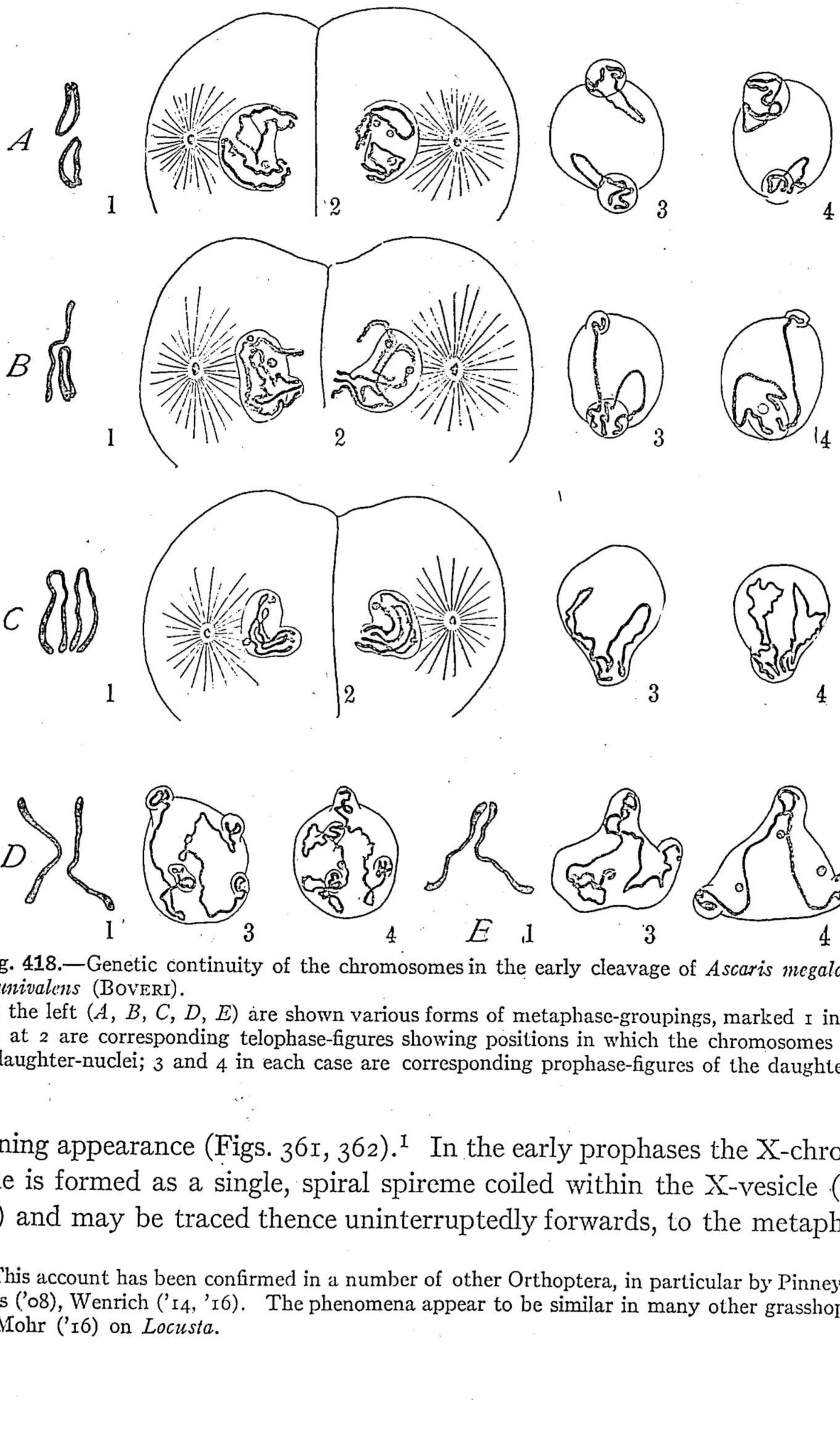

Fig. 418.—Genetic continuity of the chromosomes in the early cleavage of *Ascaris megalocephala univalens* (BOVERI).

At the left (*A*, *B*, *C*, *D*, *E*) are shown various forms of metaphase-groupings, marked 1 in each case; at 2 are corresponding telophase-figures showing positions in which the chromosomes enter the daughter-nuclei; 3 and 4 in each case are corresponding prophase-figures of the daughter-nuclei.

staining appearance (Figs. 361, 362).[1] In the early prophases the X-chromosome is formed as a single, spiral spireme coiled within the X-vesicle (Fig. 361) and may be traced thence uninterruptedly forwards, to the metaphase.

[1] This account has been confirmed in a number of other Orthoptera, in particular by Pinney ('08, Davis ('08), Wenrich ('14, '16). The phenomena appear to be similar in many other grasshoppers See Mohr ('16) on *Locusta*.

In case of this chromosome, therefore, no doubt can exist as to its genetic continuity throughout many generations of cells.

In agreement with this is the evidence in respect to the chromosomal vesicles of segmenting ova and embryonic cells. Many earlier observers had noted the irregular or polymorphic form of the cleavage-nuclei and showed [1] that it was due to an incomplete fusion of the karyomeres at the close of mitosis in rapidly dividing cells. Conklin found that exceptionally the karyomeres might remain separate through the whole of the resting-

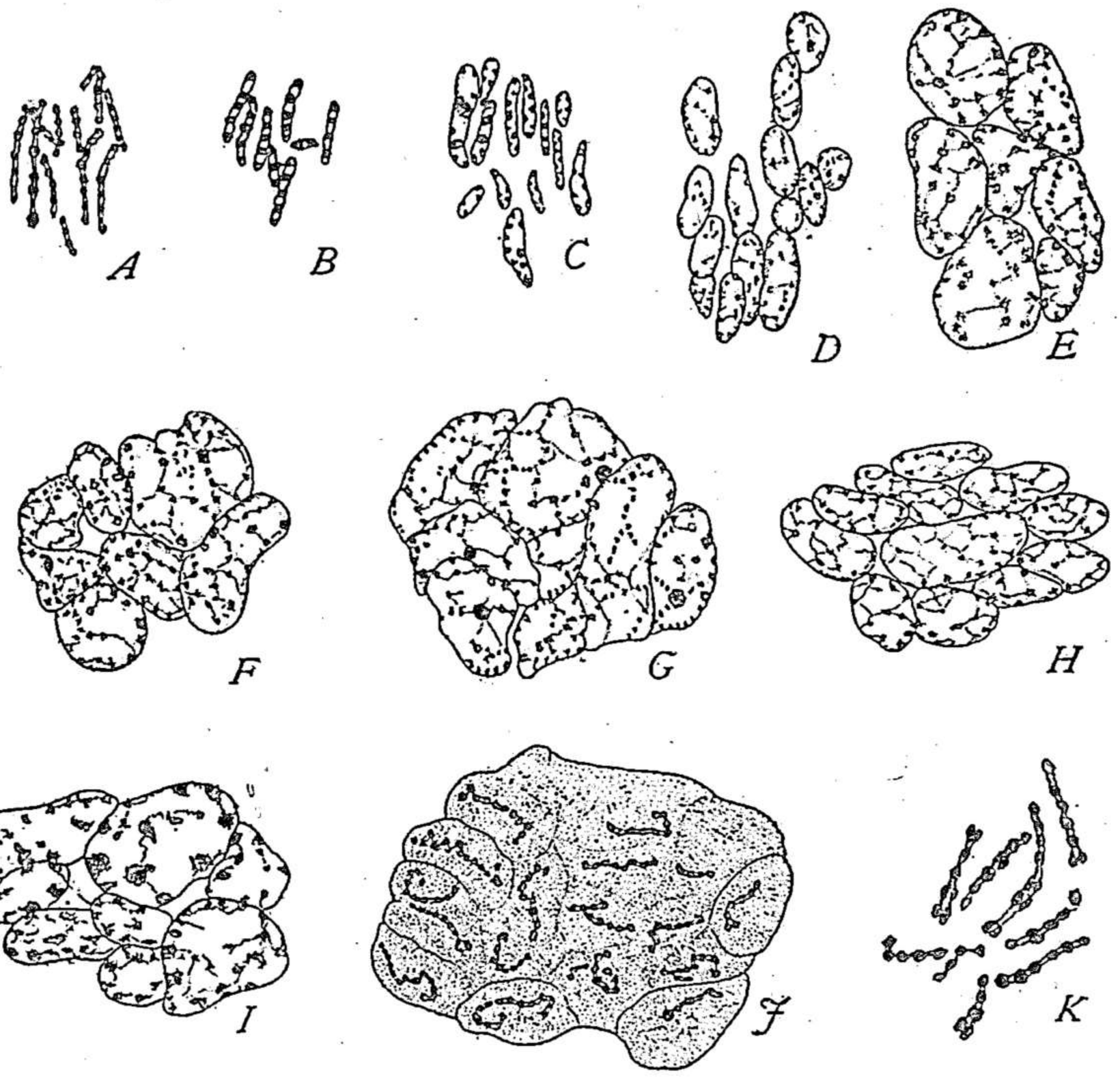

Fig. 419.—Chromosomes and karyomeres in the cleavage of the egg of the fish *Fundulus* (RICHARDS).

A–D, successive stages in transformation of the anaphase-chromosomes into karyomeres; *E*, *F*, final telophases; *G*, "resting" nucleus; *H*, *I*, early prophases; *J*, new chromosomes forming separately inside the old karyomeres; *K*, metaphase-chromosomes.

period, showing the structure and behavior of miniature nuclei. More recently Richards ('17) likewise found that in the cleavage of the teleost *Fundulus* the karyomeres do not at any time undergo complete fusion, but only become closely appressed, the partitions between them being more or less completely retained at every stage up to the ensuing prophases. The new chromosomes arise, each endogenously within one of the vesicles, the latter finally breaking down and disappearing as the prophases advance (Fig. 419). In such cases the karyomeres are seen not only in the telophases but in the *prophases* of mitosis. A striking example of this type

[1] See Conklin ('02), Rubaschkin ('05), Beckwith ('09), Boveri ('07), etc.

occurs in the prophases of the first polar spindle of the gasteropod *Haminea*,[1] where the chromosomes first appear in the form of irregular vesicles within each of which is formed a condensed chromosome (tetrad). Still more remarkable is the case offered by the mite *Pediculopsis* [2] in which the karyomeres remain completely distinct during the early cleavages throughout the whole mitotic cycle, each assuming a spindle-shape during mitosis and developing internally a thread-like chromosome that splits lengthwise and then separates into two parts. In this process (called by Reuter *merokinesis*) and the foregoing ones, the prophase-karyomeres seem clearly to correspond to the alveolized prophase-bands in the root-tips of plants.

