

CHAPTER X

CHROMOSOMES AND SEX

"The cytological evidence has revealed a visible mechanical basis for the production of males and females in equal numbers and irrespective of external conditions. . . .

"Phenomena of this kind seem likely to throw further light on the mechanism of Mendelian heredity as well as of sex-production, for they demonstrate a disjunction of different elements in the formation of the gametes; and this is a fact, not a theory."¹

The genetic aspects of our subject are most readily approached through the subject of sex-production, to the elucidation of which cytology and genetics have equally contributed. In no other field of inquiry is the close connection between cytological and genetic phenomena so readily demonstrated; nature here offers us, indeed, a series of experiments, systematically carried out on a grand scale, that afford crucial evidence concerning the causal relation between chromosomes and heredity.

I. SEX AND THE GERM-CELLS

Investigations upon the nature of sex were long dominated by the preconceived notion that it is determined by conditions external to the germ,² but the inadequacy of this view is now conclusively demonstrated. It is true that many conditions, external or internal, may influence sex-production; and in certain cases may give the appearance of determining sex. For instance, the classical experiments of Prantl ('81), Buchtien ('87) and their successors showed that in the prothallia of *Equisetum* and certain other pteridophytes the production of archegonia is favored by stronger light or more favorable conditions of nutrition while the reverse conditions favor the production of antheridia;³ and a result similar in principle in respect to soil-conditions has recently been demonstrated by Schaffner in the dioecious *Cannabis* ('21) and *Arisæma* ('22). It seems clear, however, that external conditions here operate merely to incite the development of one set of sexual characters at the cost of the opposite set in an organism that is actually or potentially monoecious or hermaphroditic.⁴

¹ Wilson, '09, p. 15; '10, p. 592.

² Compare, for instance, the account of this subject given in the preceding edition of this work, 1900, pp. 144-146.

³ See Klebs ('13).

⁴ This is clearly evident in *Arisæma dracontium* where the individuals as found in nature are often actually monoecious. The effect of soil here is to change the monoecious conditions to the staminate or the reverse.

Probably of the same type is the case of the worm *Bonellia*, in which the mature forms show a very pronounced sexual dimorphism. Here the larva, at first alike in both sexes, becomes a female if it fails to become attached (in some cases showing some hermaphroditic characters); while if it becomes normally attached it produces a male.¹ To cite a case of different type, the experiments of Shull ('10, '12) and of Whitney ('14-'17) have shown that in cultures of rotifers (*Hydatina*, etc.) composed exclusively of parthenogenetic females, males may be quickly caused to appear upon a suitable change of diet (p. 229); but this, evidently, is not a change of one sex into another but only the partial appearance of the sexual forms (both males and sexual females) in addition to the parthenogenetic. Still another type appears in the facts observed by R. Hertwig ('12, '21) in frogs, in which over-ripe eggs produce a large excess of males as compared with those from the same female when fertilized immediately.² In this case the explanation is not yet evident; but it seems probable that they are due to a modification of the chromosome-mechanism of sex-production.³

It is indeed possible—and such a view has in fact often been advocated—that all organisms are potentially hermaphroditic (see p. 819). Nevertheless a real distinction exists between true hermaphroditic and dioecious organisms; and in the latter both the genetic and the cytological evidence demonstrates the existence in the germ-cells of a definite internal mechanism that is adjusted for an automatic production of the sexes under identical external conditions. It is probable, therefore, that in so far as external conditions affect sex production it is in all cases through their influence upon the internal mechanism (p. 819).⁴

Mendel himself suggested the possibility that sex-determination might be a phenomenon of heredity and segregation; and this suggestion (later adopted by Strasburger, '00 and by Bateson, '02, and elaborated by Castle, '03) was ultimately shown to give the true key to a solution of the problem. Definite evidence of its correctness was first brought forward by Correns ('07) in experimental studies on hybrids between monoecious and dioecious species of plants (*Bryonia*). The results indicated that in the dioecious

¹ Baltzer ('14).

² In one of these experiments 500 eggs, fertilized at once, produced 226 males, 218 females and 4 undetermined. A large number of eggs from the same lot fertilized from 68 to 77 hours later gave 13 females and 673 males, with a large mortality.

³ Hertwig, assuming the female to be the homogametic sex (XX), conjectures that over-ripeness of the eggs may tend to weaken the action of one chromosome or even to cause its degeneration.

⁴ The sexual dimegaly of the eggs long known in the parthenogenesis of rotifers and phylloxerans and in the sexual eggs of *Dinophilus apatris* (pp. 277, 806) early led to the view that sex is predetermined in the germ-cells. Beard ('02, and earlier) urged the hypothesis of four-fold gametes—*i. e.*, that both eggs and sperms are predestined as male-producing or female-producing, a necessary corollary of which is the assumption of selective fertilization; but later researches rendered this particular assumption highly improbable.

species sex is determined by the pollen-grains, all the eggs being sexually of one type, while the pollen-grains, are of two classes, equal in number, one of them male-producing, the other female-producing. This led Correns to compare the sexual cross to the Mendelian "back cross" between a heterozygote, DR, and a corresponding recessive homozygote, RR, the male (which we may call XY) being in a certain sense the heterozygous sex or sex-hybrid, the female XX the homozygous (Fig. 352). In both cases the "homozygous" parent produces but one kind of gamete (R or X); the "heterozygous" parent two equal classes (D and R or X and Y). In either case, therefore, random fertilization will in the long run produce the two parental forms (DR=XY, and RR = XX) in equal numbers. In order, however, not to complicate the use of the terms "homozygous" and "heterozygous" it has been found convenient from the cytological point

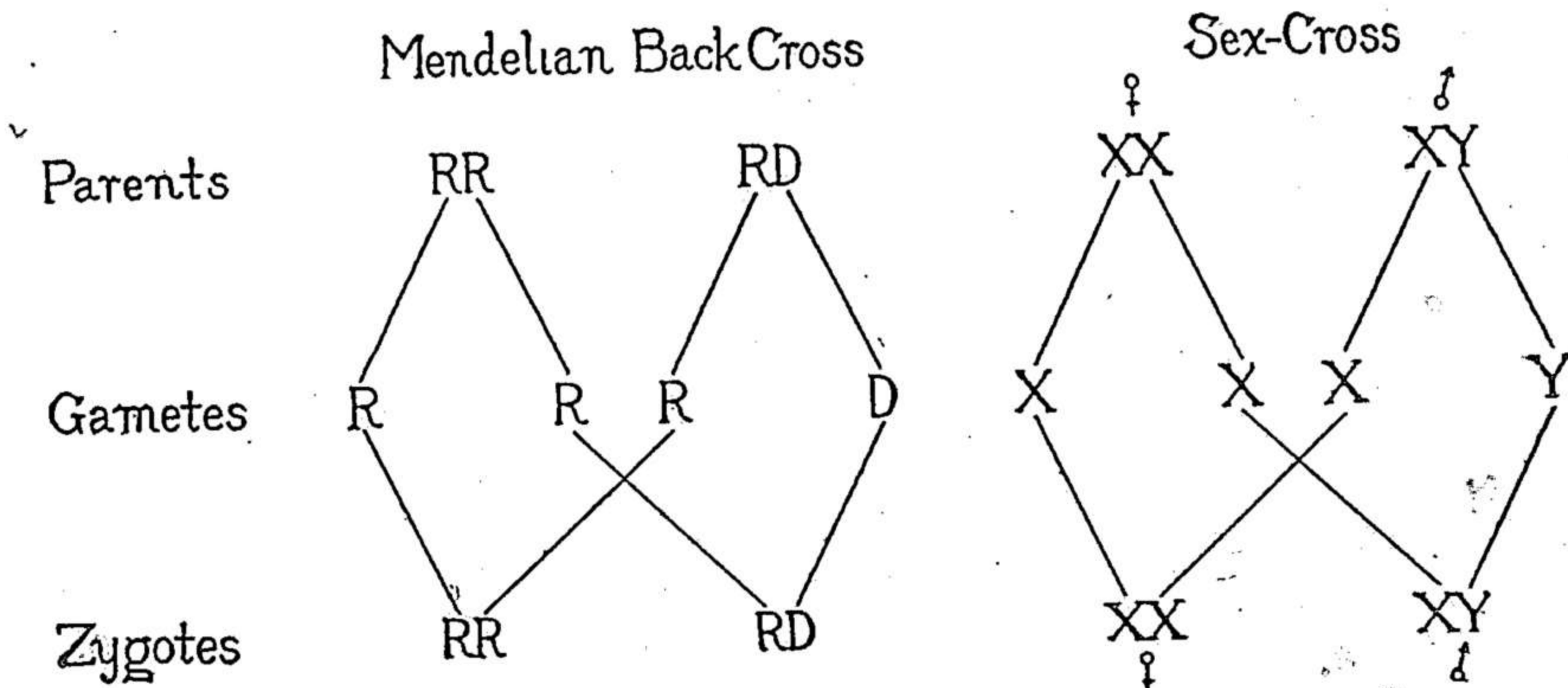


Fig. 352.—Diagram comparing a sex-cross with a Mendelian back-cross between a homozygous recessive (RR) and a heterozygote (DR).

of view to replace them when applied to sex-heredity by the corresponding terms *homogametic* and *digametic* or *heterogametic*.¹

Genetic research on the heredity of sex-linked characters (p. 945) has fully borne out the foregoing conclusion and has further demonstrated that either sex may be the homogametic one. Thus, the male has been shown to be the digametic sex in mammals and Diptera, while the reverse condition exists in birds and Lepidoptera. This means that in the former case, all the eggs alike have the constitution X, while half the sperms have the constitution X and are female-producing, and half Y and are male-producing. In the bird or butterfly, on the other hand, it is the sperms that are genetically alike, while the eggs are of two equal classes, female-producing and male-producing. The decisive or differential sex-factor is therefore the sperm in the fly and mammal, and the egg in the butterfly.

The fundamental contribution of cytology to the subject was the dis-

¹ Wilson, '10a, '11.

covery, announced in 1905,¹ that the genetic phenomena are exactly paralleled by certain particular chromosomes; so that the symbols X and Y may be applied to them in sex-production in precisely the same manner as to the genetic factors that determine sex. That these chromosomes bear the differential factors of sex has been proved to be the case by an irresistible body of more detailed and concrete evidence drawn from both genetics and cytology. The chromosomes in question may, therefore, appropriately be called the *sex-chromosomes*.² Thus far the male sex has been certainly found to be cytologically the digametic one in echinoderms, nematodes, spiders, myriapods, Odonata, Orthoptera, Hemiptera, Coleoptera, Diptera, Hymenoptera (though with an important qualification), reptiles and mammals; and there is strong indirect evidence that the same condition exists in rotifers, ostracodes and Cladocera. On the other hand, the female has been proved to be cytologically digametic in the Lepidoptera. The birds alone offer a seeming contradiction in that genetically the female is genetically heterozygous, but cytologically the male has been described as digametic. This material, however, offers great difficulties (p. 786).

The facts just outlined mean that a definite relation or predestination exists between the germ-cells and sex and one that is not dependent upon external conditions. Examples of such predestination have earlier been given in case of the rhizopods, algæ and fungi (p. 585, etc.). The evidence is now conclusive that this predestination of sexual genetic constitution in the germ-cells is established by the meiotic or maturation-divisions, *i. e.*, in general during the spore-formation in plants and during the gamete-formation in animals. In the heterothallic moulds, for instance, the male (—) and female (+) strains remain perfectly distinct so long as conjugation does not occur (p. 588). Since, however, conjugation brings together the + and — determining factors it seems necessary to assume that they are segregated or disjoined at a subsequent period. In point of fact Blakeslee showed ('06), in the case of species of *Phycomyces* that are predominantly heterothallic, that this disjunction takes place in the formation of the spores; for if on germination of the zygosporangia the germ-tube be cut across before the formation of a sporangium it may give rise by regeneration to a mycelium of the neutral or homothallic type, which is proved to be bisexual (+ —) by the fact that branches of such mycelia occasionally conjugate with one another. The sexual segregation in the spore-formation is, however, in-

¹ Stevens ('05), Wilson, '05.

² Wilson ('06). Sex-chromosomes are definitely known in sea-urchins, nematodes, arachnids, myriapods, most orders of insects, reptiles, mammals, and birds. Among plants they have thus far been found only in the liverwort *Sphaerocarpos*, and the seed-plants *Elodea*, *Rumex* and a few others (p. 812).

complete; for a certain percentage of the spores remain bisexual and give rise to homothallic mycelia.

In higher plants, where the sexes are readily distinguished by the eye, a more definite result has been reached. In *Marchantia*, a strictly dioecious liverwort, the haploid thallus or gametophyte, may be cultivated asexually (by means of gemmæ) through many generations without change of sex, however the external conditions be varied. The spores, however, as proved by isolation experiments, are strictly male-producing or female-producing, and both kinds occur in the same sporangium (Noll, '06).

In a beautiful series of experiments the Marchals ('06, '07) established the same fact in several species of dioecious mosses (*Barbula*, *Bryum*, *Ceratodon*). Isolation-cultures proved that each spore is strictly predestined either as male-producing or as female-producing. All efforts to alter this predestination by changes of the external conditions, such as nutrition, light, heat or moisture, failed to produce the least effect. Like the spores from which they proceed, both the primary protonema and the gametophyte (leaf-bearing moss-plant) are of fixed sex, and this applies to every part of the plant. Small fragments of the stem or of the leaves will readily regenerate secondary protonemas from which are budded forth new moss-plants; the latter are always of the same sex as the original plants or spores, irrespective of variations in the environment (Fig. 353). Since the diploid sporophyte (sporogonium) is produced by the zygote it must contain the potentialities of both sexes, and this is directly proved by the fact that it produces spores of both sexes. If, now, small pieces be cut from the sporangium or its stalk they may produce by regeneration (apospory) new gametophytes or moss-plants, quite similar in appearance to the original ones, but diploid in nuclear constitution and *sexually hermaphroditic or bisexual*, a condition otherwise almost unknown in the species under investigation, though common in other mosses.¹

Experimental demonstration is here given: (1) that male-producing and female-producing factors are brought together in fertilization; (2) that they remain associated in the diploid cells of the sporophyte; (3) *that they are disjoined in the course of the meiotic divisions by which the spores are formed.*² This last result received convincing confirmation in the researches of Douin

¹ This fact is not immediately shown by all the plants thus produced; many of them are plainly bisexual, but some are in appearance males, and a few females. These latter forms are, however, in reality also bisexual or hermaphroditic, as is proved by their descendants, again produced by regeneration from fragments of the stems or leaves. It should be noted that mixed or hermaphroditic gametophytes have been recorded in a number of species of mosses that are normally of separate sexes, including one of the species (*Mnium hornum*) examined by the Marchals (see M. Wilson, '15). In this case Wilson showed that such an hermaphroditic gametophyte contained the haploid number of chromosomes (6). It does not seem, however, that the Marchals' results are thus invalidated.

² See also Strasburger ('09).

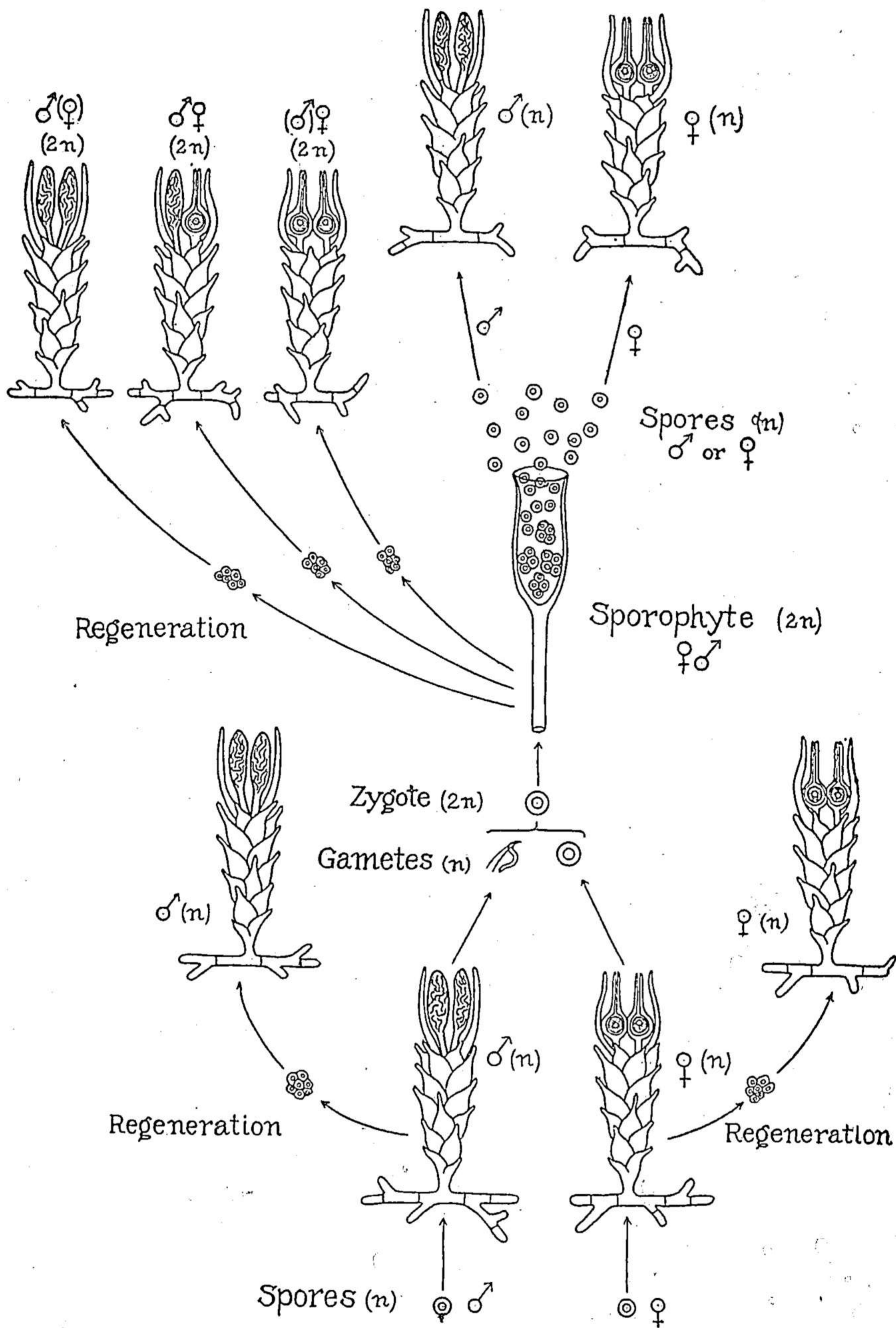


Fig. 353.—Diagram illustrating the experimental results of the MARCHALS on the diœcious mosses).

The male and female haploid gametophytes below, with the diploid sporophyte (sporogonium, above). Regeneration-products of the males or females at either side below; those from the sporophyte are externally male, female or hermaphrodite but in each case may regenerate individuals of different sex.

('09) and Strasburger ('09) on the liverwort *Sphaerocarpus*, a form especially favorable because each quartet of spores resulting from the two meiotic divisions is surrounded by a common membrane and thus held together in a single group, and the four gametophytes produced by each spore-tetrad often remain associated for a considerable time, while the sexual characters develop very early. The result showed that *two of the spores in each tetrad are male-producing and two female-producing*.¹ This can only mean that *the male-producing and female-producing factors are disjoined in one of the meiotic divisions*. Almost at the same time genetic evidence was obtained, from the heredity of sex-linked characters in animals, that in one of the sexes half the gametes are male-producing and half female-producing. It was thus firmly established that two *somethings* responsible for sex-determination are brought together by the gametes in the zygote and disjoined in the process of meiosis (sporogenesis in plants, gametogenesis in animals). Meanwhile cytological studies had demonstrated the fact that *these somethings are chromosomes*.

II. SEX AND FERTILIZATION. THE SEX-CHROMOSOMES

The sex-chromosomes were seen, and in some cases carefully described, long before their relations to sex-production were suspected. Henking, in 1891, described in the hemipteron *Pyrrhocoris*, a "peculiar chromatin-element" which in the second spermatocyte-division first lags behind the separating anaphase-chromosomes and then passes undivided to one pole, while all the other eleven chromosomes are equally divided. From this it follows that the sperms are of two numerically equal classes distinguished by the presence or the absence of the chromatin-element in question. Henking arrived at no very clear idea of the nature of this element, and (for this reason, no doubt) labels it "X"; but in the final statement of his results calls it a "nucleolus."² Nevertheless, the general implications of his brief account seem to be that this body is a chromosome which appears during the growth-period in a condensed, nucleolus-like form, divides equally in the first division, and fails to divide in the second; but its chromosomal nature was not fully established in *Pyrrhocoris* until long afterwards.³ All the essential features of Henking's description, so far as it went, were subsequently confirmed in other insects by other observers—by Paulmier ('99) in the hemipter *Anasa tristis*; by Montgomery ('01) in *Protenor*, *Alydus* and certain other Hemiptera; by Sinéty ('01) in the phasmids *Orphanina* and *Dixippus*;

¹ The more recent data of Allen ('19) are in harmony with this conclusion (as are also those of McAllister, '15; on *Thallocarpus*) though less extensive. Allen's cytological observations give a remarkable confirmation of the same result, though the actual disjunction of the sex-chromosomes has not yet been seen. (Cf. p. 812.)

² '91, p. 712.

³ Gross ('06), Wilson ('09).

by McClung ('02), Sutton ('02) and their followers in many species of grasshoppers; and a similar type of sex-chromosomes was subsequently found in many other animals. This type has received many names,¹ of which perhaps the most widely employed are the terms *accessory chromosome* (McClung, '02) and *X-chromosome* (Wilson, '09). In the meantime a second, and slightly more complicated type of sex-chromosome was described by Montgomery ('98, '01) in various Hemiptera under the name of "chromatin-nucleoli," but their real nature was not at that time suspected. Still more complicated types were subsequently discovered.

The first suggestion that the X-chromosome is concerned with sex-determination came from McClung ('01, '02b), who emphasized the parallel between the two equal classes of sperm differentiated by the X-chromosome, and the two equal sexual classes of adults. He was thus led to the hypothesis that this particular chromosome is the "sex-determiner"; but the actual proof of this was first produced a few years later.

A. MALE DIGAMETY

This condition, the most frequent and the first to be observed, shows many variations of cytological detail and may be classed in this respect under three main types all of which conform to the same general principle. The first of these, which is the simplest, may be taken as the general basis of our account.

1. The Simple XO-XX or Protenor Type

a. General Outline. In this type half the sperms contain one X-chromosome and are female-producing, while half lack such a chromosome and are male-producing. McClung assumed the X-bearing class of sperms to be male-producing, *i. e.*, that eggs fertilized by them produce males, while the no-X class of sperms are female-producing. This assumption implied that the male should contain one more chromosome than the female, and seemed at first sight to harmonize with Montgomery's discovery ('01) that in several of the Hemiptera having one X-chromosome the diploid (spermatogonial) number in the male is odd (*e. g.*, in *Protenor*, *Alydus*, *Harmostes* and *Cedancala*). Sutton ('02) actually described such a condition in the grasshopper *Brachystola*; but this was afterwards proved to be an error. Meanwhile

¹ Some of these are the "special chromosome" (Sinéty), "odd chromosome" (Montgomery), "heterotropic chromosome" (Wilson, '06), "idiochromosome" (Wilson, '05c, and '09), and "monosome" (Montgomery, '06). Montgomery also designated this chromosome as "chromosome X" in the case of *Protenor*, but in other similar cases called it the "odd chromosome" (*Harmostes*, *Alydus*, etc.). The general term "monosome" was later proposed by him (in contradistinction to "diplosome") to designate one subdivision of a more general group of specially modified chromosomes called "heterochromosomes," ('04), later "allosomes" ('06). The term X-chromosome was suggested in the interest of a simpler and more consistent terminology, and because of its convenience when transferred to the corresponding genetic phenomena (Wilson, '09).

the whole subject was temporarily thrown into confusion by the erroneous conclusion of Gross ('04, '06), and Montgomery ('04), that in some insects which possess a typical odd or unpaired chromosome both sexes have the same number of chromosomes. An exit from this difficulty was at first sought in the hypothesis, that sperms of the no-X class are non-functional,

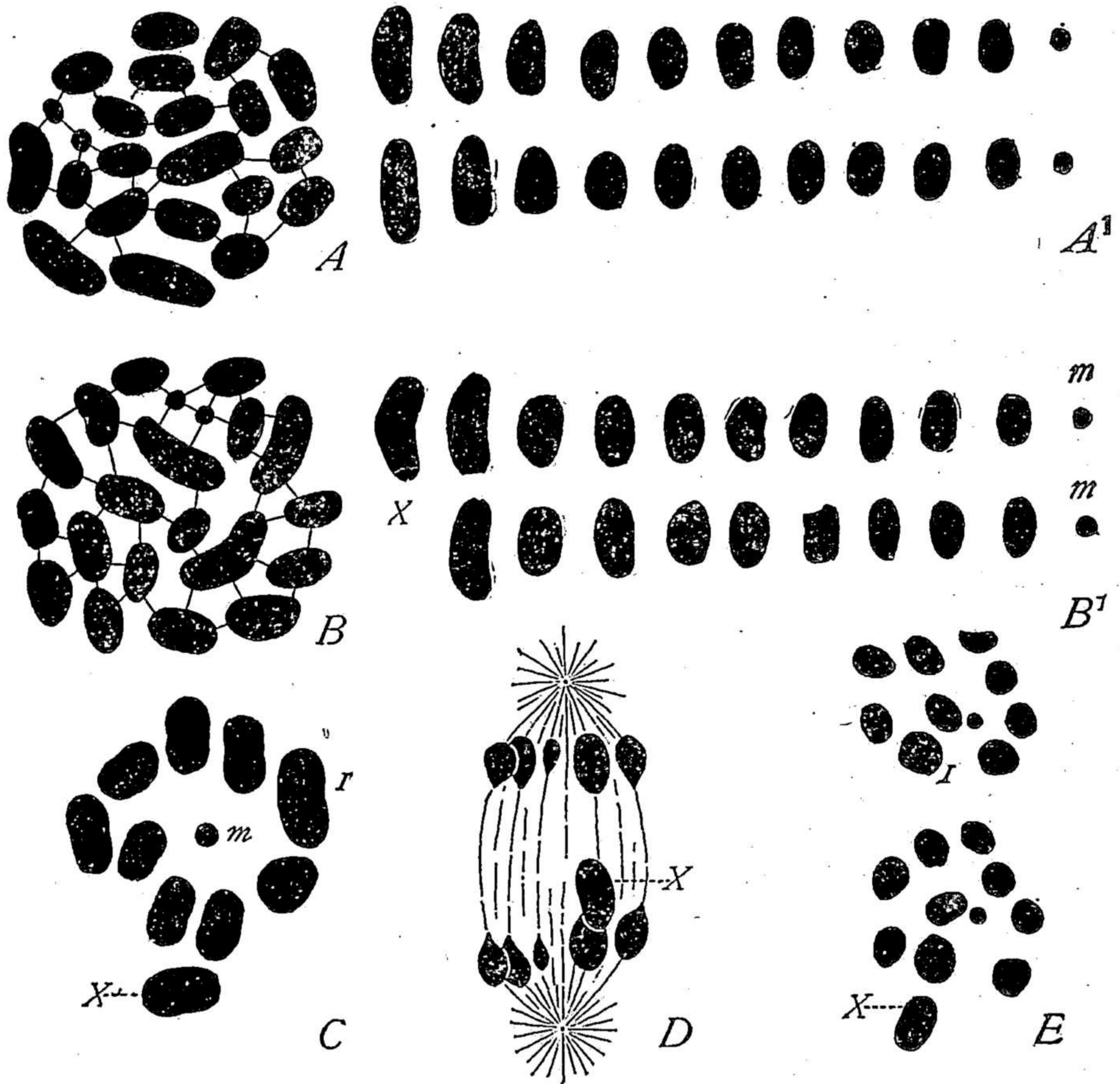


Fig. 354.—Sex-chromosomes in the squash-bug *Anasa tristis*.

A, female diploid group, 22 chromosomes; *A*¹, the same arranged in pairs; *B*, corresponding group in the male (21 chromosomes), one of the largest four (*i. e.*, one *X*) being absent; *B*¹, the same arranged in pairs; *C*, first spermatocyte-metaphase, characteristic grouping, 10 bivalents, one univalent (*X*); *D*, second spermatocyte-anaphase, *X* passing to one pole; *E*, sister anaphase-groups of same division, one with 10 chromosomes (no *X*-class) and one with 11 (*X*-class).

degenerating after the fashion of polocytes, and that either sex may be produced after fertilization by sperms of the *X*-class.¹

This confusion was dispelled by the discovery that it is the *female* that possesses one more chromosome than the male, the diploid chromosome-groups of the former containing two *X*-chromosomes, those of the male

¹ Gross, '04, '06, Wallace, '05.

but one;¹ while in respect to all the other chromosomes the sexes are of identical constitution (Figs. 354, 355). Their total chromosome-number is therefore even in the female and odd in the male. In *Protenor belfragi*, for example, the female number is 14, the male number 13, and the X-chromosome is immediately recognizable because it is at least twice the size of the next smaller. It is here seen at a glance that the male contains a single, unpaired large chromosome, the female two such chromosomes (Fig. 356).

In the female, obviously, the diploid groups consist of two similar series of chromosomes; in other words, all the chromosomes may be arranged in symmetrical pairs of synaptic mates (p. 503), one of these being the X-

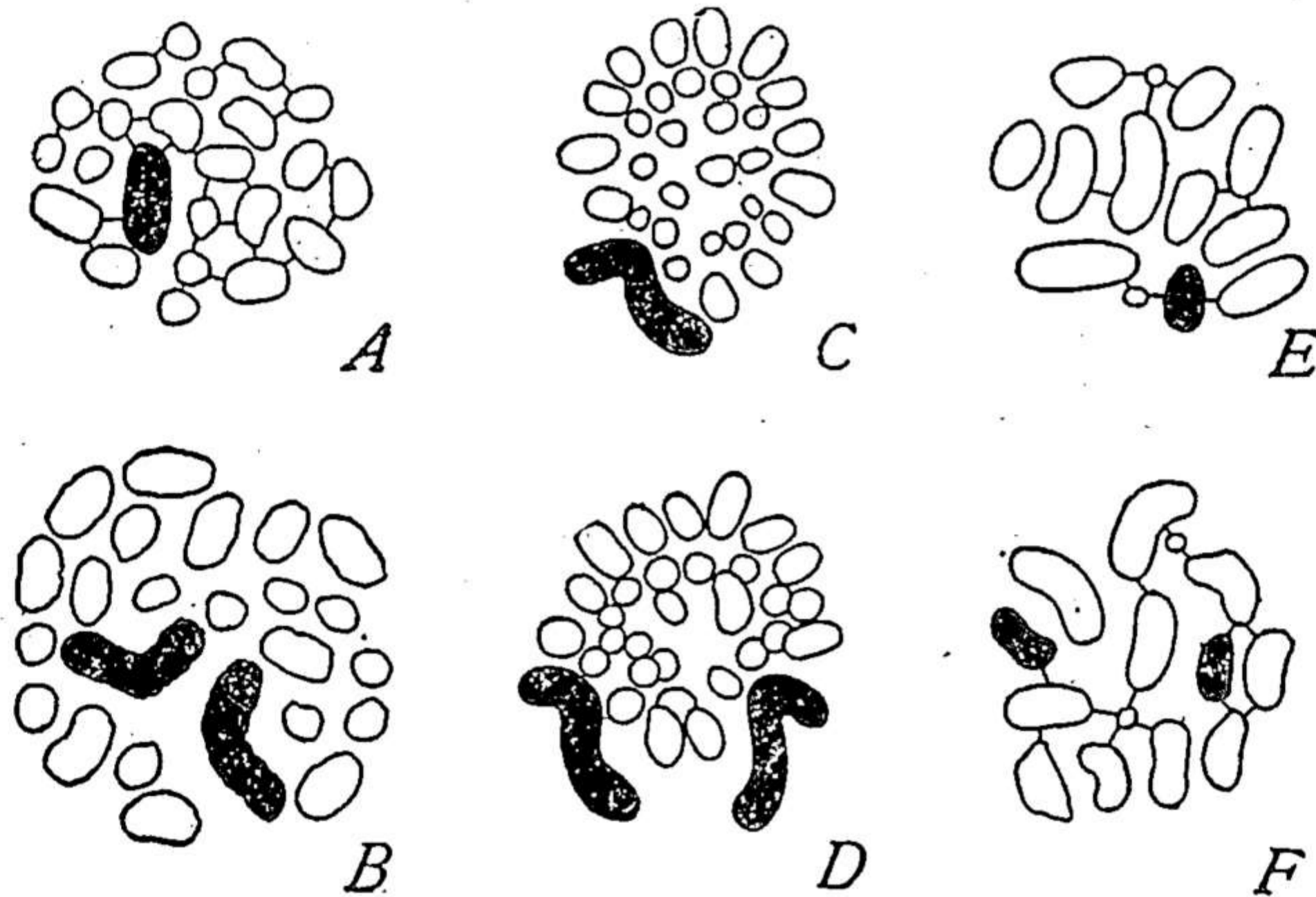


Fig. 355.—Sexual differences of the diploid chromosome-groups in insects (C and D, from MOHR). The X-chromosome black in each case.

A, B, male and female diploid groups of the hemipter *Pyrrhocoris*, 23 and 24 chromosomes; C, D, corresponding groups from the grasshopper *Leptophyes*, 31 and 32 chromosomes; E, F, from the hemipter *Alydus*, 13 and 14 chromosomes.

pair. In the male, the conditions are the same except that one member of the X-pair is missing. With this fact in mind all becomes clear. In the female synapsis produces, as usual, the haploid number of bivalents, including XX, and all the mature eggs are alike, each receiving a complete haploid series, including one X (Fig. 358). In the male, on the other hand, the unpaired X-chromosome has no synaptic mate, and hence enters but half the sperms. The latter, accordingly, comprise an X-class and a no-X class, in equal numbers (Fig. 357). The sex of the fertilized egg depends therefore upon the class of sperm that enters it in fertilization, as in the following formulas:²

$$\text{Egg AX} + \text{Sperm AX} = \text{AAXX} (\text{♀})$$

$$\text{Egg AX} + \text{Sperm A} = \text{AAX (or AAXO)} (\text{♂})$$

¹ This was first demonstrated in the hemipteran genera *Protenor*, *Anasa*, *Alydus*, and *Harmostes* (Wilson '05, '05a, '05b, '06), later in many other forms.

² In this and all succeeding formulas of this type A denotes the haploid group of autosomes or ordinary chromosomes common to all the gametes.

This is also shown in the diagram (Fig. 352) where the no-X class of sperm is designated as Y.

Two additional results of the first importance are made clear by these diagrams. (1) If fertilization take place at random, *i. e.*, if the chances be equal that a sperm of one class or the other will enter any particular egg, then the two sexes should in the long run appear in equal numbers. Departures from such equality are therefore probably to be ascribed to secondary causes, such as different degrees of activity or of viability in the two classes of sperm, or in male and female embryos. (2) *The single X-chromosome of the male is derived from the mother.* This chromosome, therefore, may alternate between the sexes in successive generations; and in fact it always passes from the male to the female in the production of females, and from the female to the male in the production of males.¹ On this fact, as will later be shown, depend some of the most characteristic features of sex-linked heredity.

Two of the conclusions involved in the foregoing interpretation, though firmly based upon our general knowledge of the chromosomes in meiosis and fertilization, were at first inferential, namely, that in maturation each egg receives a single X-chromosome, and that the observed sexual differences in the diploid chromosomes are determined by the class of sperm that enters the egg. Both conclusions were later substantiated by direct observation. The first was established through the work of Morrill ('10) on the maturation of the egg in various Hemiptera (including *Protenor* and *Anasa*); that of Boveri and Gulick ('09) and of Gulick ('11) on the nematode *Heterakis*; and that of Mulsow ('12) on the nematode *Ancyracanthus*, the last a particularly favorable object for study of the entire cycle of the chromosomes. In this form the chromosomes remain separate in the sperm, so that they may readily be counted and are visible even in life (Fig. 357). It was thus possible to establish the entrance into the egg of both classes of sperms; the formation from them of the male pronuclei, containing in one case five chromosomes, in the other six; the presence of six chromosomes in the egg-nucleus; and finally zygotes of two types, containing either 12 or 11 chromosomes (Fig. 358), the respective female and male diploid numbers. So far as its morphological aspects are concerned, therefore, the entire internal mechanism of sex-production in these animals has been clearly demonstrated.

b. Comparative. The simple XO-XX type has since been found in many animals of various groups, though in many individual cases the conditions in the female still remain a matter of inference. The chromosome-numbers in both sexes have been observed in Hemiptera, Odonata, Coleop-

¹ Wilson ('06), p. 28.

tera, Diptera, Orthoptera, sea-urchins, nematodes and mammals, and also in a considerable number of the parthenogenetic forms, such as the Hymenoptera, Hemiptera and rotifers. The unpaired X-chromosome has



Fig. 356.—Sexual differences of the chromosomes in the hemipter *Protenor*.

A, male diploid group (spermatogonium) and *B*, female group (ovarian cell) with chromosomes numbered in the order of their size; in *A*¹ and *B*¹ the same chromosomes are arranged in pairs according to size.

also been found in the males of myriapods, and spiders; and it is hardly to be doubted that further search will reveal its presence in many other groups. A partial list of the observed chromosome-numbers follows.¹

SIMPLE XO-XX OR PROTENOR TYPE

NAME	GROUP	DIPLOID NUMBERS		HETERO-KINESIS	AUTHORITY
		♂	♀		
<i>Cerastipsocus venosus</i>	Corrodentia	17	(18)	pr.	Boring, '13
<i>Anax junius</i>	Odonata	27	28	"	Lefevre and McGill, '08
<i>Tettigidea parvipennis</i>	Orthoptera	13	14	"	Robertson, '08, '15
<i>Stenobothrus curtipennis</i>	"	17	(18)	"	Davis, '08
<i>Pamphagus marmoratus</i>	"	19	20	"	Granata, '10
<i>Gryllus domesticus</i>	"	21	22	"	Baumgartner, '04, Gutherz, '07-'09, Meek, '13,

¹In the fifth column, *pr.* and *po.* mean respectively *pre-heterokinesis* and *post-heterokinesis* (p. 755).

SIMPLE XO-XX OR PROTENOR TYPE—*Continued*

NAME	GROUP	DIPLOID NUMBERS		HETERO-KINESIS	AUTHORITY
		♂	♀		
Hippiscus tuberculatus	Orthoptera	23	24	pr.	Davis, '08
Blatta germanica	"	23	24	"	Wassilieff, '07
Locusta viridissima	"	29	30	"	Mohr, '15
Periplaneta americana	"	33	34	"	Morse, '09
Aplopus mayeri	"	35	36	"	Jordan, '08
Diestrammena marmorata	"	57	(58)	"	Schellenberg, '13
Aphis saliceti	Homoptera	5	6	"	Baehr, '08, '09, '12
Aphis œnotheræ	"	9	10	"	Stevens, '05, '06, '09
Euchenopa curvata	"	19	20	"	Kornhauser, '14
Aprophora quadrangularis	"	23	24	"	Stevens, '06
Pœcilopectera (2 species)	"	27	28	"	Boring, '07
Largus cinctus	Heteroptera	11	12	"	Wilson, '07
Largus succintus	"	13	14	"	Wilson, '07
Protenor belfragi	"	13	14	po.	Montgomery, '01, Wilson, '05
Archimerus calcaratus	"	15	16	pr.	Wilson, '05
Anasa tristis	"	21	22	po.	Wilson, '05
Pyrrochoris apterus	"	23	24	"	Henking, '90 Wilson, '09
Chariesterus antennator	"	25	26	"	Montgomery, '01, Wilson, '09
Necrophorus sayi	Coleoptera	13	(14)	pr.	Stevens, '09
Limoneus griseus	"	17	(18)	"	Stevens, '09
Photinus consanguineus	"	19	20	po.	Stevens, '09
Diabrotica vittata	"	19	20	"	Stevens, '09
Pachyulus varius	Myriapoda	25	(26)	pr.	Ettinger, '09
Scolopendra heros	"	33	(34)	"	Blackman, '03, '05, '10
Scutigera forceps	"	37	(38)	"	Medes, '05
Epeira scolopetaria	Arachnida	23	(24)	"	Berry, '06
Heterakis dispar	Nematoda	9	10	"	Gulick, '11
Strongylus paradoxus	"	11	12	"	Gulick, '11
Rhabditis nigrovenosa	"	11	12	po.	Boveri, '11
Ancyracanthus cysti	"	11	12	"	Mulsow, '11
Canis familiaris	Mammalia	21	22	pr.	Malone, '18
Felis catus	"	35	36	"	Winiwarter, '14
Equus caballus	"	37	(38)	"	Wodsdalek, '14
Homo sapiens (see XY-list, p. 766)	"	47	48	"	Winiwarter, '12
Mus norvegicus (albino)	"	37	(38)	"	Allen, '18

The size of the X-chromosomes varies widely in different species and shows no correlation with sex. In some cases X is the largest of all the chromosomes and is thus readily distinguished by the eye, *e. g.*, in *Pyrrhocoris*, *Protenor* (Fig. 356) *Orphania*, *Catorintha*, *Leptophyes* (Fig. 355). In *Anasa tristis* (Fig. 354) or in *Blaps lusitanica* (Fig. 378) it is one of the two largest pairs of chromosomes. In many other cases (*Alydus*, *Largus*, *Anax*) it is one of the smaller chromosomes, not to be distinguished by the eye

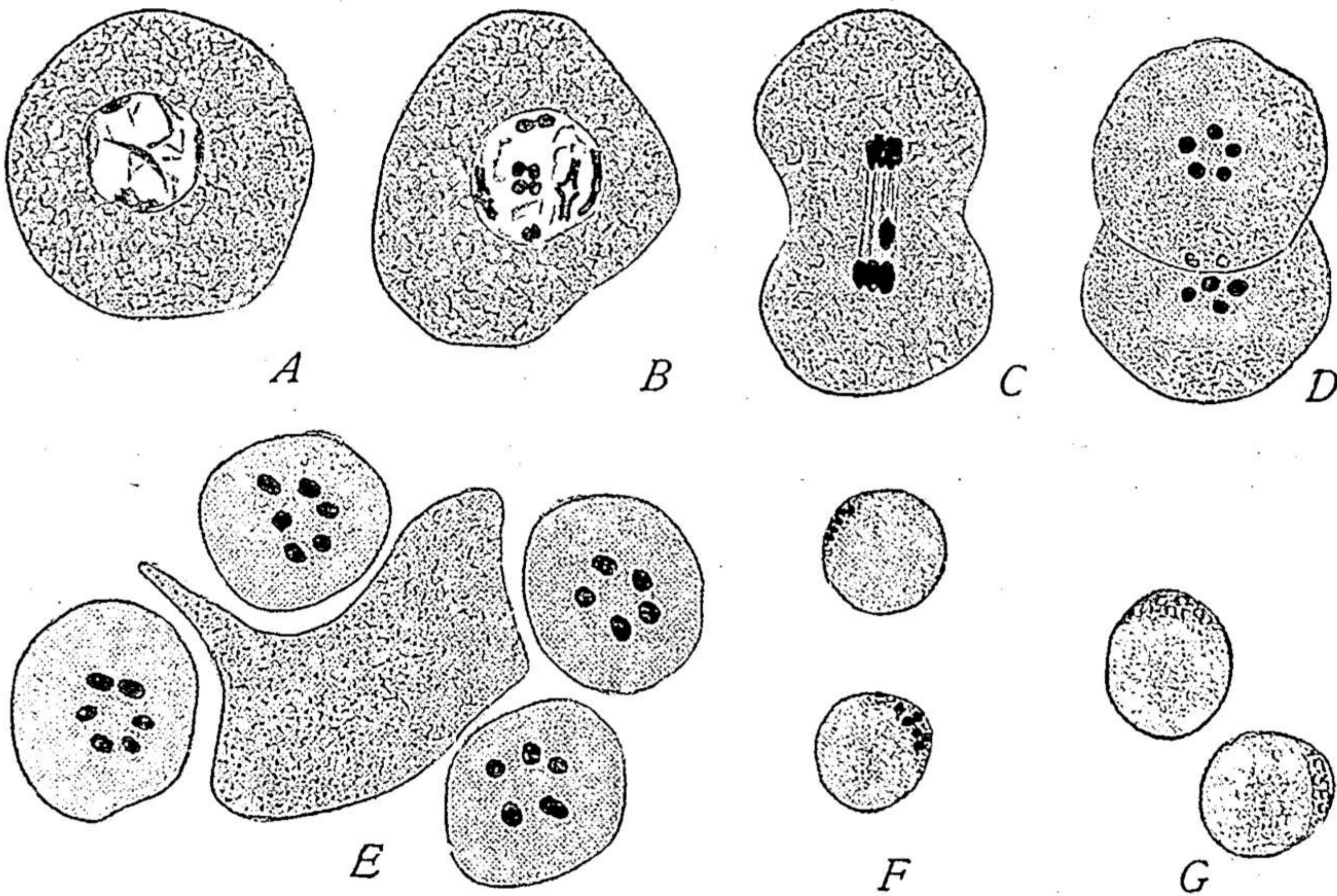


Fig. 357.—History of the X chromosome in the spermatogenesis of the nematode *Ancyracanthus* (MULSOW).

A, spermatocyte in the growth-period; C, first spermatocyte-anaphase, with X passing to one pole; D, products of this division with 5 and 6 chromosomes; E (from a smear-preparation), the four spermatids of a quartet (with spermatophore in the center) two of the X-class (6 chromosomes) and two of the 10-X (5 chromosomes); F, sperms of the two classes; G, the same, from life.

except during the spermatocyte-divisions. In others, again, X is the smallest of the chromosomes, *e. g.*, in *Philænus* (Boring, '13) or *Photinus* (Fig. 359). In still other cases it is closely linked with one of the other chromosomes and sometimes can only be distinguished under certain special conditions (*Ascaris megalocephala*, p. 779).