When we consider the various intergradations that connect the foregoing cases with less extreme ones we can hardly avoid the conclusion that even vegetative nuclei of the ordinary type must consist of definite areas or regions, each the product of a single chromosome and each the fundamental basis of a future corresponding chromosome (Boveri, '01, '04). These same facts clearly show, however, that the chromosomes are not to be regarded as fixed bodies that persist unchanged from one cell-generation to another. They grow, become vacuolated and often branched, and give rise to linin, nuclear sap, in some cases to the nuclear membrane. Only a small part of the complex thus produced is preserved in the ensuing mitosis. We cannot therefore properly speak of a persistent and unchanged *individuality* of the chromosome, but only of a genetic continuity such that each new chromosome is derived from a portion of its predecessor.

Boveri suggested that the persistent portion might completely lose its colorable (basichromatic) component only regaining it as the next division approaches; and out of this grew a controversy as to whether the basis of chromosome-continuity is "chromatin" (basichromatin) or "achromatin" (oxychromatin or linin). The latter view, adopted by Haecker ('02, '05), Strasburger ('04), Montgomery and others, has received definite support from those cases, earlier referred to, in which the chromosomes undergo a more or less complete loss of basophily during the growth period of the auxocytes without loss of their morphological identity (pp. 350, 545). This, however, is a question of secondary importance; for the theory of the genetic continuity of chromosomes need for the present go no further than to maintain that the old chromosome passes on to the new a portion of its own substance which somehow carries with it the essential features of its own organization. That the continued presence of "chromatin" (*i. e.*, basichromatin) is essential to the genetic continuity of the chromosome has, however, become an antiquated notion (p. 653).

[1] Smallwood, '01.

[2] Reuter ('09).

2. The Chromonema-hypothesis

The most noteworthy fact established by the foregoing observations is the endogenous formation of new chromosomes, each in the form of a fine spireme-thread inclosed within its predecessor; and out of this fact, now conclusively demonstrated in certain cases, grew the chromonema-hypothesis of Bonnevie and Vejdovský (p. 136). The existence of a finely coiled basichromatic thread (chromonema of Vejdovský) during the anaphases and telophases, early reported by Barenecki ('80) in the pollen-mother-cells of *Tradescantia*, was again briefly described in the telophase-chromosomes of the spermatogonia of urodeles by Janssens ('01), who found the thread coiled more or less definitely around the periphery of the chromosome and imbedded in an "achromatic" basis of "plastin." The first germ of the chromonema hypothesis appears in his suggestion that this thread may be identical with the spireme which is seen unraveling from the prochromosomes or chromatin-blocks in early prophases of the ensuing division ('01, p. 58). This idea was developed in greater detail especially by Bonnevie and later by Vejdovský,[1] both of whom believed the telophase chromonema to be converted directly into the nuclear framework and in the ensuing prophase to give rise directly to the early spireme. In evidence of this both found that in *Ascaris* the spiral prophase spireme-threads reappear with their free ends in the nuclear lobes originally formed by the ends of the telophase-chromosomes, as described by Boveri (Fig. 59).

Bonnevie argued from this that "the nuclear network arises . . . from thin, spirally coiled threads, which have arisen endogenously in the old chromosomes; and these threads develop in the prophase directly into the chromosomes of the following mitosis . . . ." ('08, p. 470). In rapidly dividing cells (root-tips) Bonnevie believed that the telophase-spirals may still be distinguished more or less clearly in the vegetative nucleus so that the individuality of the chromosomes is never wholly lost at this time.

The conclusions of Vejdovský ('12), especially in the case of *Ascaris*, were essentially similar. Like Janssens, he gives a circumstantial account of how in the telophases the chromosomes swell up and finally unite, their achromatic axial portions giving rise to the nuclear sap and membrane while the coiled peripheral thread produces the general framework. The thread itself is said to arise by the linear aggregation of originally scattered, minute basichromatic granules or chromioles.[2]

Bonnevie first found the prophase-spiral or chromonema in the anaphases or telophases of the preceding mitosis and believed this spiral to persist as

[1] See references at p. 136.

[2] *Cf.* Dobell's account of the formation of the spiral nuclear thread of bacteria from scattered chromidial granules, p. 84.

such during the interphase, uncoiling to form the prophase-spireme, and splitting lengthwise. Vejdovský's conclusion comes to the same in the end, but is complicated by the additional conclusion (in *Ascaris*), that the original chromonema first arises within the *prophase*-spireme. While, therefore, the latter, considered as a whole, splits lengthwise (as concluded by Bonnevie), the same is not true of the new chromonema, the close coils of which seem to break up more or less into rings or discoid chromomeres (Fig. 59). In either case the new chromonema is cut *crosswise* at more or less regular intervals by fission of the thread as a whole. How the continuous anaphase- or telophase-chromonema is formed from their products remains undetermined and the whole hypothesis is thereby materially weakened. As will presently be seen, however, Vejdovský's conclusions on this particular point have to a certain extent received support from the recent work of Martens (p. 898). Bonnevie ('13), on the other hand, was unable to find either spiral or rings in the metaphase-chromosomes.

The chromonema-hypothesis involves the three main postulates, each of which has been called in question by other observers. These postulates are: (1) The presence of a definite spiral or zigzag thread in the anaphase or telophase-chromosomes from which is formed the framework of the interphase-nucleus; (2) the identity of the prophase-threads, individually considered, with those of the preceding telophase; (3) the longitudinal splitting of the thread during the prophase or an earlier period. We may briefly consider these in order:

(1) Definite anaphasic or telophasic spiral formations have been described by a few other observers;[1] but some of them describe the spirals as longitudinally double, consisting of two interlacing threads (Brunelli, Schneider) while another finds the spiral single, temporary, and not in the form of a separate thread but rather a transitory ridge on the surface of a chromatic axis (Lee). A considerable group of careful observers have, however, concluded that the appearance of a coiled thread is but an optical illusion due to the vacuolization of the anaphase and telophase-chromosomes, leaving the partition-walls so disposed as to offer the appearance of a contorted, zigzag or coiled thread (Fig. 55).[2] Martens, however, in one of the most recent studies of the subject gives a very circumstantial account of the formation of a true telophasic chromonema (Fig. 420), irregularly zigzag or convoluted, and arising by a differentiation of the chromosome into an "achromatic" core and a single basichromatic peripheral thread.

[1] Brunelli ('10) in the grasshopper *Tryxalis*, Schneider ('11) in Amphibia; and Bolles Lee in the plant *Paris* ('13), and more recently ('20) in urodeles, insects and other cases.

[2] Among these may be named especially Sharp ('13, '20), and Litardière ('21), whose conclusions concerning the telophasic vacuolization are closely akin to those of Grégoire and other observers referred to above. See also Kuwada ('21), Overton ('22).

In this respect his account is close to that of Bonnevie and Vejdovský save for the irregularity of the thread; but otherwise it is wholly different.

(2) The proof that the prophase-threads are identical with the telophasic chromonema involves the same difficulties encountered under any hypoth-

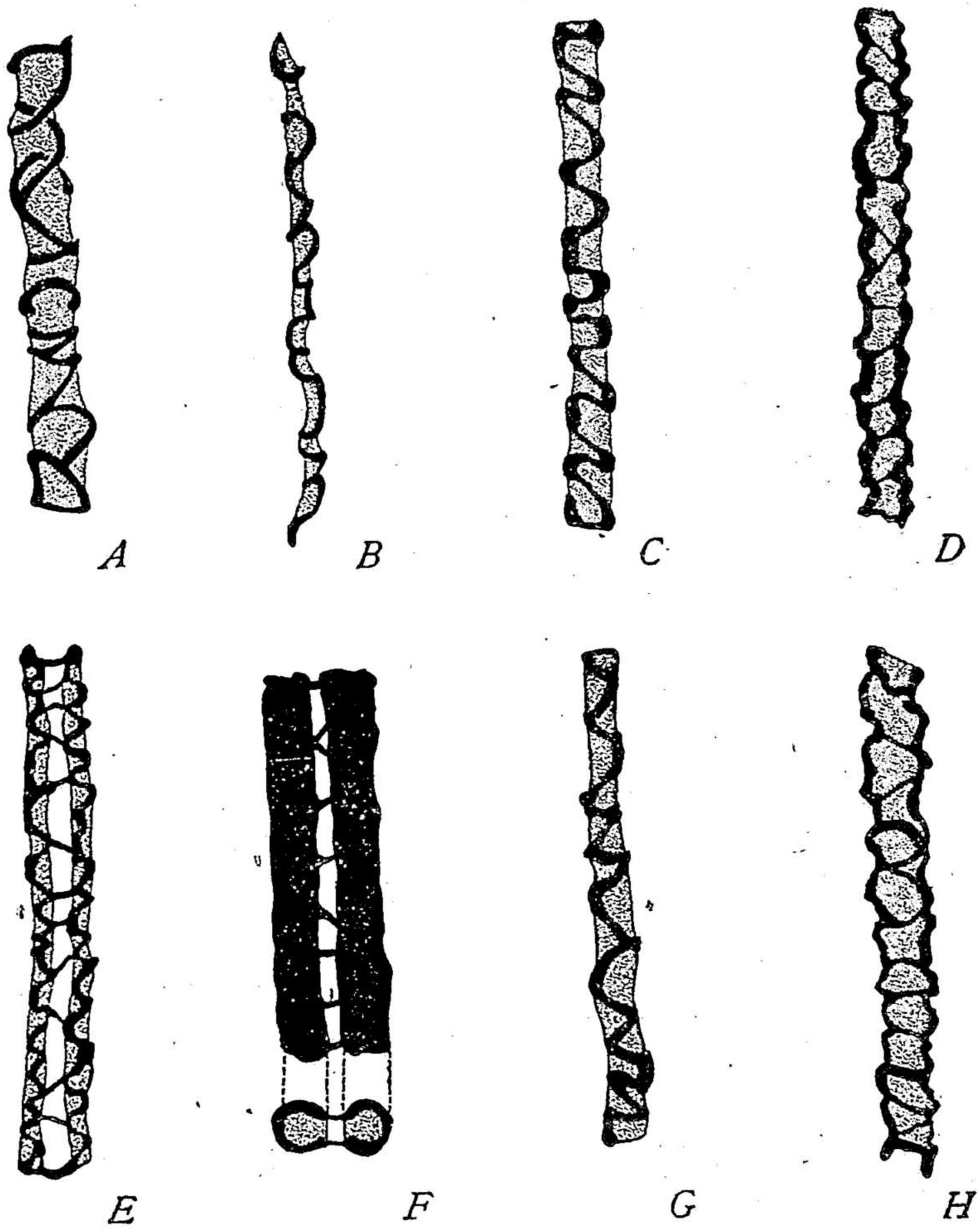

Fig. 420.—Scheme of the chromonema in the seed-plant *Paris* (MARTENS).