Pre-heterokinesis and Post-heterokinesis. Precession and Succession. In all the foregoing cases the X-chromosome shows essentially the same behavior in meiosis; it divides equationally in one division and in the second passes undivided to one pole so as to give two equal classes of sperm. It is an important fact that the differential division or *heterokinesis*¹ (*i. e.*, that in which X passes undivided to one pole) may be either the first or second spermatocyte-division, two cases which for the sake of brevity may

¹ This term is due to Gutherz '07.

be spoken of as *pre-heterokineses* and *post-heterokinesis* respectively. In the Heteroptera post-heterokinesis is the rule; in the Homoptera, pre-heterokinesis, as is also the case in the Orthoptera; but nearly related forms, even species of the same genus, may differ in this respect (Wilson, '05, Gulick, '11). The key to such variations seems to be offered in the beetle *Photinus*, in which the X-chromosome undergoes its equational division

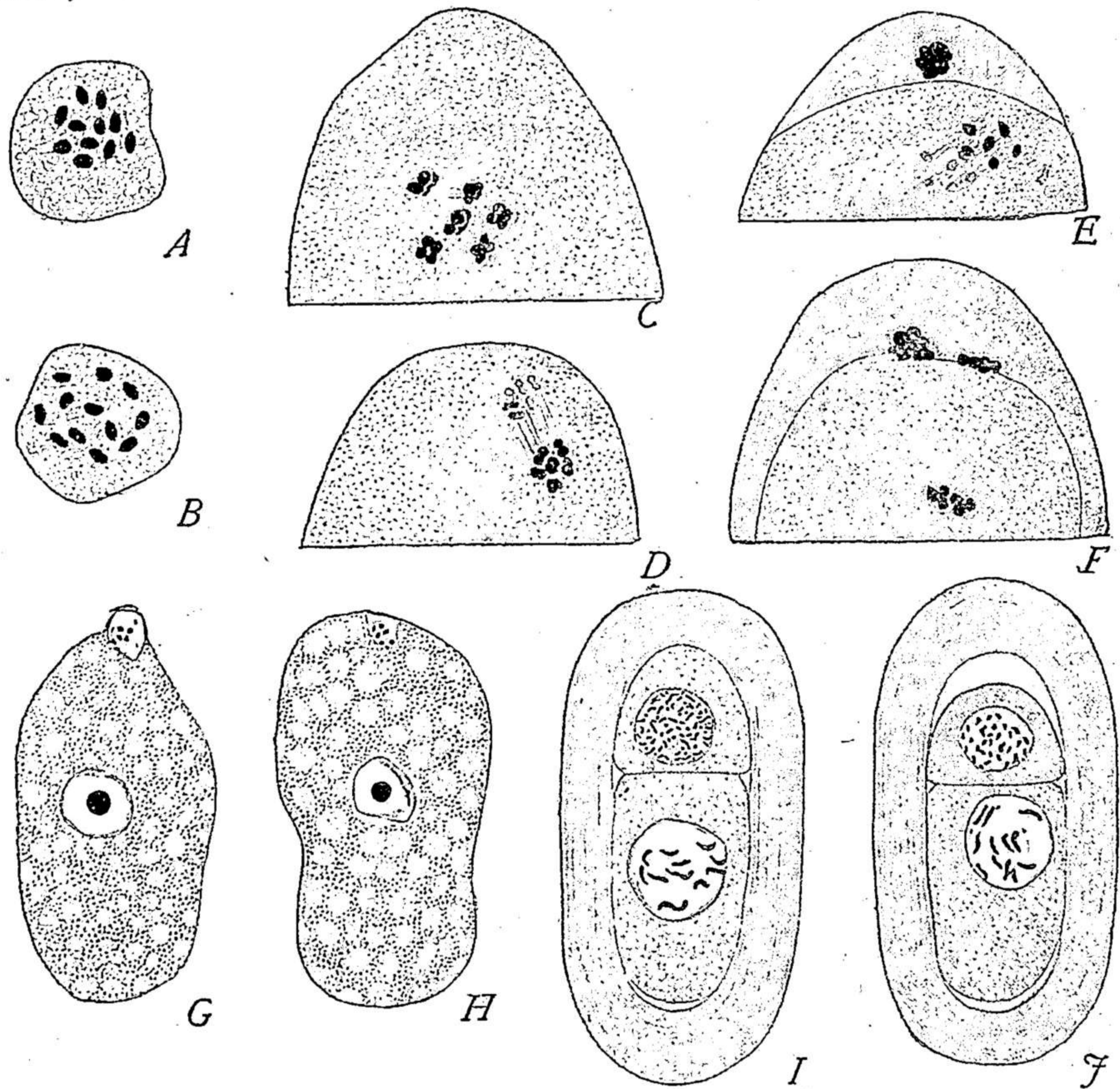


Fig. 358.—History of the X-chromosome in the oögenesis of the nematode *Ancyracanthus* (MULSOW).

A, male chromosome-group (spermatogonium), 11 chromosomes; *B*, female group (oögonium) 12 chromosomes; *C*, late prophase of first oöcyte-division, 6 tetrads; *D*, anaphase of same, 6 dyads, to each pole; *E*, second division anaphase, 6 single chromosomes to each pole; *F*, the two polarocytes above, 5 chromosomes left in the egg; *G*, entrance of no-X sperm (5 chromosomes) into upper pole of egg; *H*, entrance of X-sperm (6 chromosomes); *H*, same, female (12 chromosomes); *I*, *J*, 2-cell stages, male and female.

with the others in the first mitosis, but very commonly lags more or less behind the others. In *P. pennsylvanicus* (Fig. 359) the lagging is but slight, but in *P. consanguineus* is so marked that the two halves remain near together and separate from the other chromosomes after completion of the first division. A slight further retardation of division would cause this chromosome, longitudinally split, to pass without separation of its two

halves to one pole in the first division. This is borne out by the case of *Ascaris megalocephala* where, according to Edwards ('10), both conditions exist in the same species, the process being in some cases nearly like that in *Photinus*, while in others the two halves of X pass together into one daughter-cell (Fig. 359, H, I). We find here some ground to conclude that originally the differential division was the second.

A second fact, as yet unexplained, is that in the heterokinesis the X-chromosome in some cases precedes the others (*precession*) (Fig. 360); in

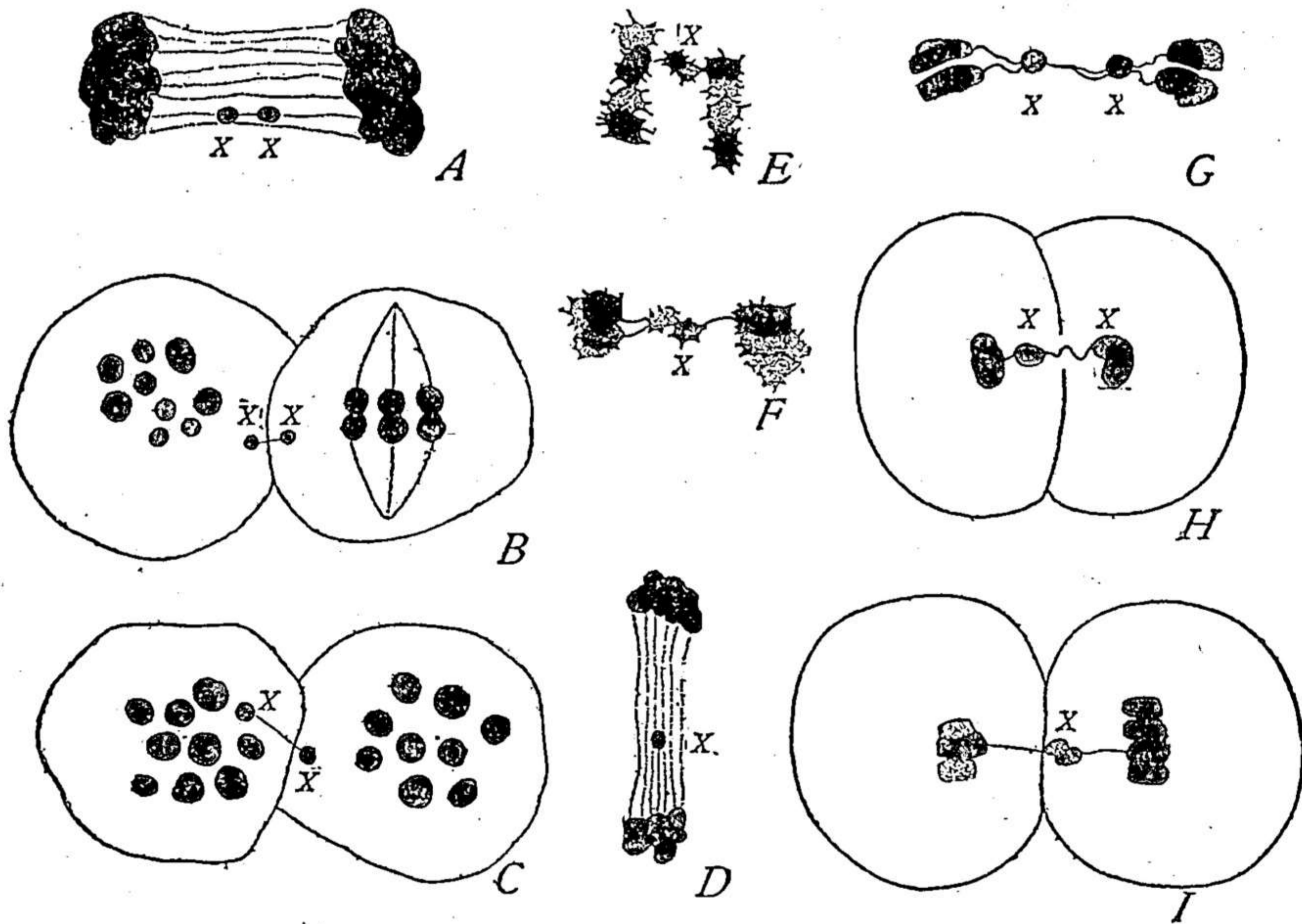


Fig. 359.—The lagging X-chromosome in insects and nematodes (A-D, from STEVENS, G-I, from EDWARDS).

A, first spermatocyte-anaphase in the beetle *Photinus consanguineus*, lagging division of X; B, pair of second spermatocytes of the same in metaphase, with lagging X's at one side; C, similar view with one X in the metaphase-group; D, second spermatocyte anaphase with lagging X; E-G, first spermatocyte-anaphases in *Ascaris megalocephala*, with lagging division of X; H, division of same, separating the two X's (leading to post-heterokinesis); I, division of same species leaving both X's in one cell (pre-heterokinesis).

other cases lags behind them (*succession*). The first case is the rule among the Orthoptera, the second case in *Hemiptera heteroptera* (an exception is offered by *Syromastes*); while both cases occur in Coleoptera and nematodes. When precession occurs in the first division the X-chromosome in some cases gives rise to a small separate nuclear vesicle in the interphase thus recalling its behavior in the spermatogonial divisions of the Orthoptera. Examples of this are offered by *Stenopelmatus* (Stevens, '05), and *Gryllus* (Gutherz, '07, Brunelli, '09) (Fig. 360).

The sex-chromosomes of sea-urchins are of interest because they were first observed in the early cleavage stages of the ovum without knowledge

of the meiotic phenomena; also because these animals were at first believed to offer a case of female digamety (Baltzer, '09); but this later proved to be an error.¹ The critical evidence was obtained from forms in which the sex-chromosome is characterized by its atelomitic or non-terminal attachment, and has accordingly the shape of a V or U (*Toxopneustes*, *Parechinus microtuberculatus*), or of a J (*Paracentrotus*, *Hipponoë*, *Moira*). All the observers named, beginning with Baltzer, have found the segmenting eggs to be of two kinds, some containing one such sex-chromosome and others none, in addition to certain atelomitic autosomes common to both; and that the two classes are approximately of equal numbers, as shown in *Toxopneustes* (Heffner, Pinney), *Hipponoë* (Pinney) and the hybrid between them (Tennent). Whether the sex-chromosome has a rod-shaped synaptic mate or is unpaired is not yet quite certain.

That the male is the digametic sex—*i. e.*, that half the sperms carry X and half lack it—was ingeniously demonstrated by Tennent, and later by Baltzer, by crossing two forms that differ in the shape of the sex-chromosome. The sex-chromosome in *Hipponoë* is J-shaped (Pinney), in *Toxopneustes* V-shaped, and in both cases it appears in only half the straight (pure) fertilized eggs. In the hybrid *Toxopneustes* ♀ x *Hipponoë* ♂ half the eggs show the J-shaped sex-chromosome and half lack it. This chromosome must be derived from the sperm (since it is peculiar to *Hipponoë*) and present in only half of them. Baltzer's similar-proof is based upon the cross between *Sphærechinus* ♀, which has only telomitic rod-shaped chromosomes, and *Paracentrotus* ♂, in which the sex-chromosome is J-shaped. The fertilized eggs are of two classes, one with a J-chromosome, the other without it, thus confirming Tennent's result.

c. Special Peculiarities of the X-chromosome. In the earlier stages of development, and in the division of the somatic cells generally, the X-chromosome does not, so far as known, differ in behavior from the others, nor do the two sexes differ in this respect.² In later stages, on the other hand, the X-chromosome in the male germ-line shows certain special peculiarities of behavior³ which sometimes appear in the spermatogonia and are almost always present in the spermatocytes. In the female line these differences do not exist, or are much less marked.

Heteropycnosis. The most characteristic of these peculiarities is that during the growth-period of the spermatocytes the X-chromosome becomes greatly condensed and often rounded in form, stains intensely with basic

¹ Heffner ('10) and Pinney ('11) on *Toxopneustes*, *Hipponoë*, *Moira*; Tennent ('11), and Baltzer ('13) on hybrids.

² See Morrill ('10), Hoy ('16).

³ Hence the term *heterochromosomes* or *allosomes* applied by Montgomery ('04, '06) to the sex-chromosomes and certain other specialized forms of chromosomes (p. 839).

dyes and thus appears as a karyosome or chromosome-nucleolus (Figs. 361, 266, 267, etc.) which shows the sharpest contrast to the thread-like or diffuse, and lightly staining ordinary chromosomes (autosomes or eu-chromosomes, p. 839). This process of *heteropycnosis*¹ was first observed by Henking ('91) in the hemipter *Pyrrhocoris* and found by later observers to be a widespread characteristic of the sex-chromosomes. It shows many variations in respect to the time at which it occurs, the extent to which it

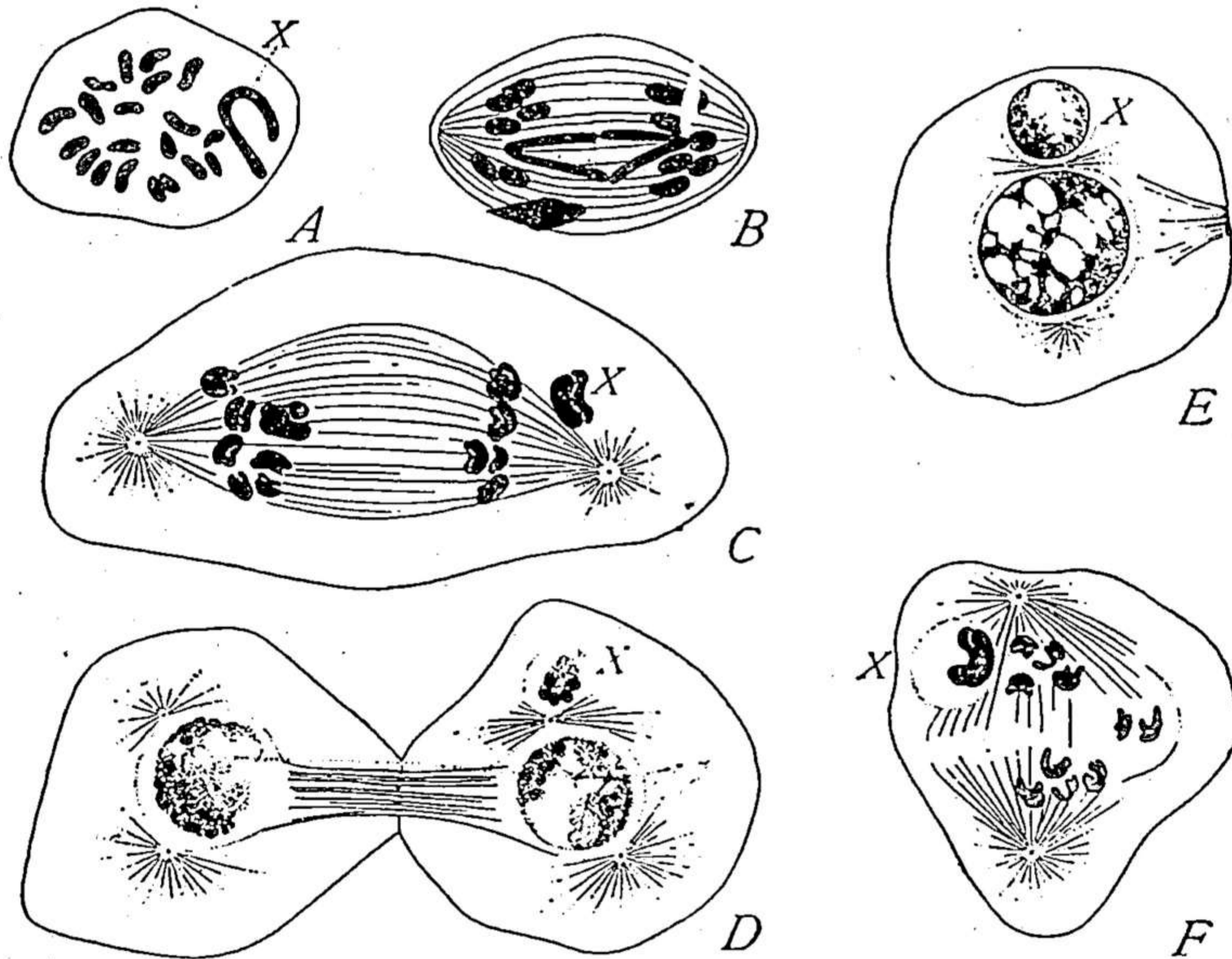


Fig. 360.—The X-chromosome in the cricket *Gryllus* (BRUNELLI).

A, spermatogonial metaphase, 21 chromosomes; B, anaphase in side-view lagging X; C, first spermatocyte-anaphase, precession of X; D, interkinesis, X a separate vesicle; E, prophase of second spermatocyte, X-class.

is carried, and the accompanying phenomena; and in a few cases it seems not to take place at any time.²

In the greater number of cases heteropycnosis first takes place after the final spermatogonial division (*e. g.*, in most Orthoptera, and in Hemiptera generally) but in a few cases it seems to occur also in the spermatogonia. In *Tryxalis*, according to Brunelli ('10) a "progressive heteropycnosis" takes place, X forming a separate reticulated vesicle in the early spermatogonia but in the later divisions showing an increasing tendency to remain in a condensed state during the interkinesis (Fig. 362).³ In Orthoptera most observers have found that the X-chromosome does not (as the other chromosomes do) break up in the telophases but retains its

¹ The term is due to Gutherz ('07).

² *E. g.*, in the spermatocytes of *Aphis saliceti*, Baehr ('12).

³ Cf. Schellenburg ('13) on *Diestrammena*.

compact form though commonly still surrounded by a separate vesicle (Fig. 265).¹

On the other hand, there seems to be no doubt that in some forms the final telophase is followed by a net-like stage or "resting-period" in which all the chromosomes are temporarily in a diffuse or reticulated condition. Examples of this are seen in certain of the Hemiptera and Coleoptera.² This condition is, however, of short duration, the X-chromosome very soon

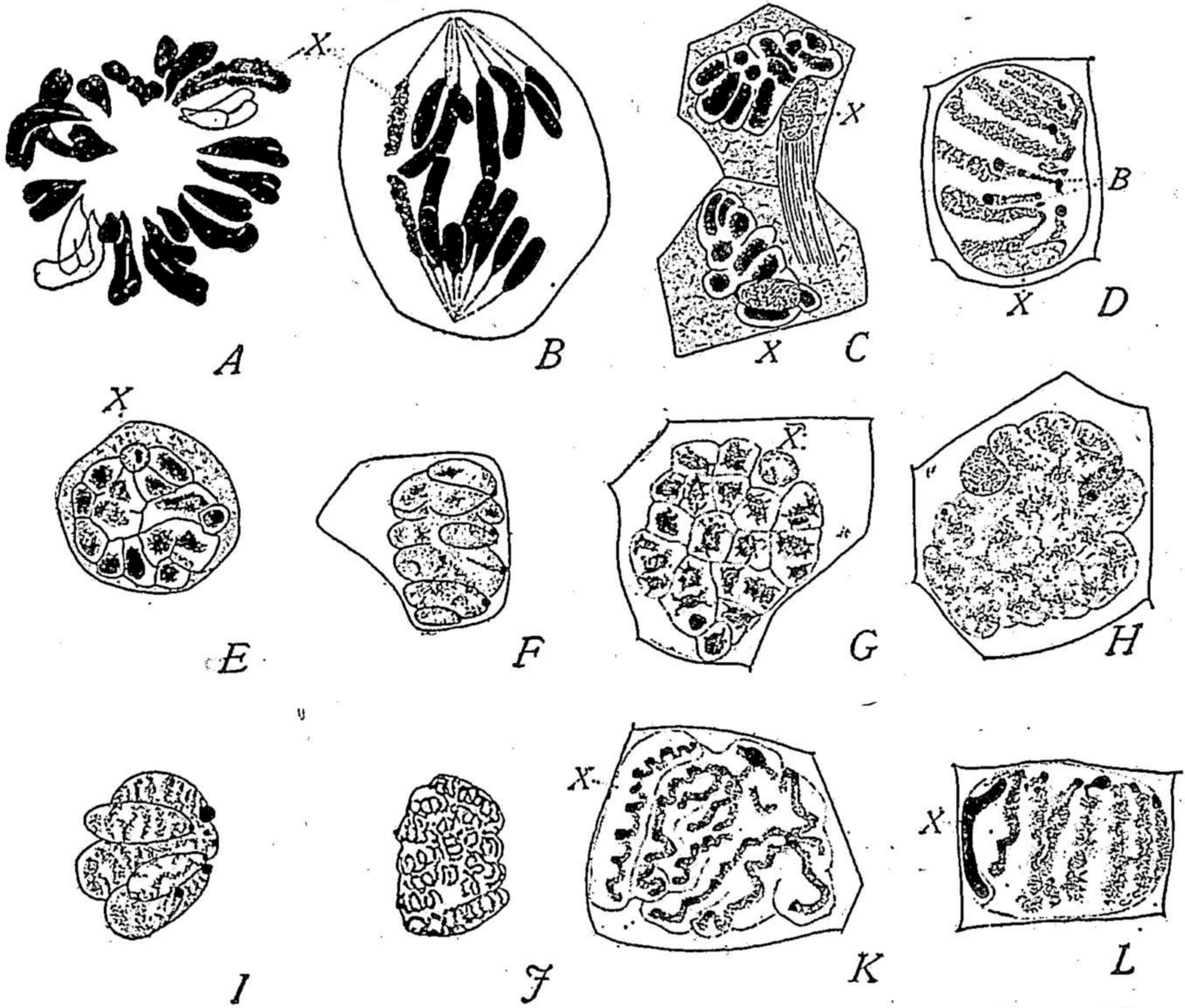


Fig. 361.—Spermatogonial nuclei, prophases and telophases in the grasshopper *Phrynotettix* (A-D, G, H, K, L, WENRICH; E-F, I-L, PINNEY).

In all the figures X designates the X-chromosome.

A, spermatogonial metaphase; B, side-view of anaphase; C, telophase, karyomeres; D, later telophase in side-view, chromosome-pair "B" and X distinguishable; E, cross-section of telophase; F, side-view, polar granules; G, later telophase; H, stage of greatest diffusion; I-K, spermatogonial prophases; L, early pre-synaptic nucleus.

reappearing in a condensed condition, though often more or less elongated (Figs. 266, 267, 361). In the latter case it takes part in the polarization, during the bouquet-stage showing the same orientation as the autosomes.³ In *Locusta* Mohr has emphasized the fact that during the bouquet-stage the X-chromosome elongates and becomes thickened and sharply flexed

¹ This is well shown in the figures of Robertson ('08), Davis ('08), and Wenrich ('16).

² Cf. for Hemiptera Wilson ('12), for Coleoptera Nonidez ('12) on *Blaps*.

³ Compare Moore and Robinson ('05), Buchner ('09), Mohr ('16), etc.

at the middle point, while the two ends, now tapering and pointed, are drawn close together. As a result of this process of "conflexion" it assumes a pear-shape with the narrow end directed towards the synaptic pole and longitudinally double. This cleft is not, however, a longitudinal split, as supposed by earlier observers, but the space between the two approximated limbs of the V. This space soon disappears while the body of the monosome again becomes vacuolated (as in the pre-synaptic stages) and finally assumes once more the form of a compact and open V, which splits lengthwise for the equational-division.

In some cases the chromosome-nucleolus may temporarily undergo a change analogous to the spireme-formation seen in the other chromosomes.

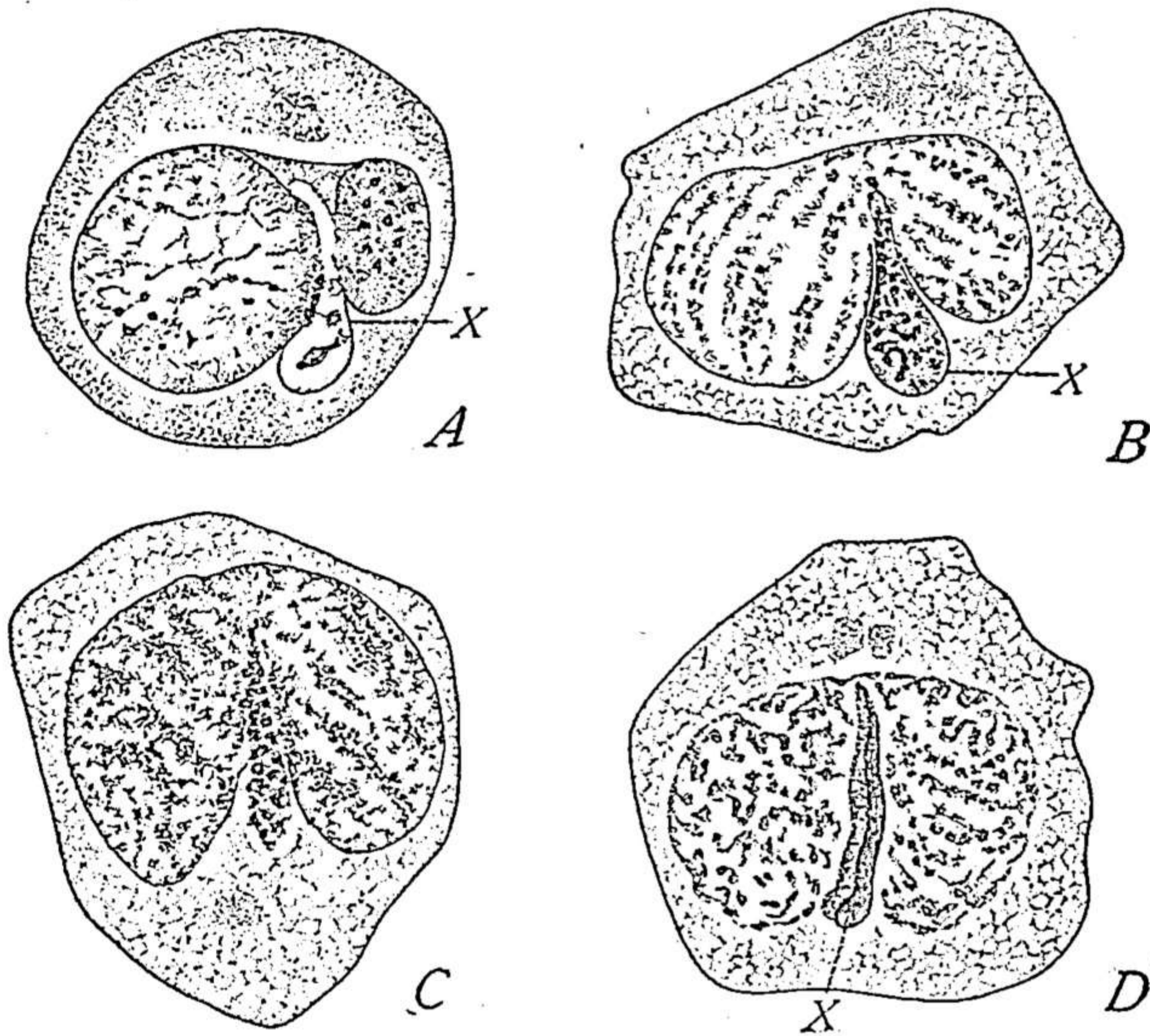


Fig. 362.—Progressive heteropynosis of the X-chromosome in the spermatogonia of the grasshopper *Tryxalis* (BRUNELLI).

A, B, earlier spermatogonia, showing separate X-vesicle; C, later, and D, penultimate generation of spermatogonia showing condensation of X.

This was first observed by McClung ('99, '00) in the locustid *Xiphidium*, where the X-chromosome, at first forming a flat, vacuolated plate lying against the nuclear membrane, is in the early prophase converted into a closely coiled spireme, which then uncoils, shortens, thickens and splits lengthwise, to form the rod-shaped accessory chromosome.¹ In the Hemiptera or Coleoptera the history of the chromosome-nucleolus appears to be simpler; but here, too, it is known in some cases to undergo during the diakinesis a process of elongation and loosening that seems to be comparable to that seen in Orthoptera.²

¹ See Mohr (*op. cit.*), also Davis ('08) and Wenrich ('16) in *Phrynotettix*.

² E. g., in *Anasa* (Foot and Strobell, '07), or *Oncopeltus* (Wilson, '12).

Sooner or later in the course of these changes the X-chromosome becomes double, owing to a longitudinal split that represents the plane of the equatorial-division. This is often plainly in evidence in the first division, even when the X-chromosome fails to divide at this time, so that it passes to one pole as a longitudinally double body (commonly the case in Orthoptera). At this time it shows no special peculiarities to distinguish it from the other chromosomes, save for the rough contour seen in many Orthoptera (Fig. 361) and sometimes also in the fact that even when it divides in this mitosis it lags somewhat behind them in the division. It is an interesting fact that in some cases the position of the X-chromosome in the equatorial plate is constant, or nearly so. For example, in the coreid Hemiptera almost without exception the bivalents are grouped in a ring with one small bivalent at the center (Fig. 354, C), while the X-chromosome lies outside the ring; but this is characteristic of the first division only.

During the interphase between the two spermatocyte-divisions the X-chromosome commonly retains its compact form and again appears as a

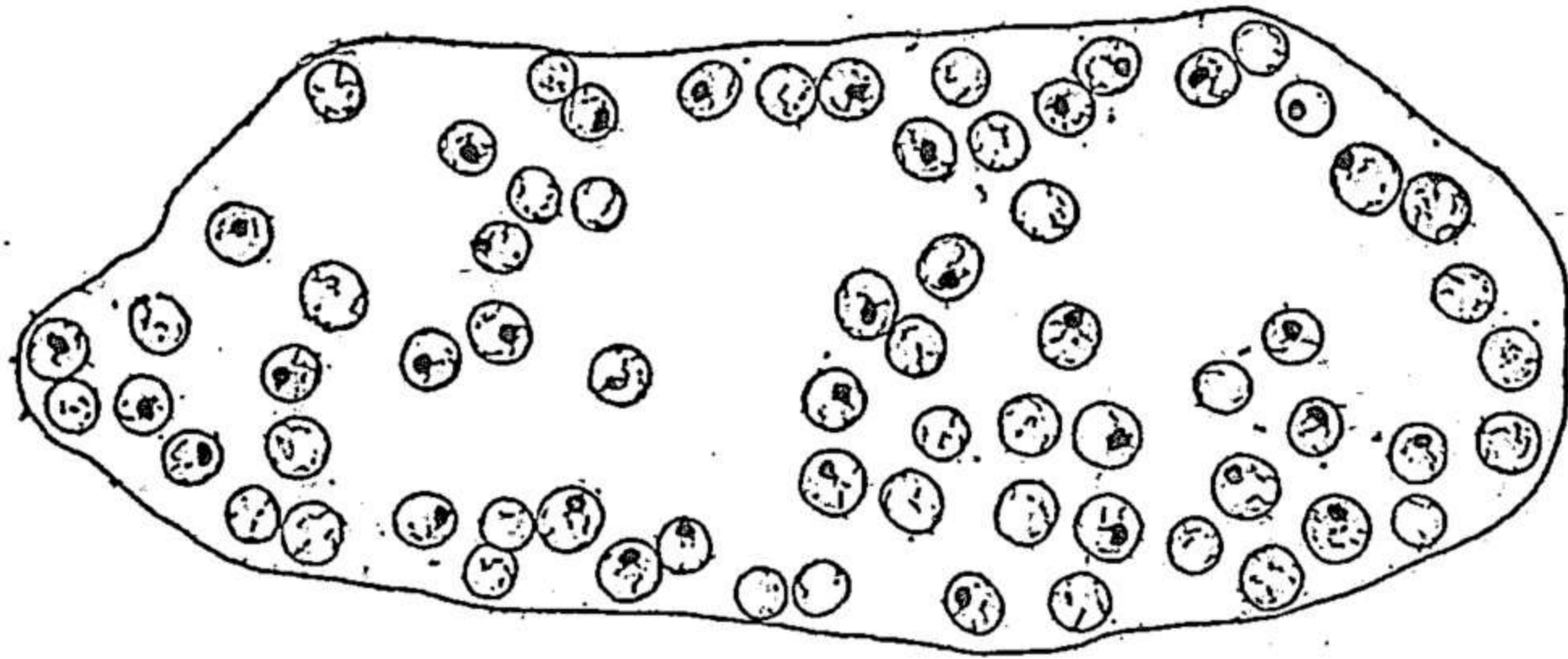


Fig. 363.—Group of spermatid-nuclei of the hemipter *Protenor*, showing 36 of the X-class (with chromosome-nucleolus) and 33 of the no X-class.

homogeneous, intensely staining chromosome-nucleolus. In the second mitosis it is again closely similar to the other chromosomes, but once more shows its distinctive quality after completion of the division by long retaining its compact and nucleolar-like form in the spermatids.¹ The latter, therefore, are for a considerable period visibly of two classes, equal in number, distinguished by the presence or the absence of the chromosome-nucleolus (Fig. 363).

An interesting feature of the chromosome-nucleolus is its almost invariable intimate relation with the plasmosome. Among many of the Hemiptera the chromosome-nucleolus is in its earlier stages accompanied by a plasmosome forming with it a typical amphinucleolus (p. 94); but in later stages the two commonly separate:² and the same has been re-

¹ This was described and figured by Henking in *Pyrrhocoris*, and has since been confirmed by many others.

² Cf. especially Montgomery, '01, '06; Wilson, '05, '06, '09, '12, etc.

corded in many other animals. At a still earlier period (synaptic and pre-synaptic stages) the plasmosome is usually absent; but in regard to its mode of origin the only safe statement is that it seems in most cases to arise in close connection with the sex-chromosomes. In the Orthoptera varying accounts of the phenomena have been given. In *Decticus*, a locustid, Buchner ('09) described the plasmosome as arising by an actual division of the X-chromosome. In *Blatta* Morse ('10) found the plasmosome as a small sphere, like a bead, attached to the spheroidal X-chromosome. From a study of *Phrynotettix* Wenrich ('16) is led to suggest a derivation of the plasmosome from one or more of the "polar granules" found at one end of certain chromosomes (p. 910). This whole subject is thus seen to be in need of further study and can hardly with advantage be followed out here.

The conditions in the female have as yet received comparatively little attention, mainly because of greater practical difficulties. It has long been known that the germinal vesicle or oöcyte-nucleus often contains one or more intensely staining nucleoli, but only in a few cases is there evidence of any relation between them and the chromosome-nucleoli of the spermatocytes. Observations on the early oöcytes of various Hemiptera (Wilson, '06), including the synaptic stages and early growth-period, failed to show anything like the chromosome-nucleoli that are so characteristic of these stages of the male; and the later studies of Foot and Strobell ('09), which extended the work to later stages of the germinal vesicle, yielded the same result, as did also those of Payne ('12) on *Gelastocoris*. On the other hand, a few observers have found a chromosome-like body in the oöcyte-nucleus which they have more or less definitely identified as the X-chromosome-bivalent; though in no case has it actually been traced into either the oögonial or the meiotic divisions.¹ Until this has been accomplished, judgment on this question will have to be reserved.

In addition to the foregoing the X-chromosome often shows other characteristics, especially in the spermatogonial chromosomes of Orthoptera. The most important of them were first made known by Sutton ('00) in his studies on the "lubber" grasshopper (*Brachystola*) and with various minor modifications have since been observed in many species, though not all of them al-

¹ Among these cases may be mentioned the following. In the homopter *Aprophora-quadrangularis*, Stevens ('06) describes one or two X-chromosome-nucleoli in the pre-synaptic and synaptic oöcyte-nuclei. Gutherz ('07) likewise finds a "chromatin-nucleolus," closely similar to that of the male, in the oöcyte-nucleus of *Pyrrhocoris* (as did also Henking); while Buchner ('09) describes in the oöcytes of *Gryllus* a very large "accessory body" that participates in the polarization during the bouquet-stage, gives rise to a large, irregular nucleolus, and finally disintegrates. There is, however, no reason whatever to identify this body with an X-bivalent, but rather the contrary. In the cat Winiwarter ('09, '14), describes a chromosome-nucleolus in both sexes and concludes that it is univalent in the male, bivalent in the female. There is no particular reason to doubt the correctness of this result; nevertheless, it should not be fully accepted until the direct proof is forthcoming.

ways coexist in the same species.¹ These are: (a) In many cases the rough contour of this chromosome, in contrast to the smooth outline of the others (Fig. 361); (b) its tendency, in some species very marked (*Orphania*, *Gryllus*, etc.) to lag behind the others in the divisions (Fig. 360); and especially (c) its relative independence of the other chromosomes in the spermatogonial interkinesis or resting-stages. In the latter the X-chromosome typically appears in the form of a separate vesicle, showing a reticulated structure often giving precisely the appearance of a small second nucleus lying beside the principal one (Figs. 361, 362).

In some respects this behavior is only an exaggeration of that shown by the other chromosomes; for in these divisions, as Sutton showed, all the karyomeres or chromosomal vesicles are very persistent and fuse but incompletely in the interkinesis or resting-stage (Fig. 361). Nevertheless, the contrast offered by the X-chromosomes is very marked, for the autosome-vesicles usually fuse more or less towards the poles, thus producing a glove-shaped lobed nucleus, while the X-vesicle remains wholly distinct. In structure also this vesicle differs markedly from the others, the X-chromosome breaking up into a finer reticulum than the others, and also lagging behind them in the ensuing transformation of the prophase, when the X-chromosome produces its own spireme, separate from the others, within its vesicle (Fig. 361), and somewhat later. The meaning of these phenomena, and of those earlier considered, is unknown; but they are of far-reaching general interest as demonstrating both the individuality of the X-chromosome and its physiological differences from the other chromosomes.²

2. The Simple XY-XX or Lygæus Type

The second type, now to be considered, includes a large number of cases, which almost certainly represent a more primitive condition from which the XO-XX or *Protenor* type has been derived, and is characterized by the presence in the male of a synaptic mate for the X-chromosome known as the Y-chromosome.³ The sex-formulas thus become $XY = \sigma$ and $XX = \varphi$. Since

¹ See Sinéty ('01) on the phasmids, *Leptynia*, *Orphania*; Baumgartner ('04) and Brunelli ('08) on *Gryllus*; McClung ('02), Otte ('07), and Mohr ('14, '16) on Locustidæ; Davis ('08) on various Acrididæ; Robertson ('08) on *Syrbula*; Pinney ('08) and Wenrich ('16) on *Phrynotettix*; McClung ('14) on various Acrididæ; and others.

² Cf. pp. 839, 920.

³ Wilson ('09). In earlier papers ('05, '06) this chromosome was called the "small idiôchromosome" and X the large "idiôchromosome," the terms Y- and X- chromosomes being later proposed ('09) in the interest of simplicity. Sex-chromosomes of this type had earlier been seen by Montgomery ('98, '01) in a number of the Hemiptera and described by him under the name of "chromatin-nucleoli" but without recognizing their relation to sex. The history of the X and Y chromosomes and their distribution to the sperm-nuclei was worked out, and possible relations to sex suggested by Wilson ('05) in the Hemiptera (*Lygæus*, *Cænus*, *Podisus*, *Euschistus*) and Stevens ('05) showed in the beetle *Tenebrio*, that the XY pair of the male is replaced in the female by an XX pair.

the autosomes are alike in both sexes the male diploid number of chromosomes thus becomes equal to that of the female; but the sexual differences are nevertheless often clearly visible since Y commonly differs from X in size, form and structure. Sex-chromosomes of this type have been demonstrated in a large number of animals, including especially Hemiptera, Coleoptera, Diptera, Orthoptera, nematodes and vertebrates (man in-

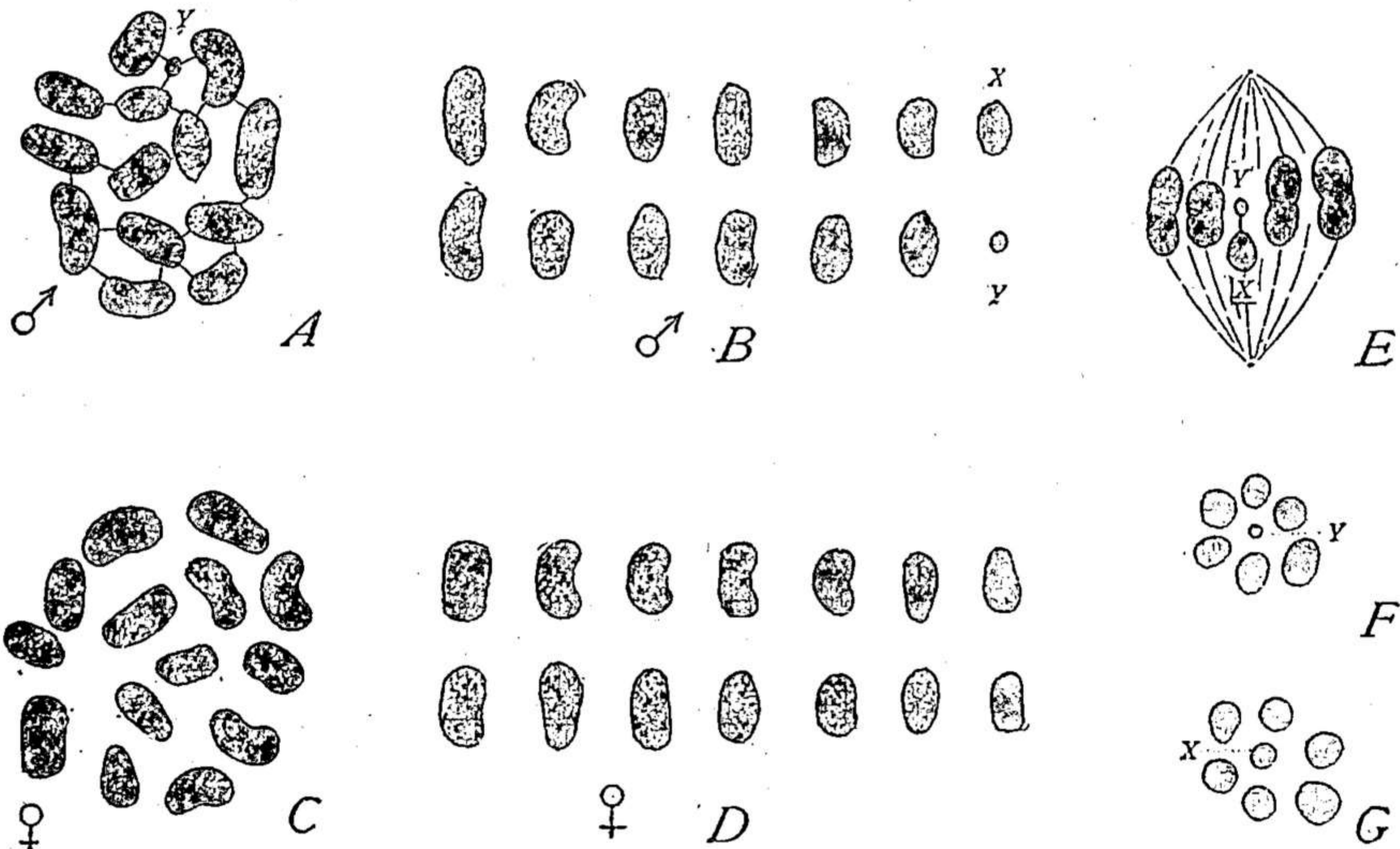


Fig. 364.—Sex-chromosomes (simple XY-pair) in the hemipter *Lygaeus turcicus*.

A, male diploid group; B, the same grouped in pairs; C, female diploid group; D, the same, in pairs; E, second spermatocyte division; F, G, the resulting sister-groups in polar view one with Y (male-producing) and one with X (female-producing).

cluded); and they will no doubt be found in many other groups. An illustrative list follows on page 766.¹

The relation of this type to the foregoing one is clearly shown in Fig. 364. It is here evident that the number of chromosomes is the same in both sexes and that all may be arranged in pairs (synaptic mates); but it is only in the female that all these pairs are symmetrical or homomorphic. In the male one pair is asymmetrical or heteromorphic, consisting of a larger member (X) and a smaller (Y). Should Y become smaller and finally disappear a condition would be produced identical with that of the *Protenor* type. It is extremely probable that such has been the actual origin of the latter.

The phenomena of maturation in this type are precisely such as might be expected from the foregoing facts.² In the male X and Y couple to form

¹ For *Hemiptera*, see Montgomery ('01, '06), Wilson ('05a, b, c, '06, '09b, '12), Payne ('09), Morrill ('10), Browne ('10, '13, '16), Kornhauser ('14); *Coleoptera*, Stevens ('05, '06); *Diptera*, Stevens ('08); Metz ('14, '16), Bridges ('16); *Orthoptera*, Randolph ('08), Stevens ('16), Voinov ('14); *Nematodes*, Edwards ('11); vertebrates, Stevens ('11), Bachhuber ('16), Painter ('21, '22, '23).

² They have been fully and repeatedly worked out in the male, much less completely in the female; but no doubt concerning them in either sex can now exist.