A, portion of the early prophase-thread; *B*, its elongation; *C*, *D*, bilateral accumulation of the chromonema-substance; *E*, *F*, longitudinal division; *G*, early telophase; *H*, later telophase, semblance of longitudinal duality.

esis of genetic continuity. Bonnevie's belief that the spirals might often be distinguished as such even in the vegetative nucleus still lacks confirmation, and even if correct the fact may be explicable because in rapidly dividing meristem-cells the nuclei often do not return completely to the "resting" state (p. 890). The substantial evidence on this point is thus practically limited to the fact, that the prophasic spiral threads in *Ascaris* reappear with their free ends in the nuclear lobes which

represent the free ends of the preceding telophase-chromosomes, as described by Boveri.

There are, however, many other facts to be taken into account. No doubt can now exist that the early prophasic spireme-threads often show a fine, contorted, zigzag or even spiral appearance, later uncoiling or straightening out as they shorten and thicken (Figs. 55, 422). It is also certain that in many cases the fine contorted threads arise by uncoiling or unravelling from larger or massive bodies (p. 902);[1] and that in some cases the prophasic spiral formations are formed in the interior of the vesicles or karyomeres resulting from enlargement of the telophase-chromosomes. Such cases differ only in degree from those earlier mentioned (p. 121) in which the spireme-threads disentangle themselves from localized areas of

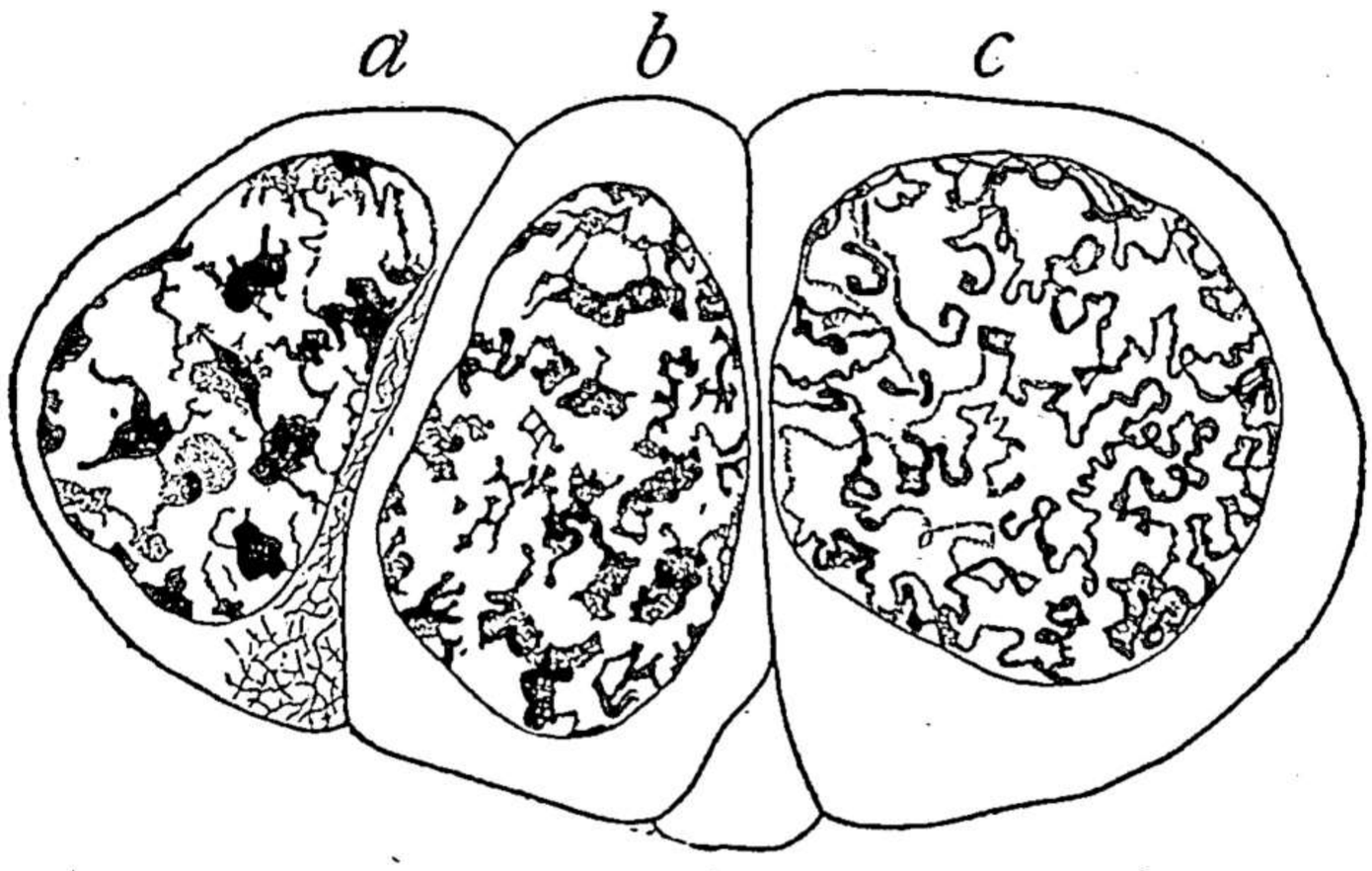

Fig. 421.—Spermatogonial prophases in the newt *Triton* (JANSSENS).

a, early stage with chromatin-blocks (chromatin-nuclei or prochromosomes); *b*, resolution into convoluted threads, which in *c* have uncoiled to form the early spireme.

the nuclear framework which become marked off in the earliest prophases[2] and, as several recent observers have especially emphasized, are closely similar to the alveolized telophase-chromosomes.[3] A step beyond brings us to cases where the threads arise by a spinning out or internal regrouping of the substance of more or less massive chromatin blocks or bodies (chromocenters or prochromosomes) as described for instance by Janssens ('01) in the spermatogonial prophases of *Triton* (Fig. 421) and more particularly by Davis ('08) and many later observers in the presynaptic nuclei of Orthoptera, by Wilson ('12) in those of Hemiptera, or by Nonidez ('10) in those of Coleoptera (Figs. 266–288).

All points to the conclusion that in these various cases, whether chromosome-vesicles, localized nuclear areas or massive prochromosomes, we are dealing with chromosomes, variously modified, derived severally from the

[1] *Cf.*, Wilson ('12, '13, '14).

[2] Mano ('04), Grégoire ('06).

[3] See especially the above cited works of Sharp, Litardière and Martens.

telophase-chromosomes and destined to give rise each to one of the prophase threads. All this, evidently, harmonizes with the chromonema-hypothesis; its present weak point, evidently, is the telophasic chromonema.

(3) Concerning the third postulate, all observers, with two exceptions, have found that the prophase-threads split lengthwise, in preparation for the ensuing metaphase. The first exception is offered by Bolles Lee's account ('20), of the phenomena in the seed-plant *Paris*, where these threads are said to be longitudinally double in consequence of a *transverse* division of the preceding V-shaped anaphase-chromosomes at the apices of the V's. This result, contradictory of those of so many other good observers, and

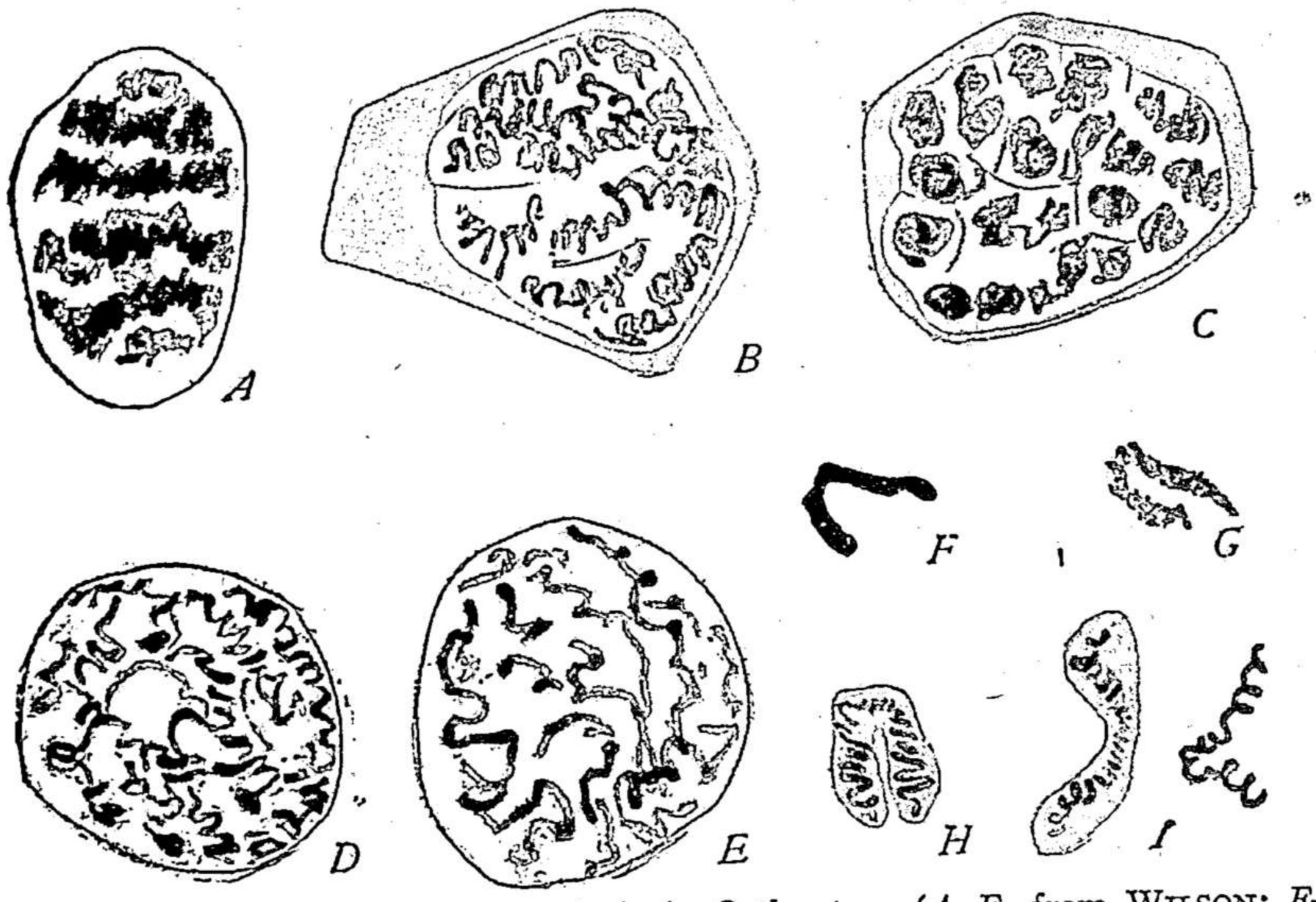

Fig. 422.—Prophasic chromonema-formations in Orthoptera (*A–E*, from WILSON; *F–I*, from MOHR).