CHROMOSOMES AND SEX

THE SIMPLE XY-XX TYPE

NAME	GROUP	DIPLOID	HAPLOID	HETERO-KINESIS	AUTHORITY
<i>Forficula auricularia</i>	Orthoptera	24	12	pr.	Stevens, '10
<i>Pentatoma senilis</i>	Heteroptera	6	3	po.	Wilson, '13
<i>Cebalus pugnax</i>	"	10	5	"	Wilson, '09
<i>Euschistus crassus</i>	"	12	6	"	Foot and Strobell, '12
<i>Euschistus variolarius</i>	"	14	7	"	Montgomery, '01,
<i>Cœnus delius</i>	"			"	'06, Wilson,
<i>Nezara hilaris</i>	"			"	'05, etc.
<i>Lygæus turcicus</i>	"	14	7	"	Wilson, '05, etc.
<i>Podisus spinosus</i>	"	16	8	"	Wilson, '05, etc.
<i>Oncopeltus fasciatus</i>	"	16	8	"	Montgomery, '01,
				"	'06
<i>Metapodius</i> (3 species)	"	22	11	"	Wilson, '09
<i>Notonecta irrorata</i>	"	24	12	"	Browne, '10
<i>Notonecta undulata</i>	"	26	13	"	Browne, '10
<i>Ranatra</i> sp.	"	40	20	"	Chickering, '18
<i>Oryctes nasicornis</i>	Coleoptera	12	6	pr.	Prowazek, '02
<i>Epilachna borealis</i>	"	18	9	"	Stevens, '06
<i>Tenebrio molitor</i>	"	20	10	"	Stevens, '05, '06
<i>Chelymorpha argus</i>	"	22	11	"	Stevens, '06
<i>Listotrophus unguatus</i>	"	26	13	"	Stevens, '09
<i>Trirhabda canadense</i>	"	30	15	"	Stevens, '06
<i>Drosophila melanogaster</i>	Diptera	8	4	"	Stevens, '08
<i>Scatophaga pallida</i>	"	12	6	"	Stevens, '08
<i>Musca domestica</i>	"	12	6	"	Stevens, '08
<i>Paracentrotus</i> (Strongylocentrotus) <i>lividus</i>	Echinodermata	36	18	"	Baltzer, '13
<i>Ascaris felis</i>	Nematoda	(18)	9	"	Edwards, '12
<i>Didelphys virginiana</i>	Mammalia	22	11	"	Painter, '22, '23
<i>Lepus</i>	"	22	11	"	Bachhuber, '16
<i>Cavia</i>	"	56?	28	"	Stevens, '11
<i>Rhesus macacus</i>	Mammalia	48	24	"	Painter, '23
<i>Cebus</i> , sp.	"	54	27	"	Painter, '23
<i>Homo sapiens</i> ¹	"	48	24	"	Painter, '22

¹ The number of chromosomes in man has long been in dispute (more recently also the character of the sex-chromosomes). The recorded diploid numbers include 16, 22, 24, 32, 36, and 48; but most of these are now seen to have been erroneous because of a failure to overcome the technical difficulties. The most careful recent observations, those of Winiwarter ('14, '21) and Painter ('21, '22) leave little doubt that the correct number is 48. Winiwarter believed man to be of the XX-XO type the numbers being 48 and 47, and the more recent work of Oguma and Kihara ('22) confirms this for the male; but Painter's work seems to show clearly that a small Y-chromosome is present in the male and that the number is 48 in both sexes. This result was reached in the case of both the negro and the white man, thus disposing of the suggestion (Guyer, '14, Morgan, '14) that some of the earlier discrepancies might be due to racial differences of chromosome-number. It is of course possible that the Y-chromosome may be absent in some individuals (as in *Metapodius*). For a list of the recorded numbers see Painter ('22).

a heteromorphic bivalent, XY, which in the heterokinesis separates into its two components so that half the sperms receive X and half Y while all the remaining chromosomes (autosomes) are symmetrically distributed. In the female all the mature eggs alike receive a single X. Fertilization of any egg by the X-class of sperm will accordingly produce the female combination

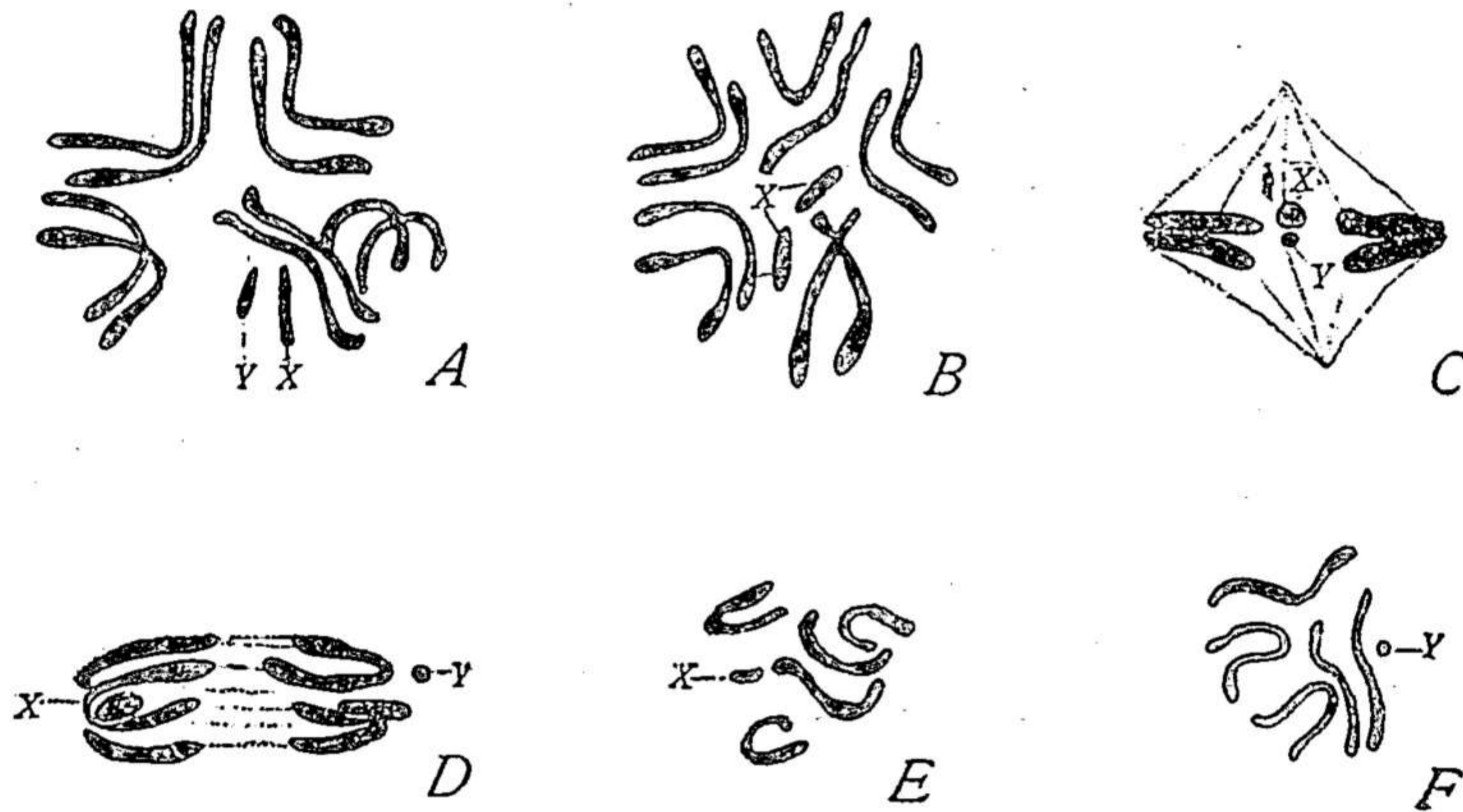


Fig. 365.—The XY-pair in the fly *Calliphora vomitoria* (STEVENS).

A, spermatogonial metaphase, 5 autosome-pairs and the XY-pair; B, corresponding view of oögonial metaphase, with XX-pair; C, first spermatocyte-division, with XY-bivalent; D, anaphase of same; E, metaphase group of X-class second spermatocyte, and F same of Y-class.

XX, by the Y-class of sperm the male combination XY, as will appear from the following formula:

Lygæus Type	Egg AX + Sperm AX = AAXX (♀)
	Egg AX + Sperm AY = AAXY (♂)

Whereas in the first or

Protenor Type	Egg AX + Sperm AX = AAXX (♀)
	Egg AX + Sperm AO = AAXO (♂)

Double proof is thus given that the sex of the zygote depends on the kind of sperm that enters the egg; for both X and Y tell the same story. The Y-chromosome is strictly confined to the male line and can be derived only from the Y-class of sperm. On the other hand, in both sexes one X is derived from the egg, while the female zygote receives its second X from the X-class of sperm.

In all certainly known cases the Y-element is a single chromosome which shows no tendency to break up into separate components such as often appears in the case of the X-element (pp. 772, 778).¹ In the most frequent case Y is distinctly smaller than X, sometimes so small as to appear almost

¹ In the remarkable case of the homopter *Pseudococcus* the facts strongly suggest that the male has a Y-element consisting of five components (p. 778). In *Rumex acetosa* the Y-chromosome (so-called) seems to be double (p. 814).

like a vestigial structure. This condition, observed in a number of *Coleoptera* and *Diptera* (Figs. 365, 366), is connected by all intergradations with one in which X and Y are very nearly or quite equal and can be distinguished by the eye only with difficulty or not at all. All these conditions have been observed in the *Hemiptera heteroptera* (Fig. 368). Finally, in *Oncopeltus fasciatus* (a form nearly related to *Lygaeus*) X and Y are so nearly equal as often to be indistinguishable by the eye (Fig. 369). Throughout this series, however, the identification of the XY-pair is made certain not alone by

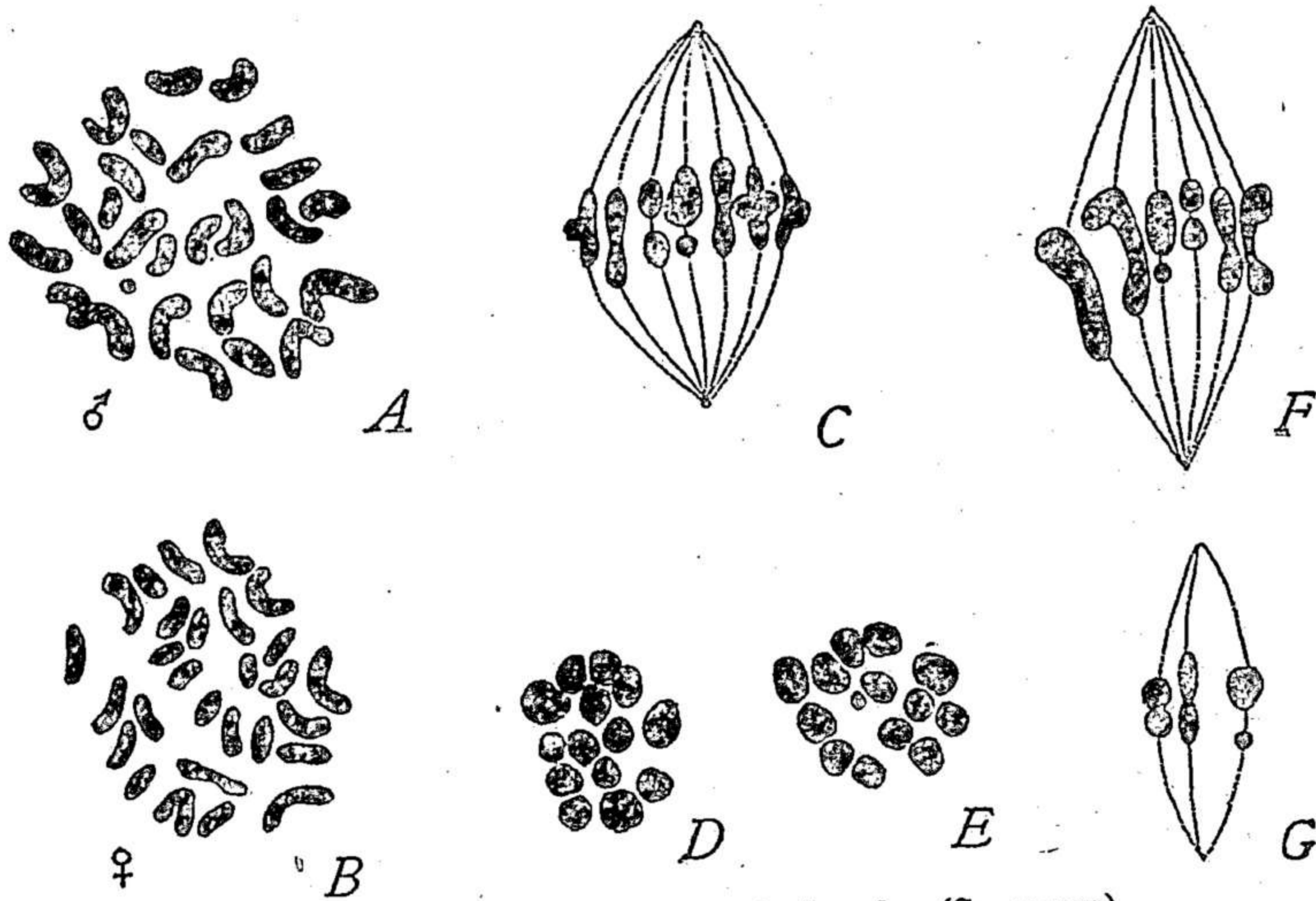


Fig. 366.—Sex-chromosomes in beetles (STEVENS).

A, spermatogonial and B, ovarian diploid groups, *Trirhabda virgata*; C, first spermatocyte-division; D, X-class and E, Y-class of second spermatocytes of same; F, first spermatocyte of *Chrysochus amatus*; G, same of *Photinus*.

the size-relations but by characteristics of behavior in the growth-period and the meiotic divisions, and in the latter also of position.¹

The extremely small size of Y in some cases, and the additional fact that even nearly related species (such as *Nezara viridula* and *hilaris*) may differ so markedly in the relative size of Y, shows how readily the size-relations may change, and how the total disappearance of Y would leave the X-chromosome without a mate (p. 765). On the other hand, those cases in which Y is as large as X (as in *Oncopeltus*) suggest that an XY-pair (or its representative) may be present in many species which seem to show no differentiated sex-chromosomes.²

Most commonly the Y-chromosome (like X) has a terminal attachment

¹ In the second division of *Heteroptera* the XY-pair always occupies the center of the group; cf. Fig. 369. See Wilson ('05, '06, etc.).

² In the hemipteron *Acholla multispinosa* (Payne '10), Y appears to be considerably larger than X (p. 775), and in *Drosophila melanogaster* (Bridges, '13, '16), slightly larger; but these are very exceptional.

to the spindle-fibers; but a few exceptions are known. In the fruit-fly *Drosophila melanogaster* Bridges ('16, etc.) found Y to have a subterminal attachment while X has a terminal one (Fig. 415); and this difference proved to be of great practical importance in analyzing the cytological aspects of non-disjunction (p. 877). In the mantids *Tenodera* and *Paratenodera*, according to Oguma ('21) Y likewise seems to have a sub-terminal attachment, at least in many cases, while in case of the X-chromosomes it is median (Fig. 373).

In the greater number of observed cases X and Y are disjoined in the first or heterotypic division (typically thus in the nematodes, beetles, flies reptiles and mammals) each dividing equationally in the homeotypic division. Such cases offer a spectacular demonstration of pre-reduction for this par-

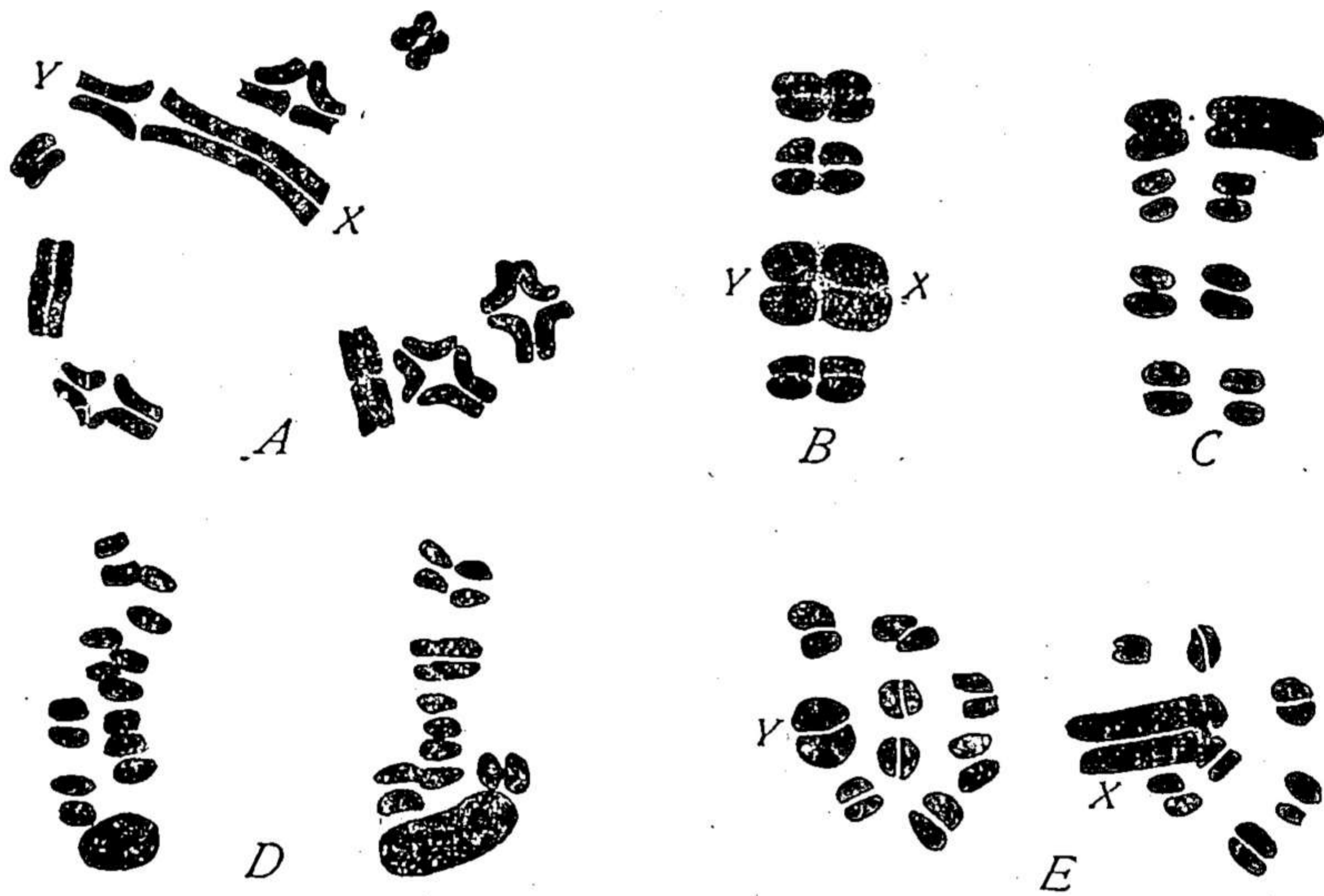


Fig. 367.—Sex-chromosomes in *Ascaris felis* (EDWARDS).

A, prophase of first spermatocyte, showing XY-tetrad; B, metaphase; C-E, anaphases.

ticular chromosome-pair, which in this respect evidently correspond precisely to the pre-heterokinetic forms of the *Protenor* type (such as the Orthoptera), save that in the latter Y is absent. In the Hemiptera heteroptera, on the other hand, the reverse or post-reductional order is almost always followed, the first division being an equational one.¹ No doubt of the facts can here exist because of the remarkable fact that X and Y, though often united during the growth-period, typically separate again during the diakinesis and divide separately as univalents in the heterotypic division lying side-by-side but not in contact (Fig. 369). In the final anaphases of this division they conjugate to form a typical XY-pair that undergoes disjunction in the second division.

¹ Wilson, '05, '06, etc.

During the growth period of the spermatocytes both the X and the Y-chromosomes typically undergo heteropycnosis, assuming a condensed and rounded condition, so as to form chromosome-nucleoli.¹ In most cases (nematodes, Coleoptera, mammals, etc.) they are united to form a single bivalent body, which in the prophases becomes quadripartite to form a tetrad and owing to the smaller size of the Y-component, is commonly asymmetrical (Fig. 367). In Hemiptera, on the other hand, X and Y often

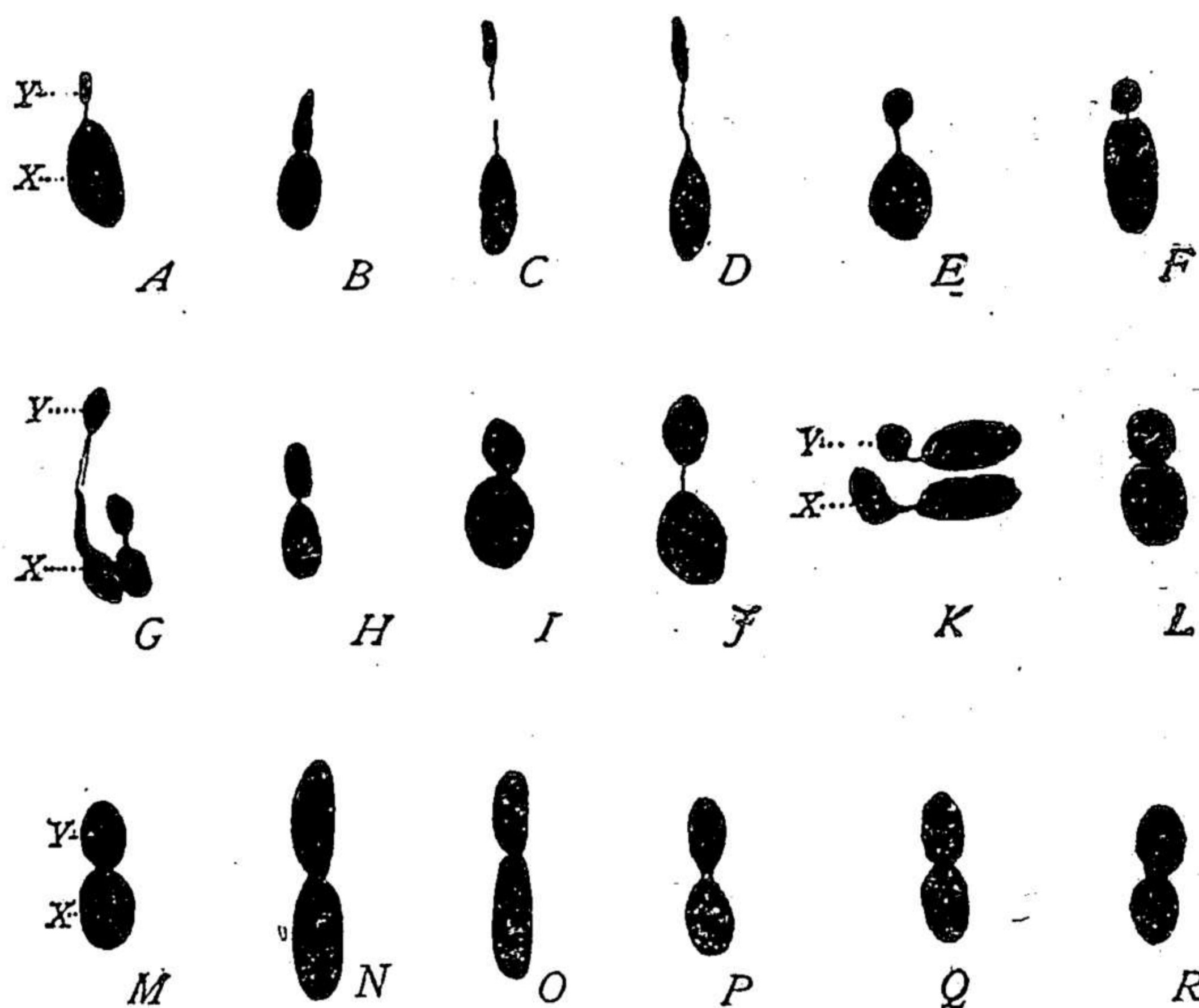


Fig. 368.—Examples of the simple XY-type of sex-chromosome in insects.

A, in the beetle *Trirhabda* (STEVENS); B, C, D, the hemipter *Nezara viridula* (WILSON); E, the hemipter *Lygæus turcicus* (WILSON); F, the beetle *Chrysocus* (STEVENS); G, the hemipter *Notonecta indica* (BROWNE); H, the hemipter *Thyanta custator* (WILSON); I, the hemipter *Euschistus fissilis* (WILSON); J, *Lygæus bicrucis* (WILSON); K, the mosquito *Anopheles*, with X and Y linked to one autosome-pair (STEVENS); L to R, various Hemiptera; M, *Mineus*; N, O, *Nezara hilaris*; P, Q, R, *Oncopeltus fasciatus* (WILSON).

remain separate during the whole growth period, or if united separate before the heterotypic division. This is very clearly seen in *Oncopeltus* (Fig. 266), where the entire history of these bodies may readily be traced (Wilson, '12).

Considerable difference exists (as in case of the unpaired X) in respect to the rate and degree of condensation of X and Y. In many cases the X-chromosome, rarely also the Y, has at first the form of an elongated

¹ An exception occurs in the homopter *Euchenopa* (p. 771). Considerable discussion has arisen concerning the chromatin-nucleolus in mammalian spermatocytes. Gutherz ('22) after a careful study of the phenomena in the white mouse, concluded that this body is not a pair of sex-chromosomes. Painter, however ('23), in a still more extended study of the facts in the opossum, has produced apparently demonstrative evidence that here at least the body is in fact a chromosome-nucleolus (XY pair). It forms in this case an irregular knotted ring which resolves into an X-chromosome and a bipartite Y.

rod, in some cases already in the presynaptic stage (Figs. 266, 267). In *Euschistus* (Montgomery, '98) or *Lygeus turcicus* (Wilson, '05) the rods condense completely to a spheroidal form; in *Lygæus bicrucis* (Wilson, '12), both X and Y shorten considerably, but still retain a rod-shape and are often plainly split lengthwise; in *Euchenopa bicurvata* (Kornhauser, '14) an elongate rod-shape is retained throughout the growth-period, by both X or Y which only assume a rounded form in the diakinesis. In this case, which is almost unique, X is always characterized by a denser consistency

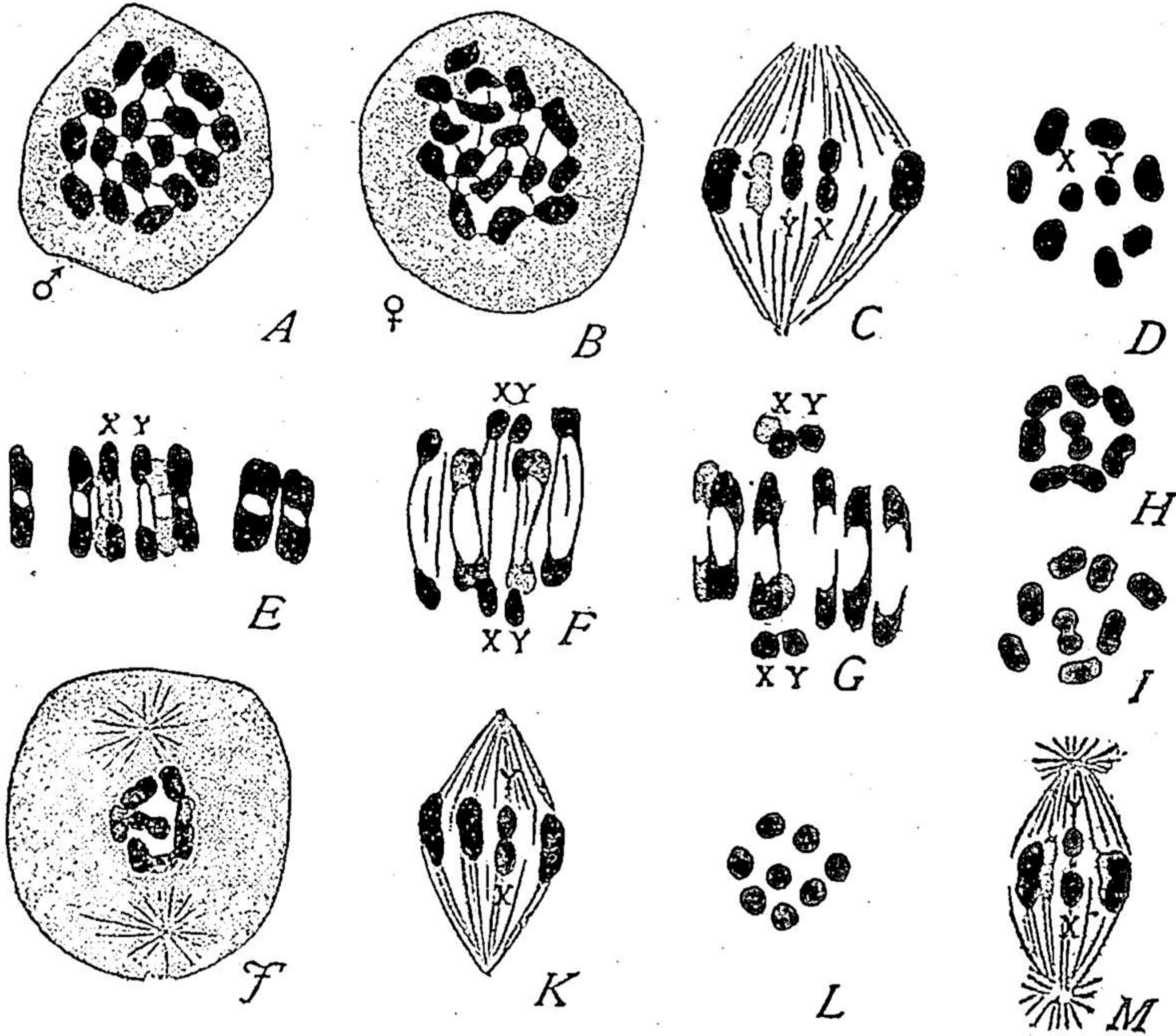


Fig. 369.—The sex-chromosomes in the hemipter *Oncopeltus*, in which the X- and Y-chromosomes are equal or nearly so.

A, male diploid group (spermatogonial); B, female diploid group (ovary), each with 16 chromosomes (X and Y indistinguishable); C, first spermatocyte-metaphase in side-view; D, in polar view; E-H, anaphases of this division, conjugation of X and Y; H, I, sister-groups from the same spindle, XY-bivalent near center; J, interkinesis; K, second spermatocyte in side-view, L in polar view; M, disjunction of X and Y.

and deeper staining-capacity, while Y remains more diffuse, in a condition like that of the autosomes.

The relations of the XY-pair to the plasmosome are similar to those seen in case of the unpaired X. When X and Y are united the plasmosome is in contact with the pair; when they are separate the plasmosome is almost always associated with X, to which it may in some cases be seen attached even when the latter has a rod-shape. The plasmosome rapidly increases in size until it is often larger than the chromosome-nucleolus and then as a rule separates from it. In the

later prophase it quickly disappears, in some cases undergoing fragmentation.

3. Compound Types. The X-Complex

Under a third type we may place those more complicated cases in which X is represented, not by one chromosome but by a group which during spermatogenesis act together as a compound X-element. The number of X-components, as thus far observed, varies from two (*Syromastes*, *Fitchia*) to

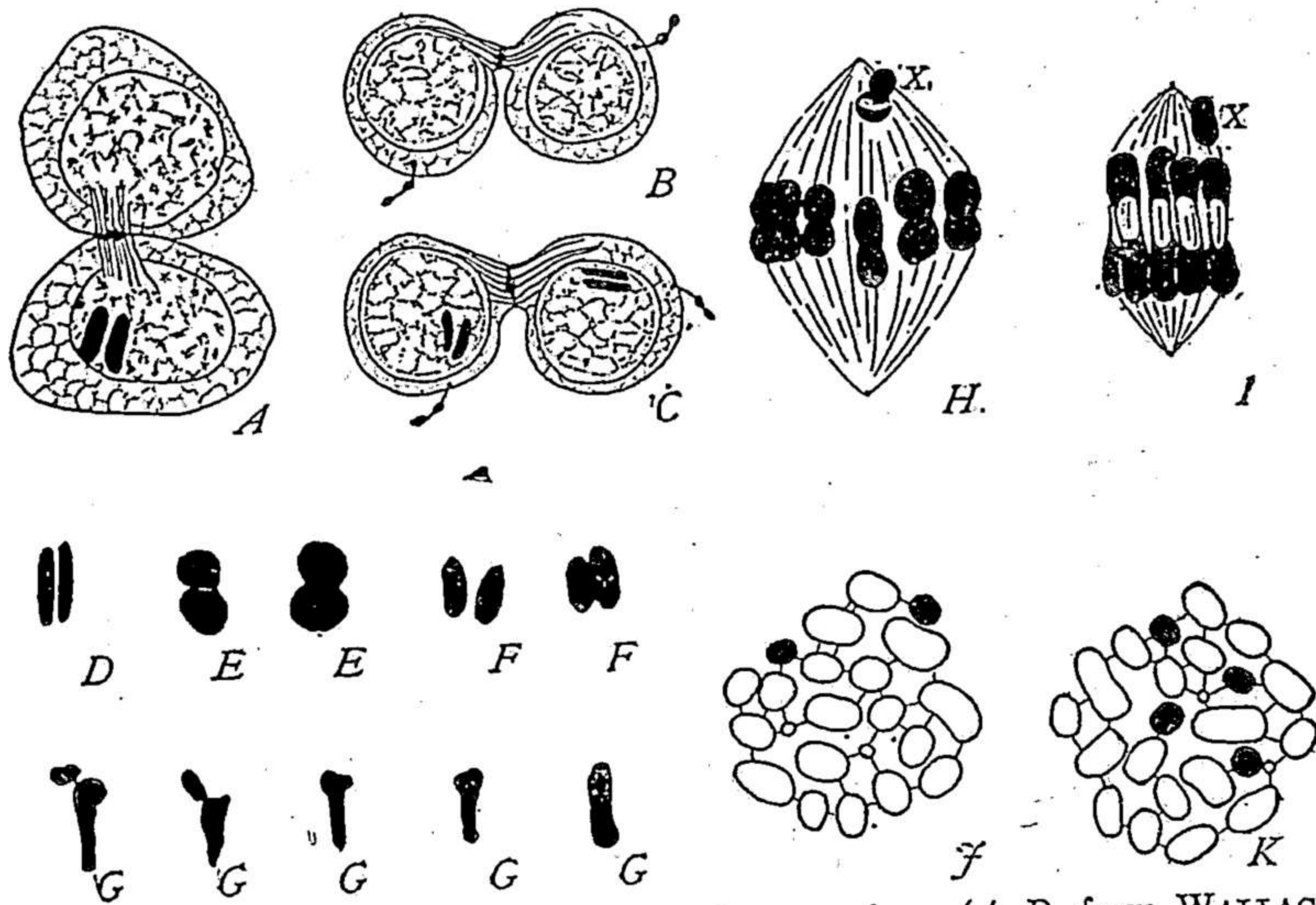


Fig. 370.—Double X-element without Y, in various species. (A-D, from WALLACE; E, from WILSON; F, G, from MORGAN; H-K from WILSON.)

A, first spermatocyte-telophase, in the spider *Agalena* with double X; B, C, second spermatocyte-telophases, showing X and no-X classes; D, X-chromosome of same; E, double X-element of the hemipter *Syromastes*; F, same of *Phylloxera fallax*; G-G, various forms of same in *Phylloxera caryæcaulis*; H, I, first spermatocyte-metaphase and anaphase in *Syromastes*, precession of X-element; J, K, female and male diploid groups of same, X-components black.

eight (*Ascaris incurva*). Whatever be their number, the X-group is single in the male, double in the female; so that these cases, too, conform to the formulas $XX = \text{♀}$ and $X = \text{♂}$. In the compound types, likewise, the X-complex of the male may or may not be accompanied by a Y-chromosome; but this is always a simple element. The compound sex-chromosomes, like the simple ones, are thus of two types which correspond, respectively, to the XY-XX or *Lygæus* type and the XO-XX or *Protenor* type. The first such case to be worked out was discovered in the "toad-bug" *Gelastocoris* (*Galgulus*) *oculatus* (Payne, '08) where X consists of four components (Figs. 372, 374). Other cases have since been found in other Hemiptera, in one or two Orthoptera (*Gryllotalpa*, *Mantis*), in some nematodes (*Ascaris*) and have been described in mammals. Without describing these cases in detail, some of them are given in the two following lists:

XJ-XX COMPOUND TYPES (Y ABSENT)

NAME	GROUP	NO. OF X-COMPONENTS	X SPERM	NO X SPERM	DIPLOID No. ♂	DIPLOID No. ♀	AUTHORITY
<i>Lepisma domestica</i>	Thysanura	2	18	16	34	(36)	Charlton, '21
<i>Syromastes marginatus</i>	Heteroptera	2	12	10	22	24	Gross, '04, Wilson, '09 a, b
<i>Phylloxera fallax</i>	Homoptera	2	6	4	10	12	Morgan, '08, '12
<i>Phylloxera caryæcaulis</i>	"	2	3(4)	2	5(6)	6(8)	Morgan, '08, '12
<i>Agalena nævia</i>	Araneida	2	27±	25±	52±		Wallace, '05, '09
<i>Anolis carolinensis</i>	Lacertilia	2	18±	16±	34±	(36±)	Painter, '21
<i>Sceloporus spinosus</i>	"	2	12	10	22	24	Painter, '21
<i>Ascaris lumbricoides</i>	Nematoda	5	24	19	43	48	Edwards, '10
<i>A. canis</i>	"	6	18	12	30	36	Walton, '16
<i>A. megalcephala</i> ¹ univalens	"	(9±)	36±	27±	63±	72±	Kautzsch, '13
<i>A. megalcephala</i> ² univalens	"	(8±)	30±	22±	52±	60±	Geinitz, '15

In all these cases the X-components behave in the diploid divisions as independent chromosomes, scattered at random among the autosomes. In the synapsis of the male they come together in a coherent group, which as a whole splits lengthwise for the equational-division and in the heterokinesis passes undivided to one pole (Fig. 375).

Phylloxera caryæcaulis forms a partial exception only in the fact that the two components of X are often indistinguishably fused at every stage in the male and almost always thus fused in the female.³ Another point of great interest is that the X-components are constant not only in number but also in size. In *Syromastes* the two components are always distinctly unequal, in *Phylloxera caryæcaulis* still more unequal; in *P. fallax* and in *Agalena* they are equal (Fig. 370). In *Ascaris megalcephala* or *canis* the components are equal; in *A. lumbricoides* four of the components of the

¹ These numbers represent the components of the original chromosomes linked to form larger chromosomes which are maintained intact as such in the germ-line but break up into much smaller and more numerous bodies in all the somatic divisions. See pp. 323, 879.

² Several additional cases of a double X-element have been reported, e. g., in the domestic fowl, Guyer ('09, '16), the pig Wodsedalek ('13) and man Guyer ('10), but all these are doubtful and the last certainly erroneous.

³ Cf. Morgan ('09, '12, '15).

pentad group are small and one large (Fig. 371). The same fact will be still more strikingly shown in some of the cases next to be considered.

Even more remarkable conditions are found among those more numerous cases in which the compound X-element is opposed by a single Y-chromosome which acts as its synaptic mate in the maturation-processes of the male. The more extreme cases of this, such as *Acholla multispinosa* or *Ascaris incurva*, offer a most bizarre appearance in the spermatocyte-divisions, particularly in case of the heterokinesis; but they are perfectly in

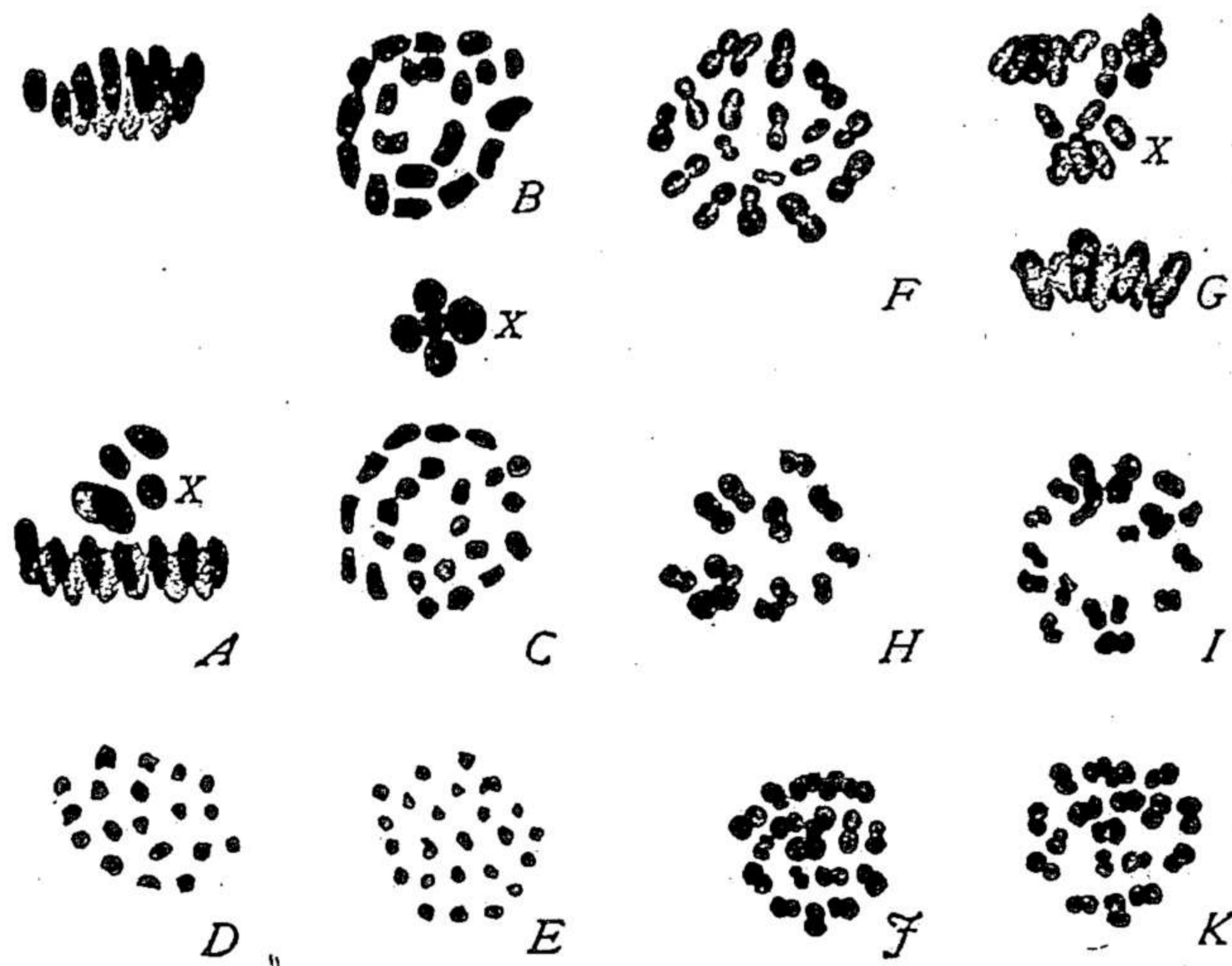


Fig. 371.—Compound X-element without Y in *Ascaris*. (A-E, *Ascaris lumbricoides*, EDWARDS; F-K, *A. canis*, WALTON).

A, first spermatocyte, anaphase; B, C, sister groups from same in polar view, showing the pentad X-element between them; D, E, the two resulting types of second spermatocyte-groups, one with 19 chromosomes the other with 24; F, first spermatocyte-metaphase, of *A. canis*, 18 chromosomes, hexad X-group in center; G, anaphase of same; H, I, sister second spermatocyte-groups, showing two types, one with 12 chromosomes, the other with 18; J, K, corresponding sister-groups from second oocyte-division, each with 18 chromosomes.¹

line with the simple XY-type. A list of the more important known cases follows on page 775.

In all these cases, as in the compound X-XX type, the X-components behave as separate chromosomes in the somatic divisions, only coming together in a coherent group during the maturation-process. It will be observed that in every case the female diploid number exceeds the male by the number of the X-components less one, because in this case the male number is increased by one owing to the presence of Y; in *Gelastocoris*, for example, the female number is $35 + 4 - 1 = 38$; in *Ascaris incurva* it is $35 + 8 - 1 = 42$.

These cases offer remarkable examples of characteristic and constant

¹ In this species all the chromosomes appear double, owing to the presence of a median transverse suture: as in copepods, etc. (see p. 904)

XX-XY COMPOUND TYPES (Y PRESENT)

NAME	GROUP	No. OF X-COMPONENTS	X = SPERM	Y = SPERM	♂ DIPLOID	♀ DIPLOID	AUTHORITY
<i>Fitchia spinulosa</i>	Heteroptera	2	14	13	27	28	Payne, '09
<i>Rocconota annulicornis</i>	"	2	14	13	27	(28)	Payne, '09
<i>Conorhinus sanguisugus</i>	"	2	12	11	23	(24)	Payne, '09
<i>Thyanta calceata</i>	"	2	14	13	27	28	Wilson, '11
<i>Tenodera (Mantis) superstitiosa</i>	Orthoptera	2	14	13	27	28	Oguma, '21
<i>Paratenodera (Mantis) aridifolia</i>	"	2	14	13	27	28	Oguma, '21
<i>Prionidus cristatus</i>	Heteroptera	3	14	12	26	28	Payne, '09
<i>Sinea diadema</i>	"	3	15	13	28	30	Payne, '09
<i>Pselliodes cinctus</i>	"	3	15	13	28	30	Payne, '12
<i>Pnirontis modesta</i>	"	4	14	11	25	(28)	Payne, '12
<i>Gelastocoris oculatus</i>	"	4	19	16	35	38	Payne, '08, '09
<i>Acholla multispinosa</i>	"	5	15	11	26	30	Payne, '10
<i>Sinea rileyi</i>	"	5	17	13	(30)	(34)	Payne, '12
<i>Pseudococcus nipæ</i> ¹ and 2 other species	Homoptera	5	5	5	10	10	Schrader, '21, '23
<i>Ascaris incurva</i>	Nematoda	8	21	14	35	42	Goodrich, '16

differences both in number and in size-relations of the X-components in different species, as may be seen in the series displayed in Fig. 372, differences often seen between even nearly related forms. In the pentatomid genus *Thyanta*, for example, the two species *custator* and *calceata* are so closely similar as to have puzzled some of the best systematists, yet in *custator* X is always a single chromosome, in *calceata* always a double element,² while the total diploid numbers of the two species are also widely different (see Table). In the reduvioid genus *Sinea diadema* and four other species X consists of three components; in *S rileyi* of five.³ In *Acholla*, a related genus, the X-complex consists in *A. ampliata*, of three small, equal components, in *A. multispinosa* of five, of which three are small and equal and two very large,⁴ the whole group opposed by a very large Y-chromosome. The chromosomal differences between the sexes in this species are perhaps the most remarkable known, since the Y-chromosome is the largest of all the

¹ The interpretation of this form, involving the assumption of 5 Y-components, is still somewhat hypothetical (p. 777).

² Wilson ('11), Barber ('11).

³ Payne ('12).