A, early spermatogonial prophase of *Phrynotettix*, side-view, polarized massive bodies, which in *B* and *C* (polar view) are seen uncoiling in the form of spiral threads; *D*, *E*, later stages; *F*, the *X*-chromosome of *Locusta*, last spermatogonial telophase; *G–I*, successive stages in its transformation into a vesicle containing a coiled thread.

evidently inapplicable to rod-shaped anaphase-chromosomes, is specifically denied by Martens ('22), after a reëxamination of the facts in the same species. This observer, however, in his turn, contradicts his predecessors by denying that the zigzag chromonema within the original prophase-spireme *is set free or straightens out to form a single fine thread.* On the contrary, the whole spireme is said to shorten and thicken, while the chromonema retains its spiral or zigzag disposition. Its substance now concentrates on opposite sides, until the chromosome gives an appearance of longitudinal duality, and finally splits lengthwise, the cleft cutting across the delicate turns of the spiral, by which the two halves are at first connected (Fig. 420). According to this account, similar in principle to that of Vejdov-

ský (p. 897), there is no longitudinal division of the chromonema at any period. Martens describes an appearance in the anaphase- and telophase-chromosomes that is closely similar except that the concentration of the chromonema on opposite sides does not in this case lead to actual longitudinal division.

How to harmonize these results with the chromonema-hypothesis, does not yet clearly appear; but in the judgment of the writer it seems impossible to doubt that the finely coiled or convoluted prophase-threads do in many cases actually uncoil and split lengthwise.[1] Until these doubts and discrepancies have been cleared up, however, the chromonema-theory of genetic continuity must await further critical study.

3. The Prochromosomes

In the foregoing section the prochromosomes have been treated somewhat incidentally as an interesting but inconstant element in the mitotic process.

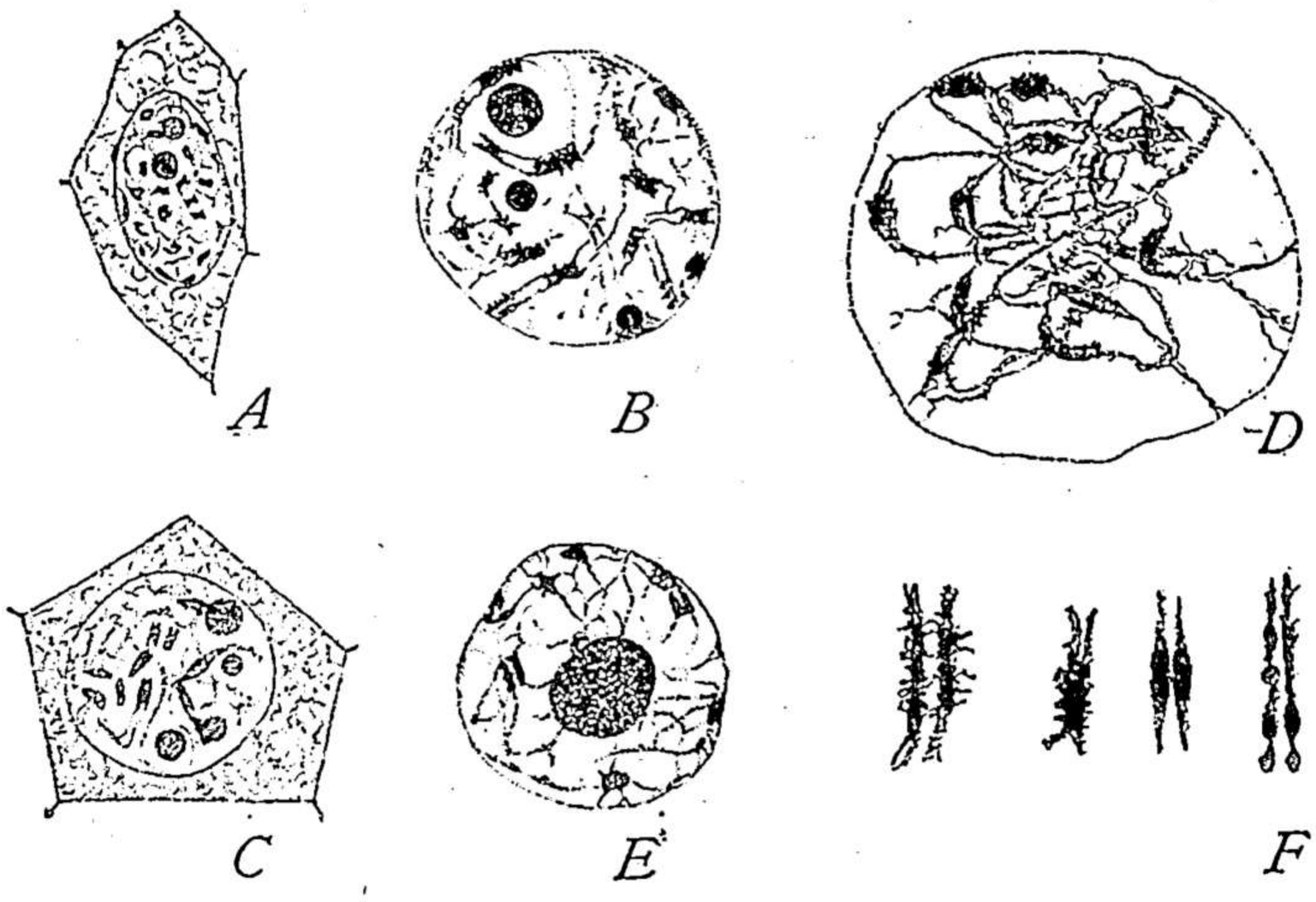

Fig. 423.—Prochromosomes in the early meiotic stages of seed-plants (OVERTON).

A–D, Thalictrum; E, F, Calycanthus.

A, somatic nucleus from anther-wall; *B*, *C*, *E*, young pollen mother-cells; *D*, early synizesis (more enlarged); *F*, paired prochromosomes before and during synizesis.

Attempts to give them a more general significance have been made by observers who were struck by the fact that the nuclei of the vegetative cells in higher plants in some cases contain numerous karyosomes which are approximately the same in number as the chromosomes.[2] A study of the behavior or these bodies in various plants led Overton to the conclusion that under favorable conditions of growth the nuclei may contain an

[1] See the figures and photographs in partial illustration of this in the early prophase of the spermatogonia of grasshoppers (Wilson, '12) and also the figures of earlier observers there cited.

[2] Rosenberg ('04, '09) in *Drosera;* Overton ('05, '09, '11) in *Thalictrum, Helleborus, Podophyllum,* etc.; Laibach ('07) in *Cruciferæ;* Tischler ('10) in *Musa;* and others.

excess of chromatin, a part of which remains aggregated about definite centers without passing out into the framework formed by the chromosomes. Around these centers the remaining chromatin collects to form the definitive chromosomes as the cell prepares for division (Fig. 423). Overton found the prochromosomes both in the vegetative somatic nuclei of various plants and in the presynaptic nuclei, where they conjugate two by two as they pass into synapsis. He also found the prochromosomes arranged in pairs in the somatic nuclei (in *Calycanthus* and *Podophyllum*); so that the synaptic mates are already associated in pairs when they enter the reconstruction-stages of the germ-nuclei ('09, p. 52). Overton describes the prochromosomes of the early prophases as local accumulations of chromatin in the spireme-thread, as first often more or less elongated, but later shortening and thickening to form the chromosomes while the intervening strands of "linin" disappear.

The phenomena on which this interpretation was based have therefore been closely examined by many cytologists. The prochromosome theory has been strongly supported, especially by Overton and by Rosenberg, and a number of other cytologists have described conditions more or less in accordance with the theory.[1] A remarkable case is that of the sedge, *Carex aquatilis*, in which Stout found about 74 small prochromosomes which could be traced continuously in both the somatic and the meiotic divisions throughout all stages excepting the synaptic knot. On the other hand, many observers have found the number of "prochromosomes" or karyosomes to be in many cases variable and often greater or less than that of the chromosomes.[2] They seem often to be quite absent; and their number and size are said to vary materially with the mode of fixation under different conditions of nutrition and apparently also with the length of the interkinesis. Rosenberg concludes, for instance, that the karyosomes are more distinct and more constant in number in the stages of "complete rest."

For these reasons the prochromosome-theory has thus far failed to provide an adequate basis for a general theory of chromosome-continuity; but the observed facts nevertheless are of much cytological interest. It is probable that prochromosomes are related on the one hand to chromatin-nucleoli or karyosomes, on the other to the chromatin-blocks, massive bodies, or nuclear areas from which the spireme-threads so often arise (pp. 122, 539). In all these cases we are dealing with localized reservoirs of

[1] *Cf.* Yamanouchi ('06), Davis ('07), Malte ('08), Tahara ('10), Frisendahl ('12), Stout ('13), and Lundegårdh ('13).

[2] *E. g.* Allen ('06), Miyake ('06), Laibach ('07), Grégoire ('07), Sykes ('08), Mottier ('07), Lewis ('08), Lundegårdh ('08, '12,' 13), Gates ('08, '10, '11), Geerts ('09), Strasberger ('05, '09), Digby ('10, 14), De Smet ('14), Litadière ('21).

basichromatin which (as was recognized by Flemming) is destined ultimately to enter into the formation of chromosomes. In the case of chromosome-nucleoli (sex-chromosomes, etc.) or of karyospheres it is evident that these chromatin-nucleoli represent chromosomes or groups of chromosomes. It is equally clear that the prochromosomes of the presynaptic stages of insects likewise represent chromosomes. There is, therefore, no reason to doubt that in some cases the prochromosomes described in the vegetative nuclei of plant-cells really are such, and that some of the observed variations in number may be due to the fact that they may often represent only portions of chromosomes, or several chromosomes united (as is certainly the case with karyospheres, p. 93).[1]

It is important to bear in mind the fact that very often, both in the presynaptic stages and in somatic prophases, no trace of prochromosomes can be discovered; and even when such bodies are unquestionably present (as in the presynaptic stages of insects), they very rarely if ever arise directly from the telophase-chromosomes [2] but from a net-like stage in which the telophase-chromosomes are for a short time at least lost to view (p. 536).