⁴ Payne ('09, '10).

chromosomes and appears only in the male, while of the X-components the male has three small and two large and the female six and four (Fig. 375).¹

A climax is reached in the nematode genus *Ascaris*. At one extreme is *A. felis* which has a simple XY-pair much like that of many insects.² At the other extreme is *A. incurva* with an X-complex of no less than eight components opposed by a single Y, one of the X-components being a very small microchromosome, and one a rather long wedge-shaped chromosome with which the Y-chromosome (here of moderate size)

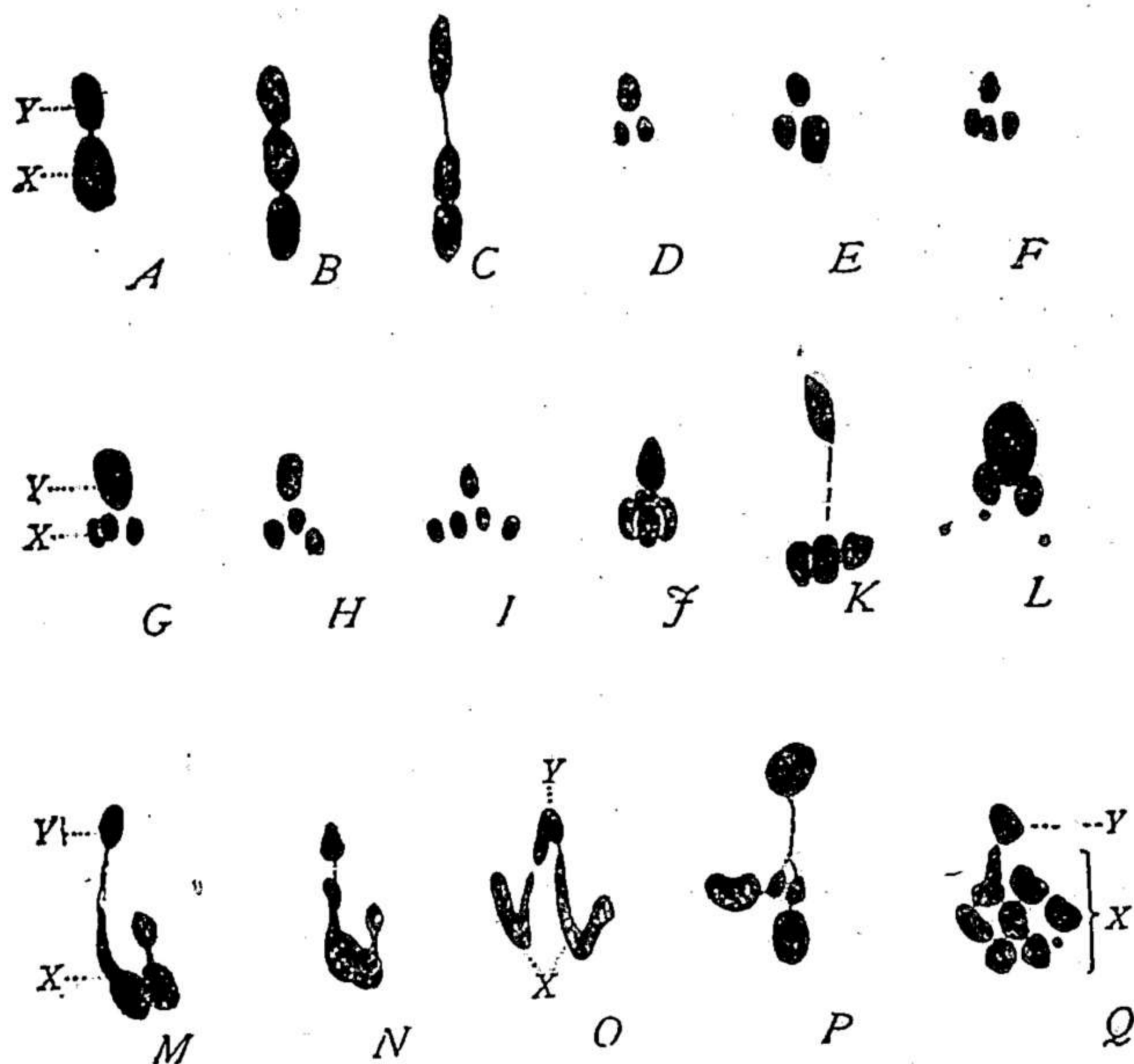


Fig. 372.—Various forms of the compound XY-pair. A to N are from Hemiptera; O, from a mantid orthopteran; P from a beetle; Q from a nematode (A–C from WILSON; D–L from PAYNE; M–N from BROWNE; O from OGUMA; P from NONDEZ; Q from GOODRICH).

A, *Thyanta custator*; B, C, *Thyanta calceata*; D, *Pitthia*; E, *Conorhinus*; F, *Sinea*; G, *Pselliodes*; H, *Prionidus*; I, *Sinea rileyi*; J, K, *Gelastocoris*; L, *Acholla multispinosa*; M, N, *Notonecta indica*; O, *Tenodera superstitiosa*; P, the sex-complex in *Blaps lusitanica*, probably a quadruple X-element opposed by a single Y; Q, *Ascaris incurva*.

is always coupled (Fig. 376).³ In *A. megalcephala* there are eight or nine components closely linked in the germ-cells but separate in the somatic divisions (p. 781).⁴ Intermediate between these conditions are *A. canis* with its six components⁵ and *A. lumbricoides* with five⁶ in each case without a Y: and we may look for the discovery of other species in which X consists of fewer components. In certain nematodes of other genera, such as *Heterakis dispar*⁷ or *Ancyracanthus cystidicola*⁸ X is a simple chromosome without a Y.

¹ See also *Pselloides*, Fig. 374.

² Edwards, '10.

³ Goodrich ('14, '16).

⁴ See Geinitz, ('15) and Kautzsch ('12).

⁵ Walton ('16, '18).

⁶ Edwards ('10).

⁷ Gulick ('11).

⁸ Mulsow ('12).

Such facts clearly indicate the conclusion, supported by many other facts, that the X-element is in general a compound and definitely organized but also highly plastic body, consisting of many components that may be closely associated in a single body or may readily appear in the form of separate chromosomes which in meiosis become associated to form a unit-complex. We find here strong ground for the conclusion that other forms of chromosomes are likewise compound bodies, a result supported by numerous additional facts (pp. 903, 906). The conclusion is also indicated that the sex-determining component or "X-chromatin" may form but a small, perhaps a very small, part of the X-element, the remainder of the

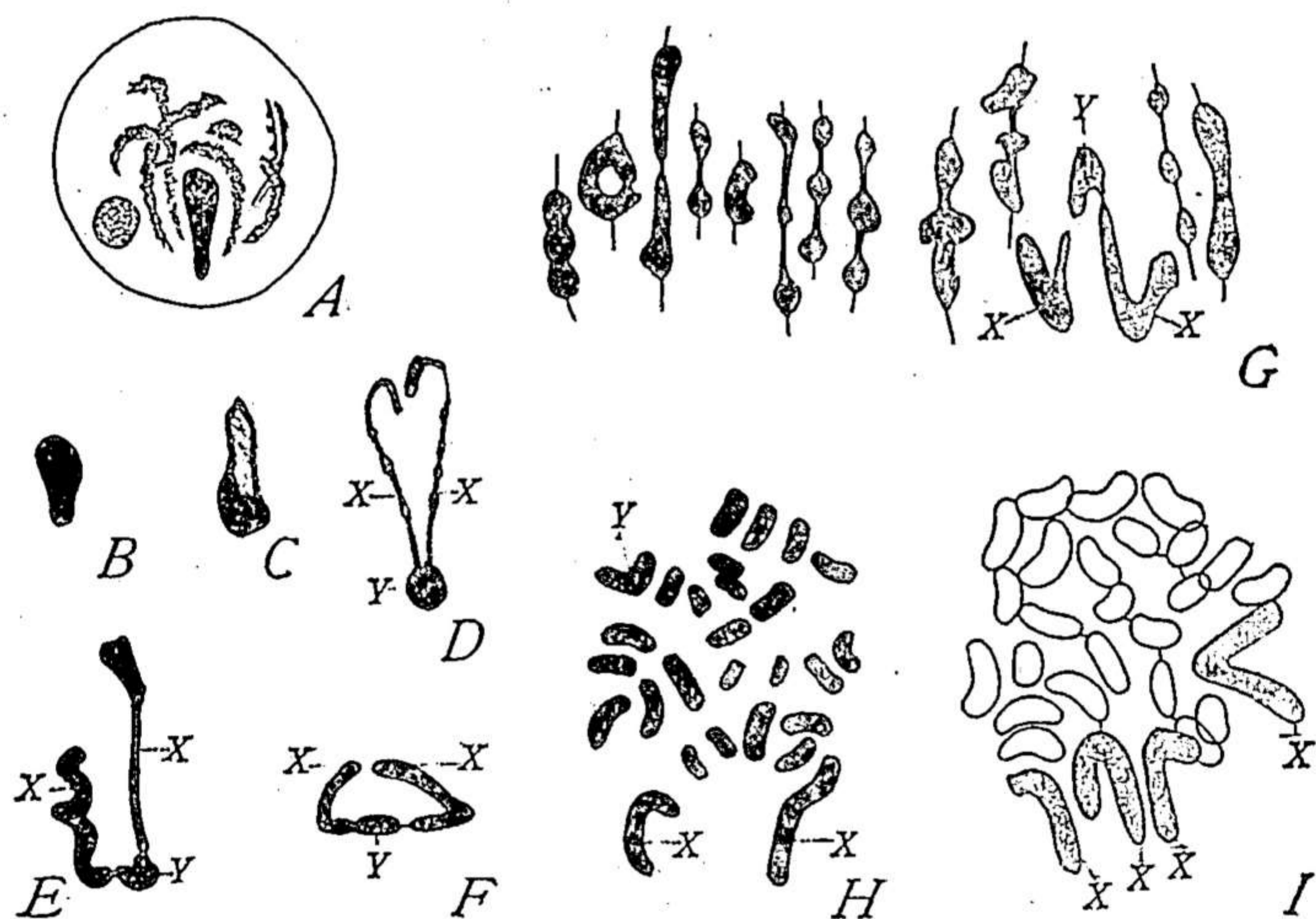


Fig. 373.—Sex-chromosomes in the mantid *Tenodera superstitionosa* (OGUMA).

A, diplotene, with XY-chromosome-nucleolus; B-D, formation of the XY-complex from the chromosome-nucleolus; E, F, later stages of same; G, the chromosomes of the heterotypic division, arranged in serial order; H, spermatogonial metaphase; I, female diploid group (follicle-cell).

complex consisting of chromatin which has nothing to do with sex as such but may form the basis of sex-linked characters.¹

It is interesting to compare the foregoing cases with such a one as that of the hemipteran *Notonecta indica*.² Here X is in the spermatogonia a single chromosome (the largest of the group), which shows no visible sign of compound structure, but in the later prophase and during the divisions very clearly shows such a structure, consisting of one large and five small components or chromomeres, which remain more or less distinct until the anaphases of the second division (Fig. 426). A slight increase of independence on the part of these components would convert them into separate chromosomes, forming an X-complex consisting of six components (as in *Ascaris canis*) opposed by a single Y.³

¹ Cf. Wilson ('11). See p. 903.

² Browne ('16).

³ A remarkable case described by Schrader (21, '23) occurs in certain of the coccids (*Pseudococcus*).

The history of the compound forms in the growth-period has been but partially cleared up; but so far as it has been examined the facts indicate that here, too, the sex-chromosomes undergo a process of condensation or heteropycnosis quite comparable to that seen in the simple types. In some of these cases the X-components unite to form a single spheroidal chromosome-nucleolus accompanied by a plasmosome which later disappears. In others all the components of the XY-complex remain separate, but are imbedded in a large plasmosome.¹

Peculiar conditions, not yet fully understood, but interesting for the study of the sex-chromosomes, are found in the mantid Orthoptera *Tenodera*

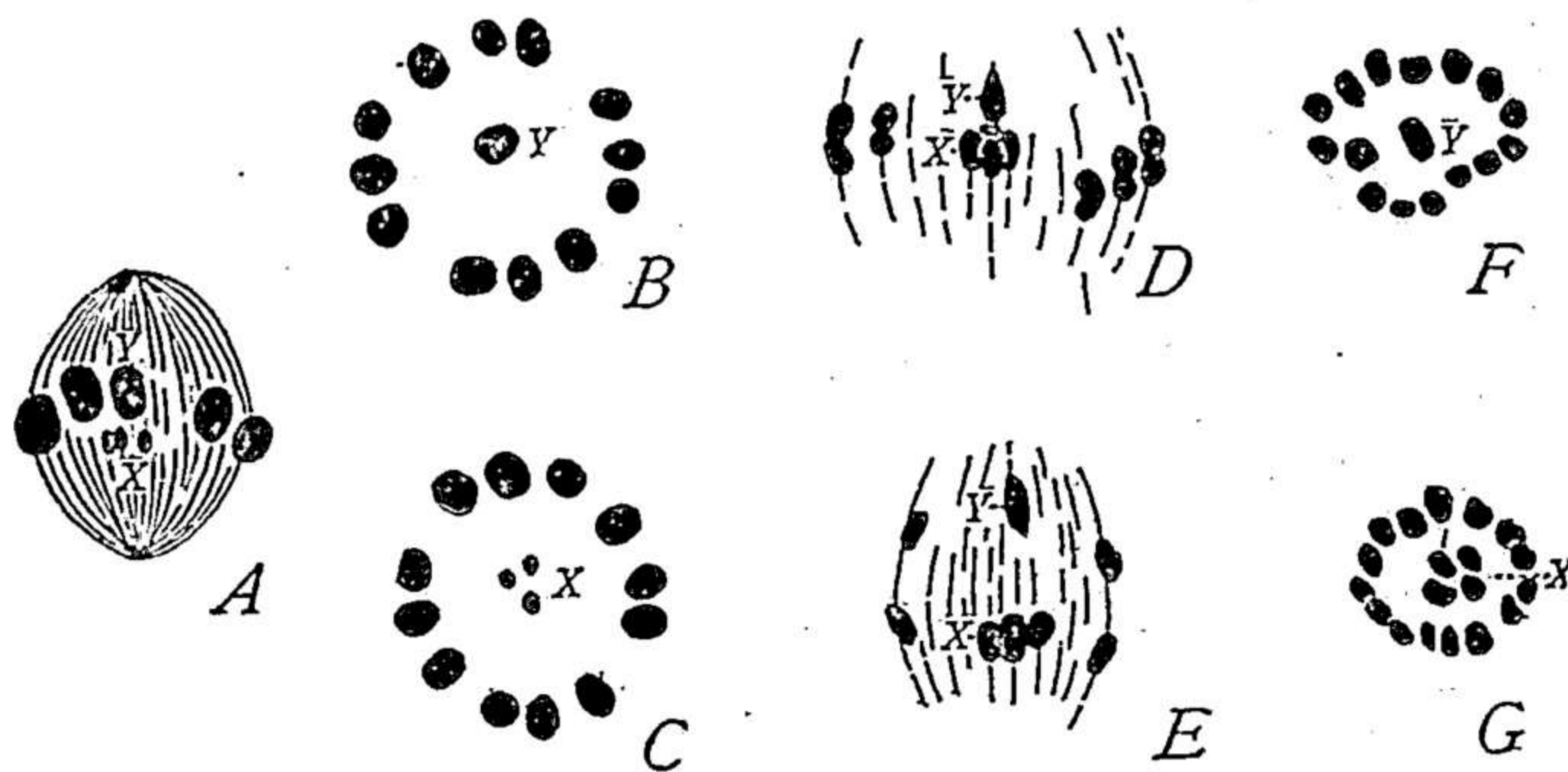


Fig. 374.—Compound XY-pair in Hemiptera (PAYNE).

A, *Pselloides cinctus*, side-view of first spermatocyte-metaphase, triple X and single Y; *B*, the Y-class and *C* the X-class, of resulting second spermatocyte-metaphase-groups; *D*, *Gelastocoris*, first spermatocyte-metaphase, quadruple X and single Y; *E*, anaphase of same; *F*, the Y-class, and *G* the X-class, of resulting second spermatocyte-metaphases.

and *Paratenodera* (Oguma, '21) and the beetle *Blaps* (Nonidez, '20). In the mantids X consists of two components which early in the growth-period unite with Y to form an apparently single compact chromosome-nucleolus. Later the X-components again become extended to form long threads while the Y-component (assuming its correct identification) remains condensed until it enters the metaphase (Fig. 373). *Blaps lusitanica* shows an X-complex somewhat similar to this but consisting of five components, two small and three large, the latter at once recognizable in

The diploid number in both sexes is here 10, while the X-element seems to be composed of five components. In the male these five remain in a compact group during the spermatocyte growth-period, divide equationally in the first division, and in the second pass together to one pole while the remaining five ("autosomes") pass to the other. In the female all the chromosomes, so far as observed, behave alike, and form five ordinary tetrads. The conclusion seems to be indicated that all the 10-chromosomes of the female here represent X-components while in the male only five such are present. This may mean, as Schrader suggests, that all the chromosomes of the female carry sex-chromatin (X-chromatin). In this case the five autosomes of the male must be confined to that sex and in this respect are analogous to a compound Y-element. It seems possible, however, that only one of the X-components carries X-chromatin, and that only one of the five "autosomes" is comparable to a Y. (Cf. the case of *Trialeurodes*, p. 704).

¹ E. g., in *Fitchia spinulosa*, *Roconota annulicornis*, *Sinea diadema*, *Prionidus cristatus*, and one or two others.

the diploid groups by their large size and non-terminal attachments (Fig. 378, from Nonidez, '20). In the heterotypic division these form a pentad element, of which one large component passes to one pole, while two large and two small pass to the opposite one. Though the interpretation of this is uncertain (since the female groups are not known) it is a plausible

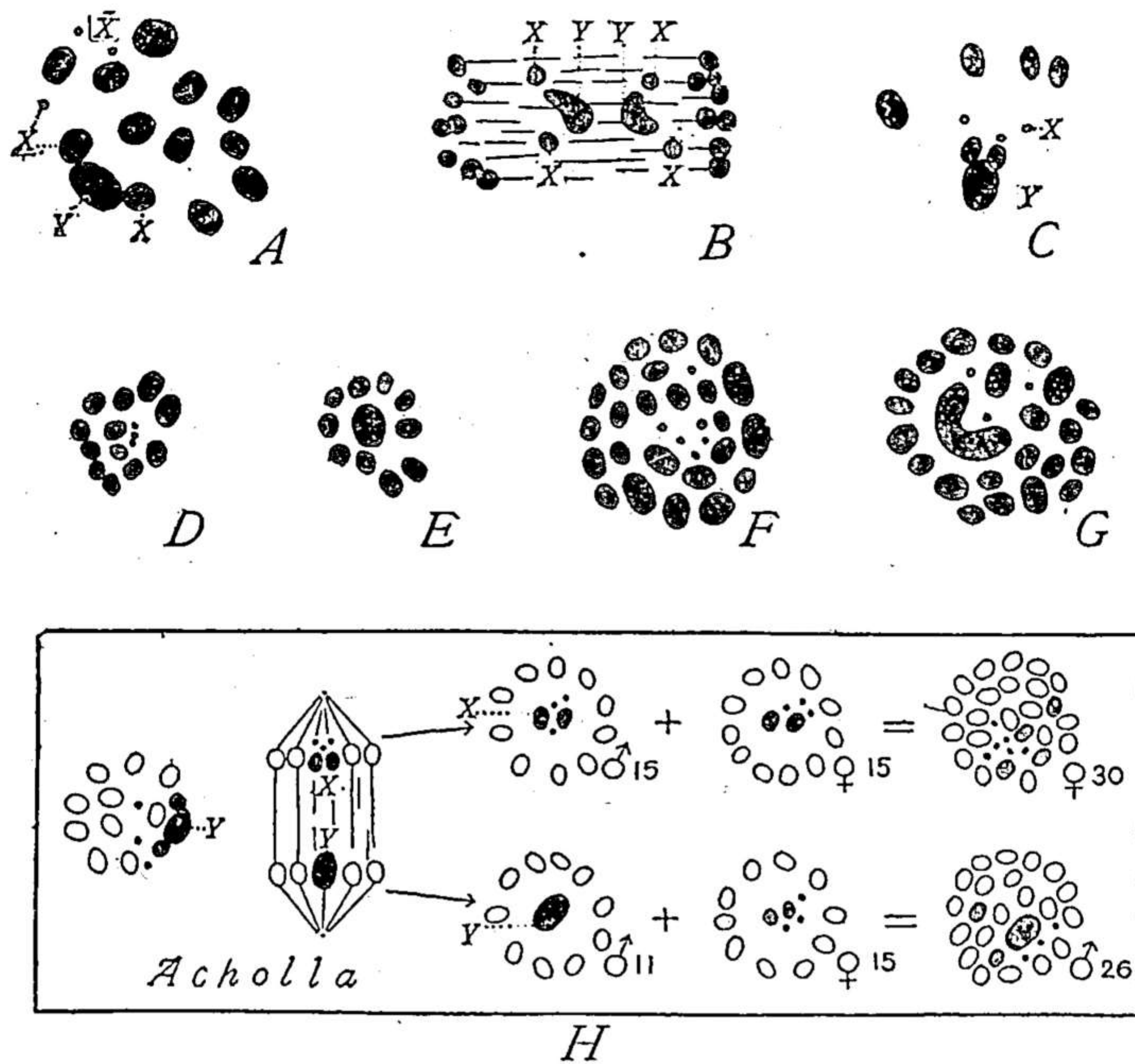


Fig. 375.—The compound XY-pair of sex-chromosomes in the hemipter *Acholla multispinosa* (PAYNE).