VIII. ORGANIZATION OF THE CHROMOSOMES

There are many grounds for the conclusion that the chromosomes possess a complex and definite internal organization, and one that varies not only from species to species but also from one chromosome to another in the same species. The most cogent of this evidence is perhaps that offered by genetic experiment (p. 949); but although the direct cytological evidence still lags behind, it points unmistakably to the same conclusion.

1. The Chromosomes as Compound Bodies

The metaphase-chromosomes often show no visible structure, appearing as nearly or quite homogenous bodies. That they are nevertheless to be regarded as compound bodies at this time is proved both by their earlier history and by comparative studies. The fact is obvious in cases of linkage; and equally convincing is the evidence offered by the multiple X-element in various species of insects, and nematodes, such as *Ascaris incurva* or *lumbricoides*, *Gelastocoris*, *Acholla multispinosa*, etc. (pp. 772–779). All the evidence indicates that this is not due to linkage in the ordinary sense, and that the group as a whole corresponds to the single X-chromosome

[1] *Cf.* Rosenberg ('09), Lundegårdh ('09, '13).

[2] Such a mode of origin is described by Janssens ('05) for the "chromoplast" or karyosome of the early spermatocytes of *Batracoseps*, by B. M. Davis for the "chromatin bodies" of the premeotic nuclei of *Œnothera* and by Lundegårdh ('13) in *Cucurbita*. The same was believed to be the case by Montgomery and some other observers for the presynaptic prochromosomes in insects.

of other forms. We might consider its multiple character as a simple fragmentation; but this leaves unexplained the remarkable fact that *the X-components are constant not only in number but in size-relations*, the latter often extremely marked and characteristic. No other explanation of this is apparent save that these components are qualitatively different. The force of these facts is evident when we consider, for example, the remarkable X-chromosome of *Notonecta indica*, in which X likewise consists of several components during the late prophases, metaphase and anaphases of the heterotypic division, but in the spermatogonia appears as a single and simple chromosome (Fig. 424). A slight increase of independence on the part of these components would cause them to appear as separate chro-

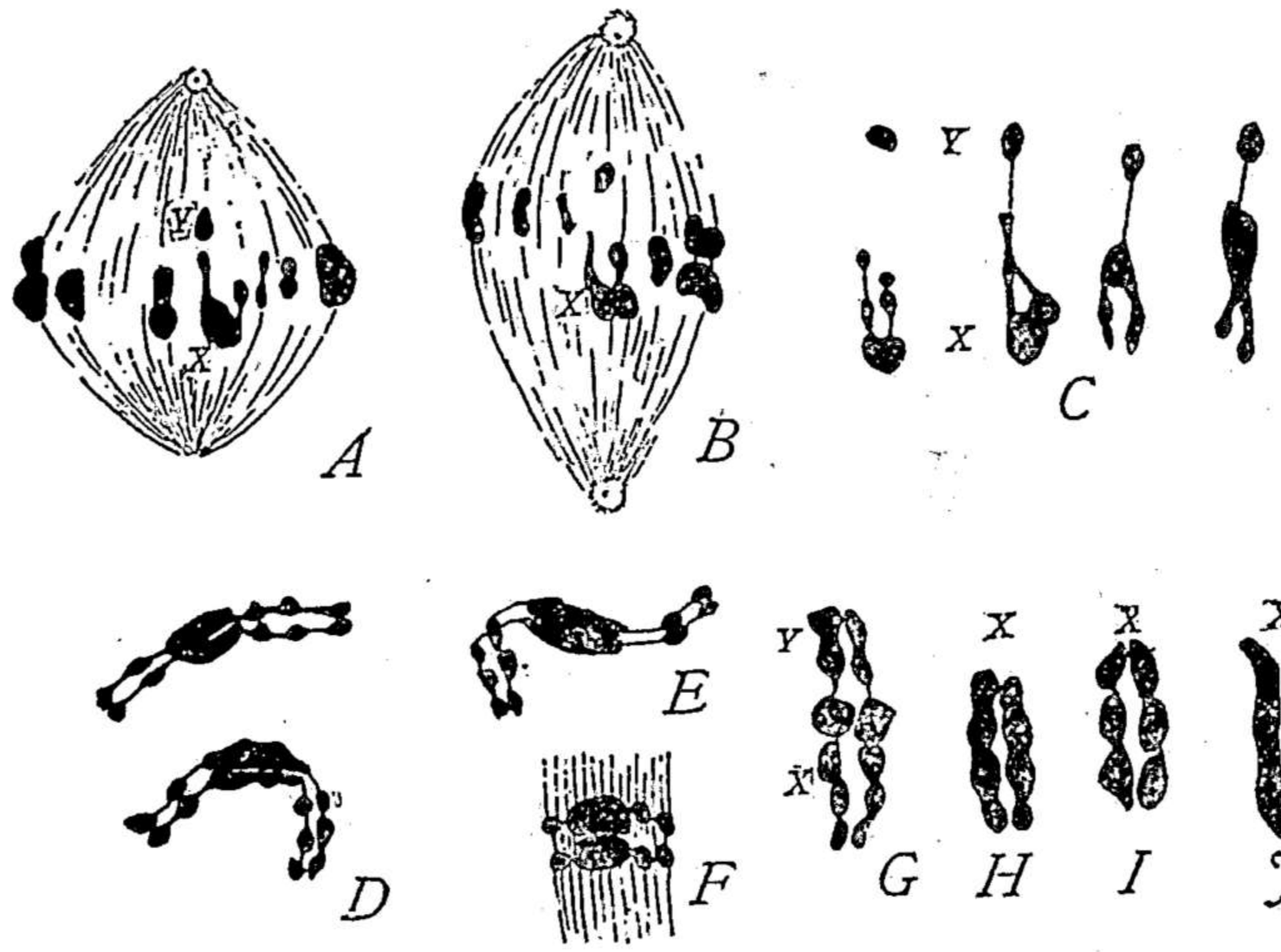

Fig. 424.—Structure of the sex-chromosomes in Hemiptera (*A–F* from BROWNE).

A, *B*, second spermatocyte-metaphases in *Notonecta indica;* *C*, four examples of the *XY*-pair from same; *D–E*, the *X*-chromosomes in the prophases; *F*, same in metaphase of first division; *G–J*, the sex-chromosomes in the growth-period of *Lygæus bicrucis;* *H*, *I*, and *J* show the *X*-chromosome only, *G* probably the *X*- and *Y*-chromosomes united end to end.

mosomes. Further evidence in the same direction is afforded by the earlier mentioned cross-sutures or constrictions (p. 889) which, as many observers have noted, often appear in certain chromosomes and *at particular points*. The classical case of this is the median cross-suture ("Querkerbe") described by Haecker ('95, '02, etc.) in the bivalents of copepods (Fig. 425). This suture was regarded by Haecker as representing the point of telosynaptic union of the two synaptic mates; but later researches [1] showed this interpretation to be untenable. The suture does not mark a plane of division, either in meiosis or mitosis; and it is found in the univalent chromosomes of the somatic divisions as well as in the bivalents. All points to the conclusion that it marks the point of juncture of two closely united components

[1] Lerat ('05), Schiller ('09), Braun ('09, '10), Matschek ('10), Krimmel ('10), Kornhauser ('15).

that have not, as yet, the value of separate chromosomes but might easily become such.[1] Similar transverse sutures or constrictions have been described by many other observers both in plants and animals.[2]

These sutures or constrictions may be median or at any other point; but in some cases at least are constant in position for each particular chromosome, as has been emphasized by all the observers named. In *Vicia*, for example, Sakamura found that several of the chromosomes show a subterminal constriction and that those of one pair of these characteristically

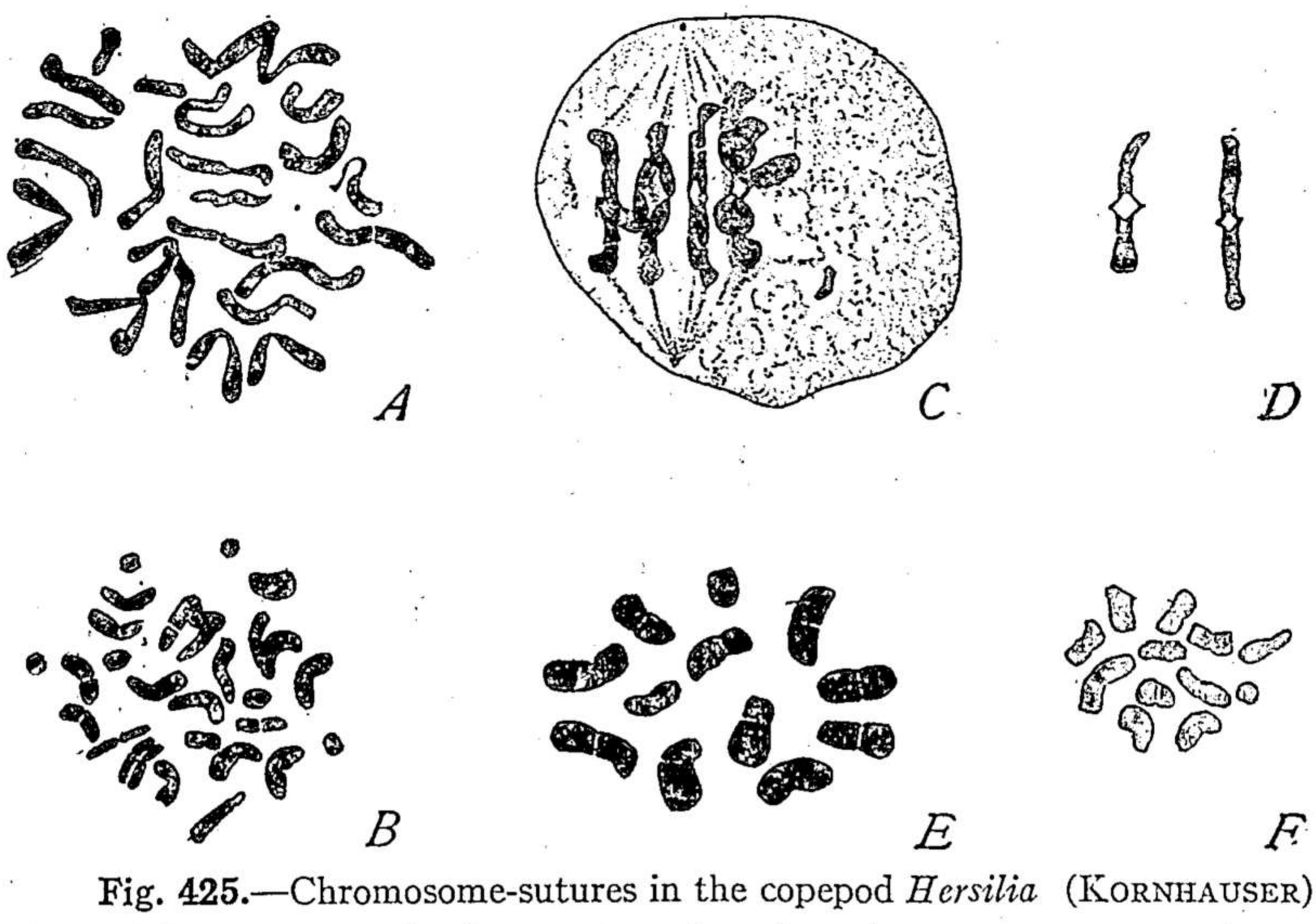

Fig. 425.—Chromosome-sutures in the copepod *Hersilia* (KORNHAUSER).

A, metaphase of cleavage-stage *B*, of spermatagonium, in each case a cross-suture in certain chromosomes; *C*, 1st spermatocyte-division in side-view, cross-sutures in two tetrads; *D*, similar tetrads; *E*, first oöcyte-division in polar view, *F*, second spermatocyte-division.

show also a median constriction in addition (Fig. 426). Agar found further, in *Lepidosiren* that these sutures (varying in position in different chromosomes) *correspond with the points of attachment to the spindle* [3] and that their position in the chromosomes of the meiotic divisions corresponds with that in the spermatogonial groups, just as does the point of attachment in case of the Orthoptera, as shown by McClung, Carothers and other observers (p. 511).

Some of the so-called "tetrads" described by various authors in the somatic divisions [4] particularly after treatment by narcotics or when in a

[1] Wilson ('11). *Cf.* Vejdovský, ('11–'12).

[2] See Janssens, '01 (*Triton*); Grégoire and Wygærts, '04 (*Trillium*); Lundegårdh, '10 (*Allium*), Fraser and Snell, '11, Sharp, '14 (*Vicia*); Kowalsky, '04, Della Valle, '07 (urodeles); Rosenberg, '09; Digby, '14 (*Crepis*); Sakamura, '20 (*Triticum*, *Lathyrus*, *Pisum*, etc.); Hance, '18, Gates, '20 (*Œnothera*); Agar, '12 (*Lepidosiren*), Nawaschin, '14, '15 (*Fritillaria*); Litardière, '21 (ferns).

[3] It is important to note that the sutures or constrictions are visible in the prophases before the spindle has been formed, and hence are not caused by the attachment.

[4] See Della Valle ('08), Popoff ('07), Nemec ('04, '10), Schiller ('09), Kemp ('10), Nawaschin ('14). etc

pathological condition, are no doubt due to the presence of such constrictions or sutures. Schiller has in fact demonstrated that upon treatment of developing *Cyclops* eggs by chloroform or ether the cross-suture is exaggerated so that a perfect tetrad appearance is given by the univalent chromosomes during the process of cleavage and in other somatic divisions (Fig. 426).

Such facts [1] indicate that each chromosome possesses a constant serial differentiation, and that the nature and order of the components are constant in each particular chromosome; and this is borne out by direct observations on the actual structure of the spireme-threads. They make

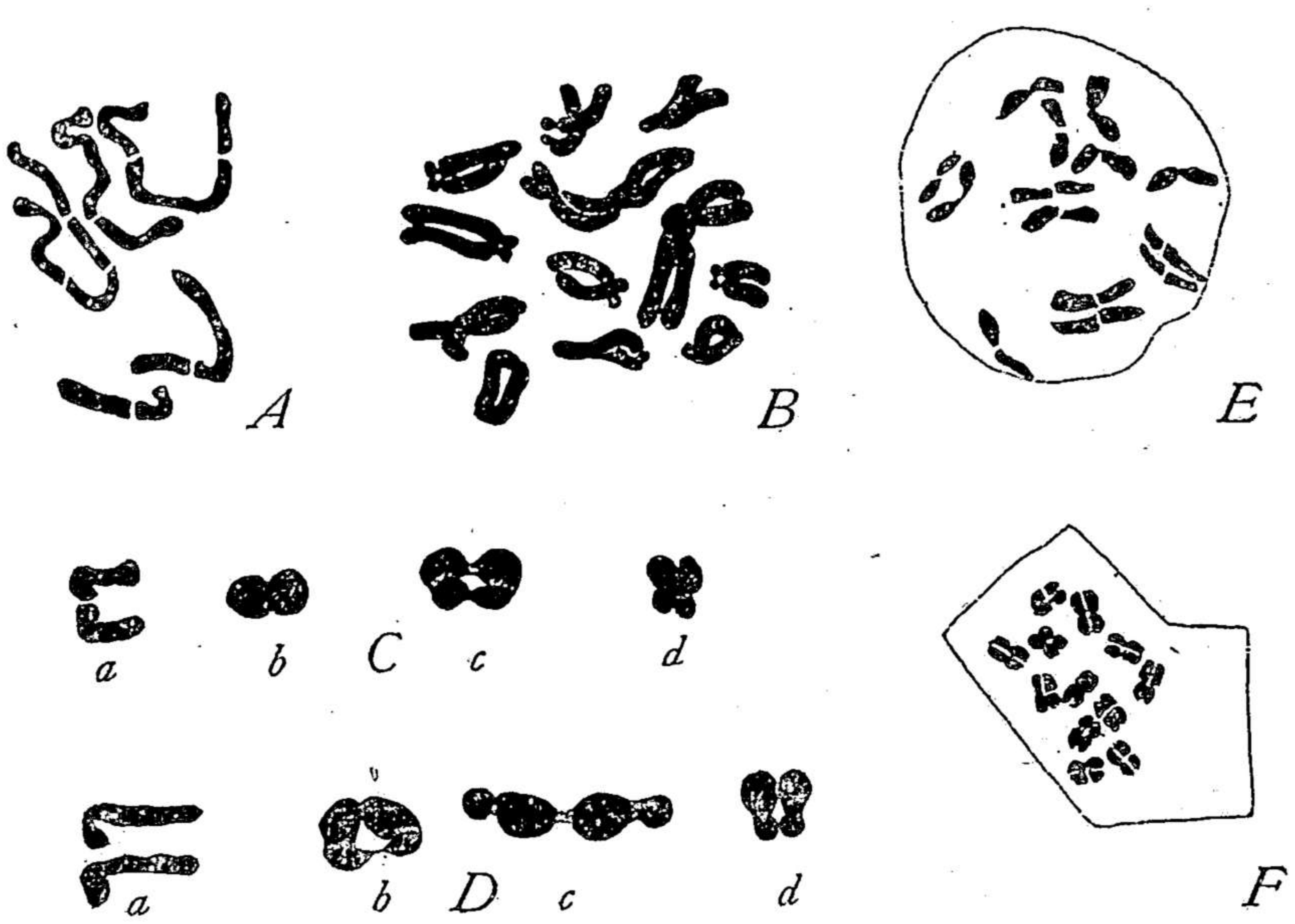

Fig. 426.—Chromosome-sutures in plants and animals.

A, spermatogonial chromosomes of *Triton* (JANSSENS); *B*, from root-tips of *Vicia*, with sub-terminal constrictions (SAKAMURA); *E*, *F*, from blastomere-divisions of *Cyclops*, slightly etherized (SCHILLER); *C*, *D*, from *Lepidosiren* (AGAR). In the latter two *a* shows a pair of somatic chromosomes with sub-terminal constriction and attachment, *b* and *c* the corresponding bivalents and *d*, late anaphase-forms of same.

easy the assumption that single chromosomes may readily break apart into separate components which thenceforth behave as independent chromosomes. A partial explanation is here offered of the origin of supernumerary chromosomes, of fluctuations of chromosome-number in the individual, and of permanent changes of chromosome-number (p. 868).

2. The Chromosomes as Linear Aggregates. The Chromomeres

We are thus brought, finally, to one of the most fundamental conceptions of cytology and genetics, namely, that the spireme-threads are linear aggregates of much smaller self-perpetuating bodies, aligned in single series, and

[1] See Wilson ('11), Agar ('12).

in definite order. The importance of the spireme-formation in mitosis was early perceived by Strasburger and Flemming (hence Flemming's term *mitosis*); but its fundamental significance was first fully grasped by Roux ('83) with whom arose the conception of a differentiation of the thread along its longitudinal axis, so that it represents a linear series of smaller components ("qualities") that are to be distributed to the daughter-cells in a particular manner. To this conclusion the whole course of later discovery, in both cytology and genetics, has continually added weight.

In *Ascaris megalocephala* it is certain that the long chromosomes of the early cleavage-stages (and of the later germ-line) are each the equivalent of a much larger number of smaller chromosomes in linear series, as is proved by the fact that in all the somatic cells it actually breaks up into such smaller independent chromosomes which approximate in number to those observed in other species of this genus in which no linkage occurs, *e. g.*, in *Ascaris lumbricoides* or *A. incurva* (p. 855). It is therefore highly probable that in *A. megalocephla* the long chromosomes of the early cells and of the germ-track are plurivalent as compared with the small chromosomes of the somatic cells or of other species.

Somewhat similar to this in type is the case of the sedge *Carex*, as described by Stout ('12). In the prophases of mitosis appear about 74 small, rounded chromosomes which become aligned in a single linear series, like beads upon a string. The continuous spireme thus formed seems to persist even during cell-division, and splits lengthwise in the metaphase. Only in the synaptic and leptotene stages do the small chromosomes spin out into thin threads and disappear from view. A similar case is offered by *Amœba glebæ*, in which Dobell ('14) describes 16 small globular "chromosomes," which seem to arise by the coalescence of a much larger number of smaller granules derived from the large "karyosome" of the vegetative nucleus. As in *Carex* these chromosomes become aligned in a single linear series to form a continuous spireme, which in this case forms a closed ring and as such splits lengthwise and divides at the equator of the spindle.

The foregoing three cases show how conventional and artificial is our common conception of "univalence," "bivalence" or "plurivalence." In *Amœba glebæ*, for example, we might equally well describe the facts by saying that division takes place with a single, ring-shaped chromosome composed of a linear series of chromomeres. In *Ascaris megalocephala* such a description seems inadmissible because the smaller bodies may become wholly independent, to divide as separate chromosomes.

The Chromomeres. We are thus brought to the fact that even the so-called single or univalent chromosomes (spireme-threads) often give a beaded appearance, as if consisting of a linear series of smaller basichro-

matic bodies suspended in a more lightly staining or oxychromatic substance. It was long since suggested that these bodies might have a persistent identity (Balbiani, '76, '81) and that *longitudinal splitting of the threads might be due to their fission.* (Pfitzner, '82). This was supported by Van Beneden who showed (in *Ascaris*) that the granules are of different sizes, emphasizing especially the fact that after splitting of the thread the granules of the daughter-threads exactly correspond to one another.[1] These bodies (Fig. 8) first known as "Pfitzner's granules" and later as *chromomeres*, were later found in many plants and animals. Their existence has been disputed by a considerable group of observers, including especially Grégoire and his followers, who have either failed to find the chromomeres or have considered them as due to accidents of coagulation, local differences of density, or the like without further significance.[2] Such scepticism, however, cannot be maintained in view of the positive results of recent careful studies. Chambers has shown that chromomeres can be seen as paired swellings in the diplotene stages of the spermatocytes of grasshoppers examined *in vivo* and that they are not destroyed but only moved further apart by stretching the double threads under the microscope by means of the microdissection-apparatus (Fig. 429). The evidence from sections, though less direct, is hardly less convincing.

The chromomeres have been described as spheroidal bodies (Pfitzner, Van Beneden), or discs (Strasburger, Carnoy, etc.); sometimes as rings surrounding a central "achromatic" core (Van Beneden, '83, Merriman, '04, Vejdovský, '11–'12) and by some observers as irregular both in shape and in size (Allen, '04, '05; Sands, '22, '23). Many observers, beginning with Eisen ('99, '00) have considered them to be compound bodies or aggregates of smaller granules or "chromioles." This lacks confirmation but we should not take too sceptical an attitude towards the principle here involved.

The chromomeres are most readily seen in the spireme-threads during the earlier stages of mitosis or meiosis before the condensation of the chromosomes has proceeded very far. As the threads shorten and thicken the chromomeres undergo various changes, often becoming less evident and in many cases disappearing from view so that many observers have been unable to find them in the metaphase-chromosomes. During this process, the chromomeres often seem to diminish in number and also to increase in size, so that we may infer that they become closely associated, per-

[1] "What strikes us is the perfect symmetry of the two filaments; they are identical with each other. Each chromatin-granule of the one has its counterpart in the other; and there is not the least peculiarity of one that is not found exactly duplicated in its fellow" ('83, '84, p. 541).

[2] See Grégoire and Wygærts ('03), Bonnevie ('08), Grégoire ('05, '06, '07, '10), Mano ('04), Maréchal ('04, '07), Berghs ('09), Stomps ('10), Sharp ('13, '20), Lundegårdh ('12), Litardière ('21), etc.

haps even fuse, to form larger bodies. Certainly the original disposition of these bodies must be greatly altered during the condensation that takes place in course of the prophases; and perhaps it is partly owing to these changes that some observers have described the chromomeres as having a quite irregular grouping. In spite of these complications some of the most careful recent studies in this field have confirmed Van Beneden's results on the size-differences of the chromomeres, and have made it nearly certain that in some cases at least these differences are constant and that *the chromomeres display a definite serial order in the spireme-threads.* A simple example is seen in the hemipter *Lygæus bicrucis* (Fig. 424), where

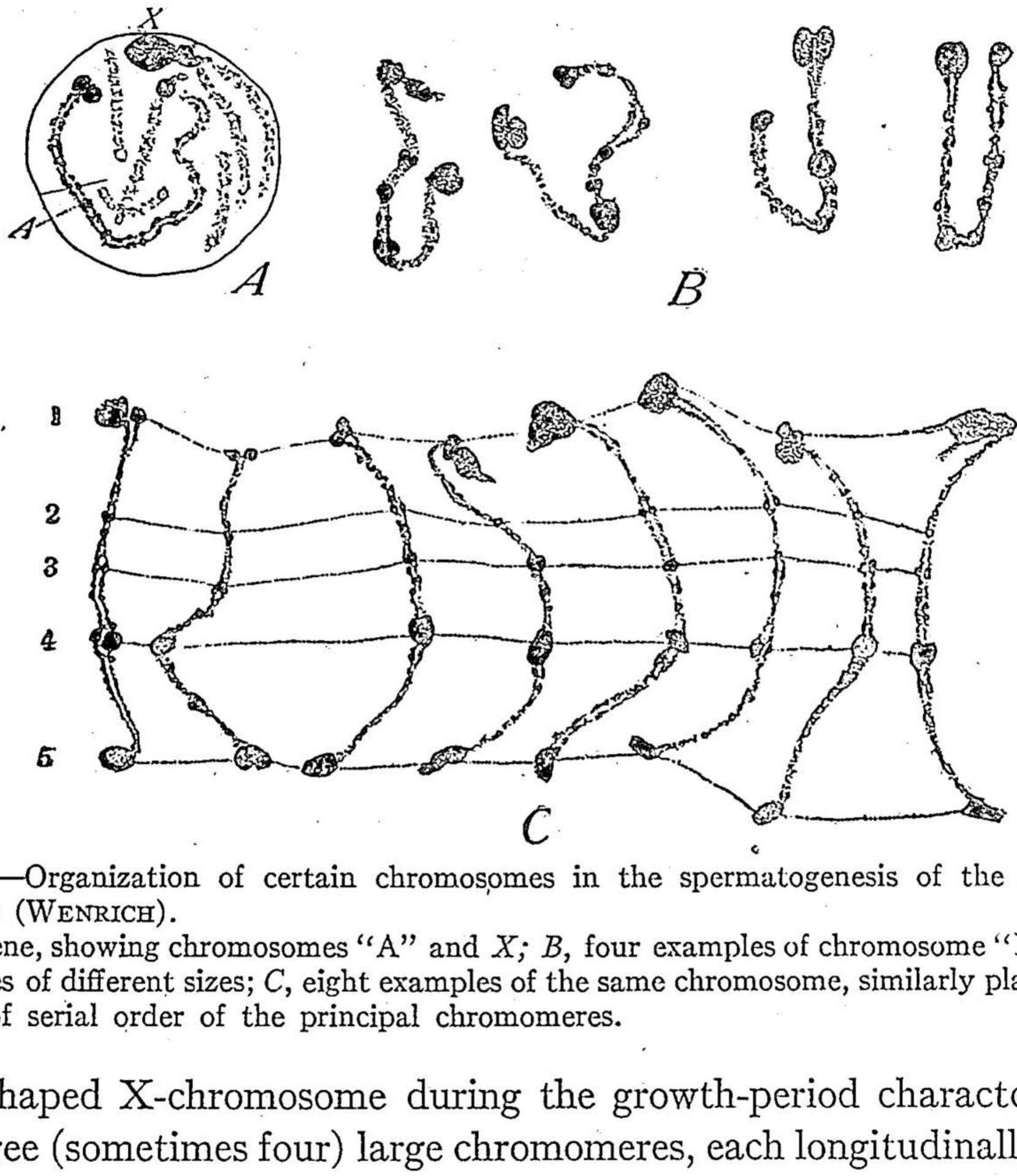

Fig. 427.—Organization of certain chromosomes in the spermatogenesis of the grasshopper *Phrynotettix* (WENRICH).

A, diplotene, showing chromosomes "A" and *X; B*, four examples of chromosome "B," showing chromomeres of different sizes; *C*, eight examples of the same chromosome, similarly placed to show constancy of serial order of the principal chromomeres.

the rod-shaped X-chromosome during the growth-period characteristically shows three (sometimes four) large chromomeres, each longitudinally double, (Wilson, '12). Still more definite and striking is the X-chromosome of *Notonecta indica* (Browne, '16) which in the diakinesis consists of six chromomeres, a large central one with two small ones at one end and three at the other, all longitudinally split and connected by thin threads (Fig. 424). These components are still clearly distinguishable at the time the chromosomes pass upon the spindle and even, in a measure, during the anaphases.

Still more remarkable conditions have been found in the autosomes of Orthoptera by Pinney ('08), Carothers ('16), and especially by Wenrich

('16). The latter observer found in the spermatocytes of *Phrynotettix* that certain of the autosome bivalents are individually distinguishable in the early diplotene stage by the characteristics of their chromomeres. In the most striking of these cases ("Chromosome B") the constancy of the size-differences and of the serial order is strikingly demonstrated (Fig. 427); and this bivalent is also characterized during the heterotypic division by a peculiar roughened or brush-like contour at one end.[1] Wenrich was able to distinguish at least one other bivalent in *Phrynotettix* ("chromosome A") which differs from "chromosome B" both in the size relations of the chromomeres and their serial order; and he gives reason to conclude that other

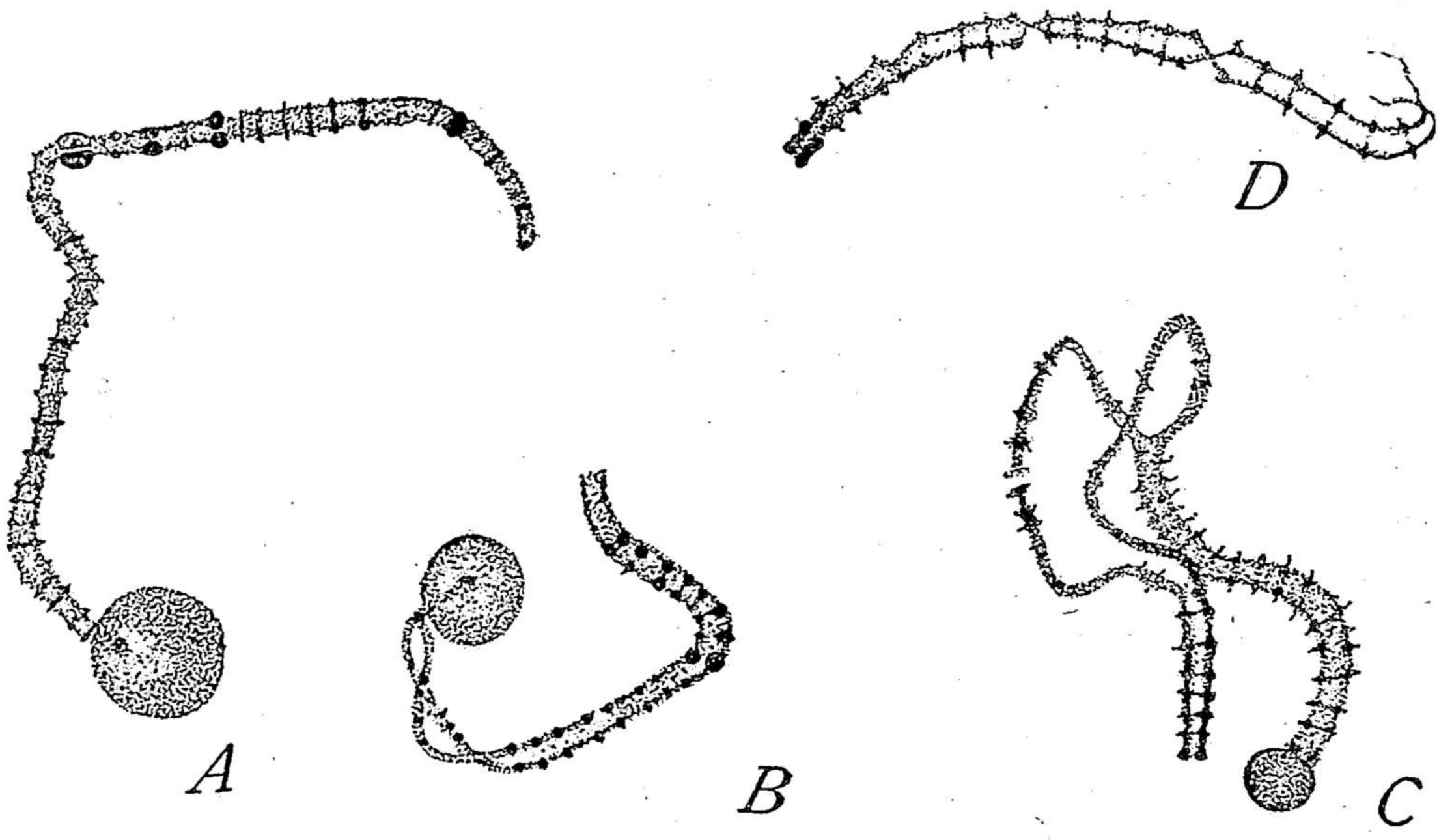

Fig. 428.—Early stages of meiosis showing chromomeres in *Dendrocœlum* (GELEI).

C, bivalent from amphitene, with parasynapsis in progress; *B*, early diplotene thread seen in the conjugation-plane; *D*, early diplotene to show twisting (?chiasmatype); *A*, somewhat later stage, viewed from the side, to show the first indications of the secondary (equatorial) longitudinal cleft, the conjugation-plane being that of the paper. Size-differences of the chromomeres.

autosome-bivalents likewise show constant differences in this regard. More recently Gelei ('21, '22) shows with great clearness that the post-synaptic chromosomes of the platode *Dendrocœlum* consist of regular series of chromomeres, showing marked size-differences, accurately paired in the diplotene stage, and quadipartite after the appearance of the secondary or equational cleft (Fig. 428).

Closely connected with the foregoing, are the "polar granules" as first described by Pinney ('08) in *Phrynotettix*. These are very distinct, deeply staining and often enlarged granules, typically found at the proximal or

[1] See also McClung, '14.

attached end but said also to occur at the distal end. In the spermatogonia these granules are single and persist in a compact form in the vesicular stage of these chromosomes (Fig. 361). In the leptotene-nuclei, when the threads form polarized loops, the polar granules are crowded together at the pole and often unite to form large composite granules; but Wenrich ('16) believes that their identity is not lost at this time, the granules separating again in the pachytene-stage, and retaining their original connections. The studies of Carothers and of Wenrich make it probable that these bodies are derived from terminal chromomeres, serially homologous with those of the central region; and they also raise interesting questions concerning their relations to the plasmosomes. Wenrich found that in certain cases the polar granules become enlarged, more or less vesicular in appearance and stain less deeply, thus assuming somewhat the character of a plasmosome, and is thus led to suggest a relationship between these granules (enlarged chromomeres) and plasmosomes. Carothers ('13, '16) had observed such vesicular chromomeres in the central region of the thread (Fig. 438) and has produced evidence that they are constant both in number and position (p. 142).

Such observations, made by cautious observers, are not to be explained away by the supposition that the chromomeres are coagulation-products of no significance. Coagulations they undoubtedly are as observed in sections; but the significant fact is the *constancy of the result*, which demonstrates the existence of a definite longitudinal differentiation in the spireme-thread, the expression of a serial organization in the living object. As a working hypothesis, therefore, we need not hesitate to accept the cytological evidence at its face value so far as concerns the essential point at issue.

If, as the foregoing facts indicate, smaller chromomeres may aggregate or fuse to form larger ones, we once more reach the conception that in many cases they may themselves be compound bodies having perhaps a definite internal architecture. In point of fact it seems clear that at least the larger chromomeres, as seen in sections, are aggregates of still smaller granules; and in case of *Batrachoseps* Eisen went so far as to maintain that the number of granules is constant. This conclusion, certainly a rash one in view of the fact that proteins generally so often coagulate in the form of minute granules, has not been confirmed by later observers; and the problems here arising lead us into a region beyond the present reach of our technique. Nevertheless the cytological evidence points unmistakably to the conclusion that the chromosomes arise from spireme-threads which in some sense or other are serial aggregates which have a perfectly definite organization, and one that differs specifically from chromosome to chromosome and from species to species. This is a surprising conclusion, but it involves further

consequences more astonishing still. The serial organization of the chromosomes, as displayed by the chromomeres is not only duplicated in the daughter-threads produced by fission in the somatic divisions, but also in the bivalent chromosomes of the meiotic period, where the longitudinal duality arises (if the theory of parasynapsis be correct) by the side-by-side conjugation of previously separate threads. We thus come in view of the possibility that the chromomeres, whatever be their ultimate significance,

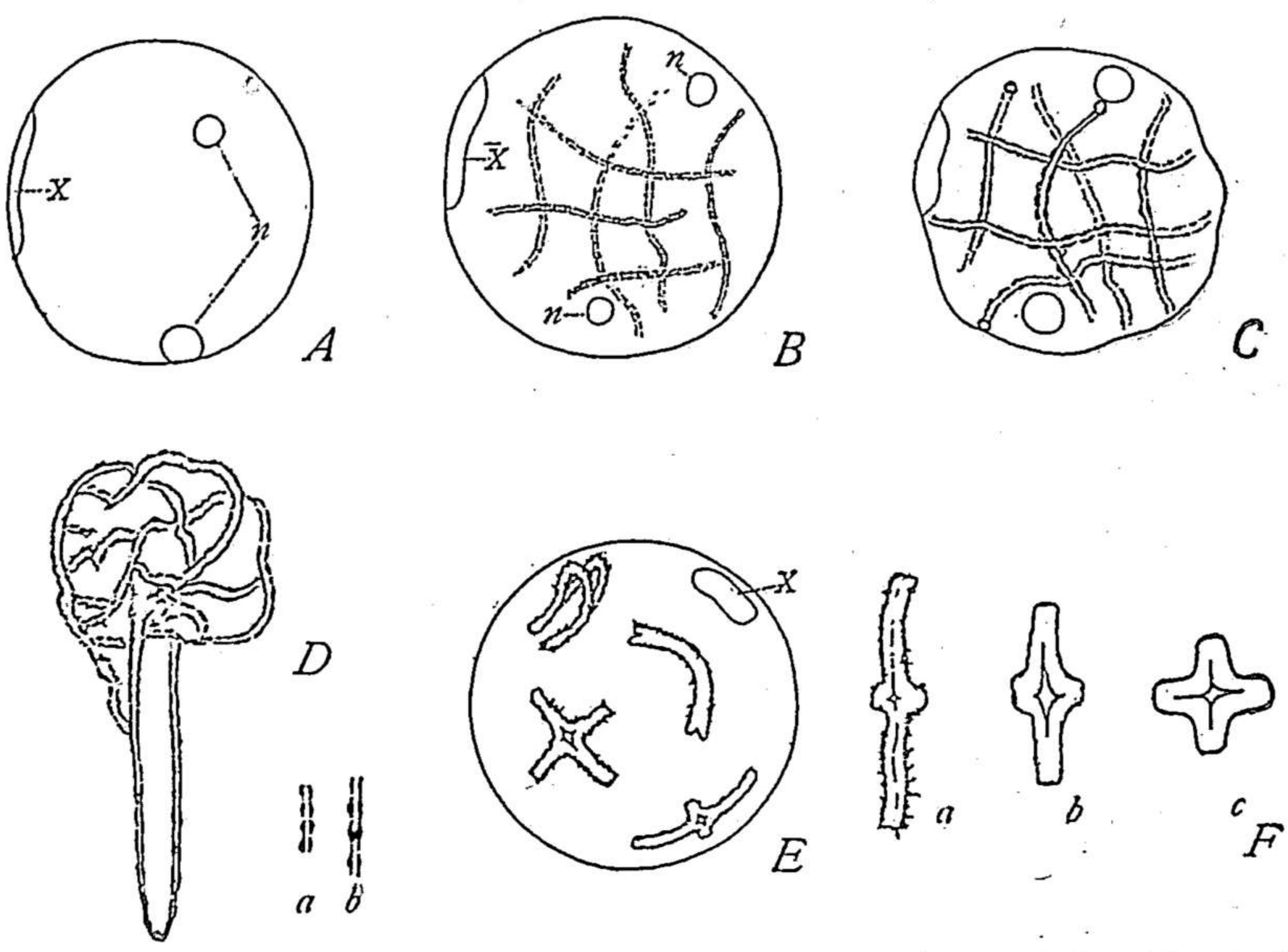

Fig. 429.—Nuclear structures in the spermatocytes of the grasshopper *Dissosteira* studied *in vivo* with the micro-dissection needle (CHAMBERS).

A, nucleus of intact living cell, showing only the chromosome-nucleolus (*X*) and plasmosomes (*n*); *B*, appearance of double threads on puncture of the cytosome; *C*, four minutes later; *D*, diplotene loop pulled out by needle (chromomeres); *a*, portion of the thread before stretching, *b* upon stretching; *E*, late diakinesis, tetrads and *X*-chromosomes; *F*, *a–c*, successive changes in a tetrad removed from the nucleus, in the body-fluid.

are capable not only of growth, definite alignment and division, but also of conjugating two by two and like with like (p. 952).

To some minds, perhaps to many, this result may seem too staggering for serious consideration. If so we may with advantage reflect on the fact that precisely the same result concerning the relations of the Mendelian unit-factors or genes of heredity has been independently reached by the exact experimental methods of modern genetic analysis. That these two lines of research are but dealing with different sides of the same problem is demonstrated by evidence now to be outlined in the following chapter.

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