A, first spermatocyte-metaphase, large Y coupled with two large X-components; B, anaphase of same division, with lagging Y and 2 X's; C, metaphase-figure, showing compound XY-pair; D, E, anaphase-groups, the former of the X-class, the latter of the Y; F, female diploid group (30 chromosomes, 10 X's); G, corresponding male group (26 chromosomes, Y and 5 X's); H, diagram showing the general relations of the chromosomes in this species.

assumption that this complex represents a quadripartite X-element (two large and two small components) coupled with a single large Y.¹

4. Linkage of Sex-chromosomes with Autosomes

The subject of chromosome-linkage in general belongs to a later stage of our discussion (Chap. XI) but must here be considered in relation to the sex-chromosomes. In a considerable number of species the X-chromosome has been found closely linked or united to one end of one of the autosomes, remaining constantly in association with it during the whole chromosome-cycle, including both mitosis and meiosis and no doubt also fertilization. Such a case was first observed by Sinéty ('01) in the orthopteran (phasmid)

¹ Nonidez himself identifies only one of the large components as an X-chromosome considering it to be associated with a large pair (MM) and with two small chromosomes.

genera *Leptynia* and *Dixippus*, where the X-chromosome is coupled with one of the bivalents in the meiotic divisions to form an L-shaped trivalent element. Similar relations were discovered by McClung in *Anabrus*, *Hesperotettix* and *Mermiria* ('05, '17). In all these cases the X-linkage appears to be constant for the individual, being already in evidence in the spermatogonial divisions, where X is linked with one of the larger rod-shaped autosomes to form a V or L attached to the spindle at the angle where the two limbs join (Fig. 377). In synapsis the autosome-component couples with its mate to form an unsymmetrical or heteromorphic trivalent, which splits lengthwise (equation-division) to form a hexad. The identity of the X-compound is revealed already in the spermatogonia by its less

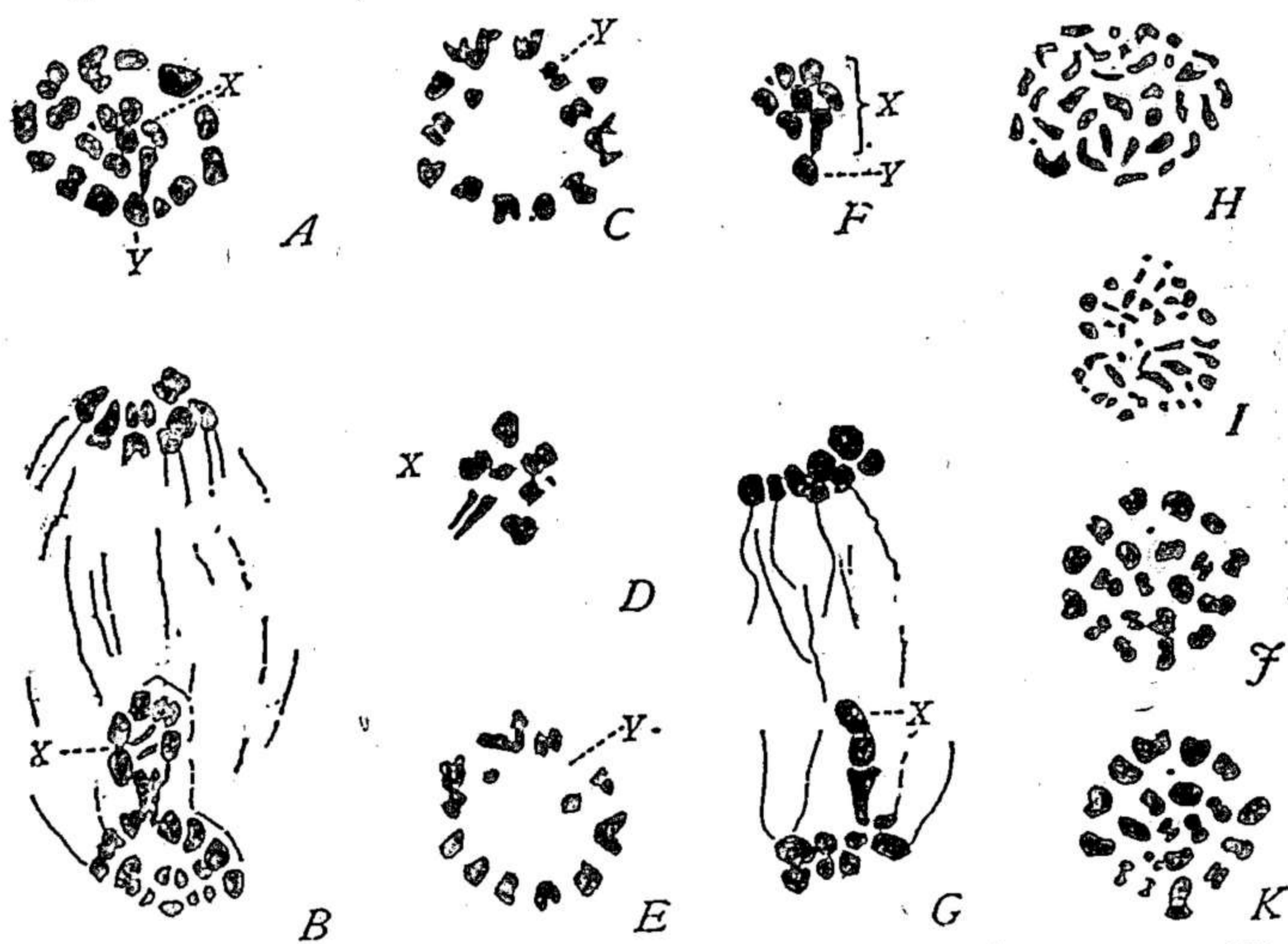


Fig. 376.—The compound XY-pair in the nematode *Ascaris incurva* (GOODRICH).

A, first spermatocyte-metaphase, 21 chromosomes with octopartite X in center and Y at margin; B, anaphase of same in side-view; C, D, E, sister-groups, in polar view, with X-complex between them; F, the XY-pair; G, anaphase in side-view; H, spermatogonial metaphase, 35 chromosomes; I, oögonial division, 40 chromosomes (expected number 42); J, K, sister-groups, first oöcyte-metaphase, 21 dyads each.

regular outline and lighter staining-capacity (*Mermiria*) and later, in the spermatocyte, by its more condensed condition while the autosome-compound is diffuse (Fig. 377, F, G). In the first division the hexad divides transversely, so as to separate the two autosome-compounds, which pass to opposite poles with the X-element attached to one of them.

Whether the X-linkage in these cases is permanent, so as to be continued from one generation to another, is not yet certainly known; but there is reason to suspect that such is the case. McClung ('17) found that X is always linked with the same autosome in a given individual but in other individuals may be otherwise linked or may be free. Most often it is joined to the largest of the 11 bivalents, but often also to the fourth or to the fifth largest;

in *Hesperotettix viridis* four individuals out of 37 were found in which X is entirely free, behaving as an ordinary accessory chromosome. Nevertheless it seems probable that when once established the particular mode of linkage may persist from one generation to another as Carothers ('21) has proved to be the case with different modes of spindle-attachment (p. 934).

Certain other cases of this type are of especial interest as examples of linkage so intimate that we are in doubt as to whether it should properly receive this name. In *Culex* (Stevens, '10), the presence of sex-chromosomes

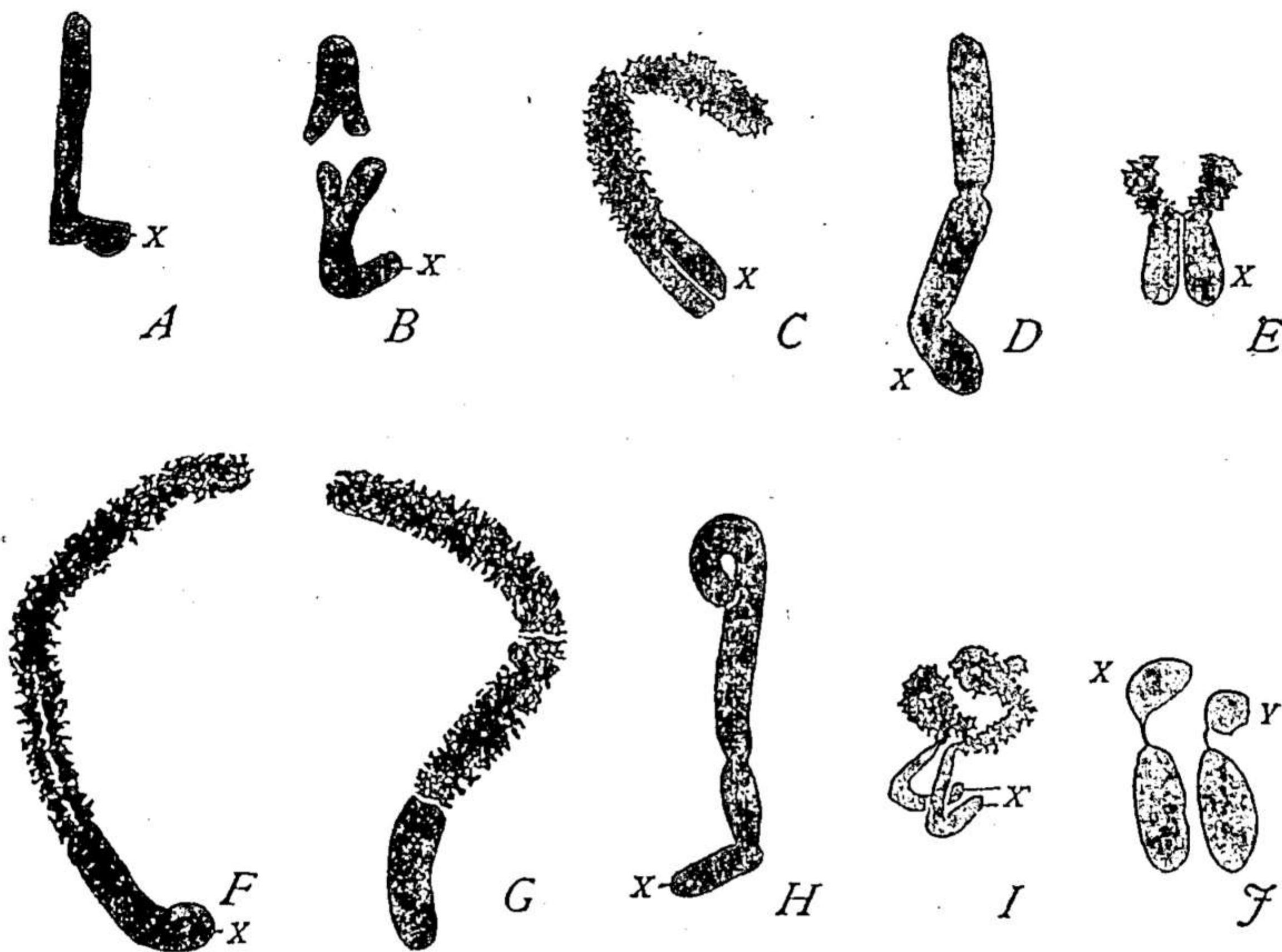


Fig. 377.—Linkage of sex-chromosomes with autosomes. (A, B, from SINÉTY, C-I, McCLUNG, J, STEVENS.)

In all the figure X is the X-chromosome linked to an autosome.

A, first spermatocyte-division of the phasmid *Leptynia*; B, the same in the phasmid *Dixippus*; C-E, the grasshopper *Hesperotettix*, C in prophase, D, metaphase, E in the interkinesis; F-I, corresponding stages in *Mermiria*; J, from the mosquito *Anopheles*, spermatogonial chromosomes, linkage of both X and Y.

would not ordinarily be suspected from either the meiotic or the spermatogonial divisions.¹ In a few cases, however, one of the spermatogonial chromosome-pairs was found to be slightly heteromorphic, each consisting of two unequal components, the larger ones equal, the smaller unequal, and the latter are conjectured by Stevens to be the equivalent of an XY-pair intimately coupled with one of the autosome-pairs. Another interesting case is that of the classical object *Ascaris megalocephala*, in which the X-element is usually intimately united to one of the autosomes though in some individuals it appears in the form of a small extra chromosome. In

¹ The later observations of Whiting ('17) are inconclusive on this point.

this case it shows in every respect the behavior of an X-chromosome.¹ In the female the two X-chromosomes in some cases form a bivalent which appears in the form of a typical tetrad and undergoes the usual distribution so that each mature egg receives one X (Frolowa, Geinitz). As will later be shown, the X-chromosome in all these cases is itself a multiple, though this fact is not apparent during the meiotic divisions (see p. 879).²

These various cases, together with that of *Blaps* (p. 779), show how difficult it may be to distinguish between a secondary linkage of chromosomes

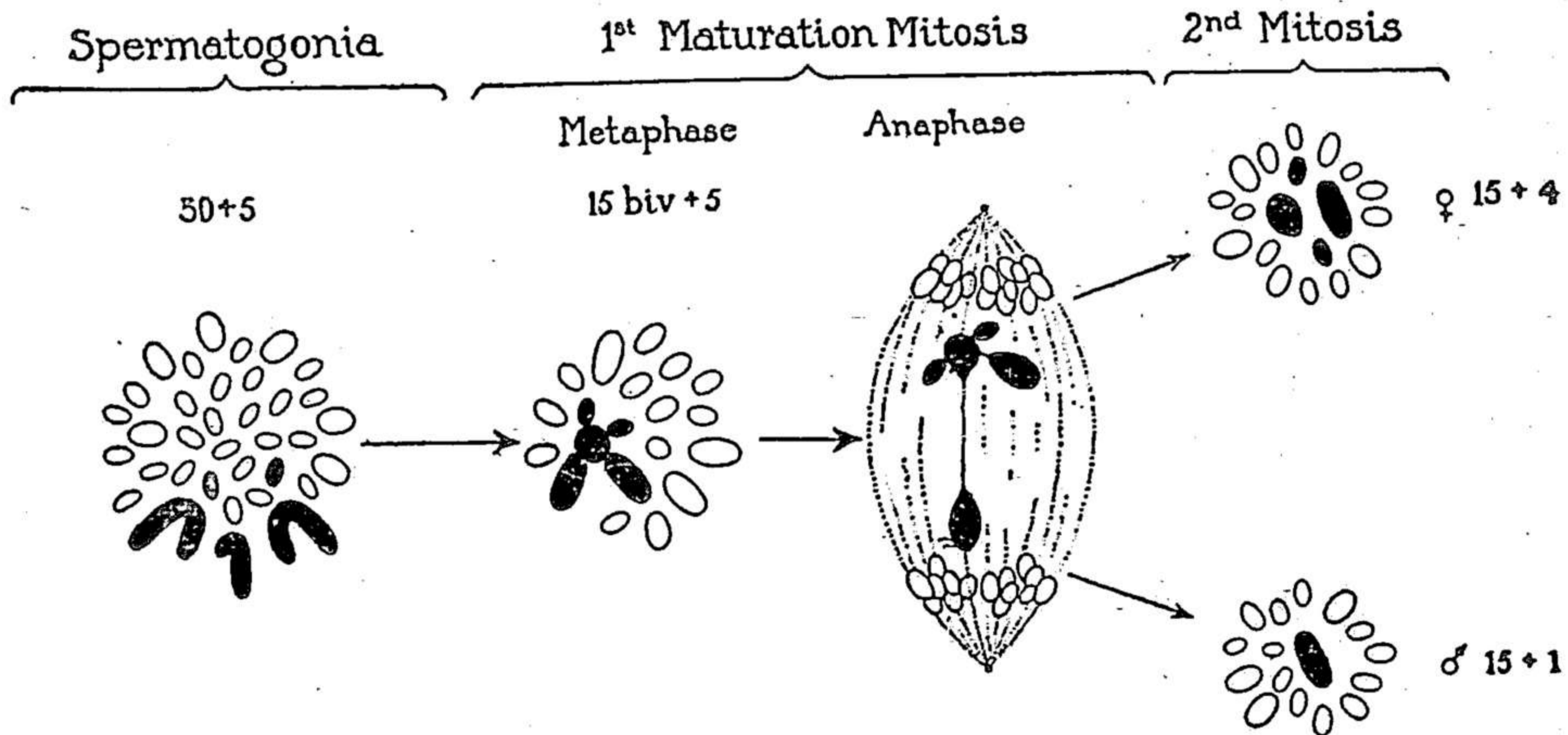


Fig. 378.—The XY-complex in the beetle *Blaps*, slightly schematized (NONIDÉZ).

It consists of five components³ (in black) of which four pass to one pole and one to the other. The simplest interpretation is that it consists of a single Y and a quadripartite X.

and a primary association; and also indicate the comparative unimportance of the question from a physiological standpoint. It seems to be immaterial, so far as sex-production is concerned, whether the X-material appears in the form of a single separate and readily recognizable chromosome; or as one temporarily or permanently linked to another chromosome; or finally as an indistinguishable component of a chromosome which outwardly seems not to differ from others. Morphologically, however, the questions here raised are of great interest in their bearing on the organization of chromosomes generally and the evolution of the sex-chromosomes (pp. 822, 823).

5. Sexual Dimegaly of the Sperms

In most cases the X- and Y- (or no-X) classes of sperm, when fully matured, do not show any differences that are visible to the eye. Only in

¹ The free X-chromosome was first observed in *Ascaris* by Herla ('94), Boveri ('99, '08) and Boring ('09) who found it very rarely present *var. univalens*, but frequently in *bivalens*. Its behavior in the meiotic divisions was elucidated by the work of Edwards ('10), Frolowa ('12), Kautzsch ('13) and Geinitz ('15).

² King ('12) describes in *Necturus* an "X-chromosome" that is linked to one of the bivalents in the spermatocyte-divisions, but the identification of this as the X-chromosome is doubtful.

certain nematodes (*Ancyracanthus*, etc., Figs. 357, 358) are the two classes of mature sperm readily distinguishable, since the chromosomes are still visible as such. Since, however, the nuclei of the two classes commonly receive different amounts of chromatin, and since the sperm-heads consist almost wholly of chromatin, we might expect to find the sperms, or their heads (or nuclei) of two corresponding sizes; and such appears actually to be the fact. Several observers¹ have made numerous measurements of sperm-heads (or nuclei) and plotted the results in curves of variability to show the distribution of size frequency. In nearly all cases the curves have been bimodal, indicating the existence of two size-groups. A test of this result is offered by differences in the relative size of X or (allowing for Y when present) of chromatin-content in different species; for such differences evidently should find expression in corresponding differences in the curves.

In the nature of the case it is difficult to obtain a very precise result; nevertheless expectation and observation show a certain agreement. In the pig, Wodsedalek found the ratio of head-length in the two maxima to be 11.5:14.25 (1:1.21), in the horse 9.5:11 (1:1.05). Zeleny and Faust found various ratios in the curves as compared with the expectation derived from measurements of the X-chromosomes. These and other similar results involve a very considerable, perhaps very large, probable error owing to the relatively small size of the sex-chromosomes and similar causes. More convincing than any of these is the similar result afforded by *Ascaris incurva*, a form which as above stated, has one of the largest known X-elements, and is also very favorable for exact measurements of the nuclei (Fig. 376). Clay models of the second spermatocyte metaphase-groups of the X-containing and X-lacking classes, when weighed, gave a ratio between the two of 21:14 (1.5:1) while the bi-modal curve from measurements of 600 sperm-nuclei showed maxima having the ratio 21:15 (1.4:1), a much greater difference than in any other observed case. This result seems to confirm the conclusion that the two modes of the frequency curves really correspond with the two sex-classes of the sperm.

B. FEMALE DIGAMETY

Digamety in the female is of two widely different types concerning which it is easy to fall into confusion. One is a digamety in the constitution of the nuclei after meiosis precisely analogous to that seen in the sperm in the cases of male digamety. The second is a dimegaly of the eggs, which are of two sizes, the larger being female-producing and the smaller male-producing (p. 806). These two types must carefully be distinguished since they do not

¹ Wodsedalek on the pig ('13) and horse ('14); Faust ('13) on *Anasa tristis*; Zeleny and Faust ('15) and Zeleny and Senay ('15) on various insects and vertebrates; and Goodrich ('16) on *Ascaris incurva*.

parallel each other. At this point we are concerned only with the first of them.¹

1. Sexual Nuclear Digamety of the Ova

Cytologically this type has been clearly demonstrated only in the Lepidoptera, though the genetic evidence proves that in birds also the female is the heterozygous sex. The Lepidoptera were examined cytologically by several earlier observers² but the sex-chromosomes were first made known by the work of Doncaster and especially of Seiler.³ Seiler's studies, on certain moths of the family of Psychidæ have demonstrated a chromosome-mechanism exactly parallel to that of male digamety but showing a relation to sex in all respects the opposite. In male Lepidoptera all the chromosomes are equally paired and symmetrically distributed, so that but one visibly distinguishable class of sperms is produced. Seiler clearly showed that while the chromosomes are also paired in the female in certain species (*Solenobia pineti*, and *triquetrella*), thus corresponding to the XY-XX type, in other species one member of one pair is missing in the female; while the male has one more. Thus, in *Fumea casta* the diploid groups of the male (spermatogonia) have 62 chromosomes, equally paired (31 + 31), the female but 61 (31 + 30). In *Talæporia tubulosa* the corresponding numbers are male 60 (30 + 30) and female 59 (30 + 29). The meiotic divisions show corresponding relations. In the male all the chromosomes are equally distributed in both spermatocyte-divisions, producing but one class of sperm. In the female, on the other hand, the unmated or odd chromosome passes undivided to one pole (either the inner or the outer) in the first polar division of the egg. The second division, accordingly, is of two types, one showing one chromosome fewer than the other (in *Talæporia* 29 or 30), all the chromosomes dividing equationally. In *Talæporia* Seiler found this chromosome passing to the outer pole in 134 cases, to the inner in 89 cases, a ratio of 1.50:1.00, the observed primary sex-ratio being about 1.75:1. Whether these particular figures are significant or not, the facts as observed make it extremely probable that fertilization by any sperm will produce either a male or a female according to the class of egg which it enters, e. g., in *Fumea casta*

$$\begin{aligned} \text{Egg } 31 + \text{sperm } 31 &= 62 (\sigma) \\ \text{Egg } 30 + \text{sperm } 31 &= 61 (\text{♀}) \end{aligned}$$

These relations seem to be exactly the reverse of those seen in the *Protenor* type, and it becomes a doubtful question how the sex-chromosomes

¹ For the second see p. 806.

² Henking ('90, '92), Grünberg ('03), Stevens ('06), Munson ('07), Dederer ('07, '15), Cook ('10), Federley ('13), etc.

³ Doncaster ('10-'15), Seiler ('14, '17, '21, '23).

should here be designated. There are several possible nomenclatures that will satisfy the observed results, both cytological and genetic. We might simply reverse the symbols employed in male digamety, employing the formulas $XXAA = \sigma$ and $XOAA = \varphi$ (Goldschmidt); or the formulas might be written $OOAA = \sigma$ and $XOAA = \varphi$ (Castle); or $YYAA = \sigma$ and $XYAA = \varphi$ (Wilson). Evidently, however, in none of these cases does the symbol X have the same meaning as in male digamety. Some writers, therefore, have preferred to use a different and non-committal terminology by substituting W and Z for X and Y, *i. e.*, $AAZZ = \sigma$ and $AAZO = \varphi$; or, in case Z has a mate in the female (*Solenobia* or *Phragmatobia*) $AAZZ = \sigma$ and $AAWZ = \varphi$ (Morgan).

To the physiological questions here involved we shall later return (pp. 815, 821). They do not affect the fact that in a broad sense the same kind of chromosome-mechanism is involved in female digamety as in male.

Earlier work on Lepidoptera, though less decisive, indicates an essentially similar condition. In *Abraxas* Doncaster ('10, '11) found that all males and most females have 56 chromosomes, and that all the gametes receive 28. In some individuals, however, and always in a certain strain, the female number is 55, half the mature eggs receiving 27 and half 28. This result possibly indicates the presence of a supernumerary chromosome, but was interpreted by Doncaster to mean that the 28-chromosome eggs are male-producing, the 27-class female-producing ($28 + 28 = 56\sigma$, $27 + 28 = 55\varphi$); further, that typically there is a pair of sex-chromosomes in each sex (*e. g.*, WZ in the φ and ZZ in the σ) but that in the female one of these (*e. g.*, W) may be absent. If this be correct the case would closely parallel that of *Metapodius*, where it is known that the Y-chromosome may be either present or absent in the same species (p. 874).¹

More satisfactory, though more complex, is the case of *Phragmatobia*, where Seiler ('14) found in the first polar mitosis of the egg one large heteromorphic bivalent, distinguishable by its size, which in the male is replaced by a symmetrical one. During the heterotypic mitosis in the female one member of this bivalent as it passes to the pole separates into two unequal components, so that the daughter-groups are of two types, one containing 29 chromosomes, the other 28. Comparison shows that the bivalent in question lies indifferently with the double element turned either outward or inward, *i. e.*, this element may either be retained in the egg or passed out into the polar nucleus. It thus comes to pass that there are two classes of eggs, one with 28 chromosomes, and one with 29. In the male on the other hand the corresponding bivalent is symmetrical or homomorphic, and all the sperms receive 28 chromosomes.

Despite some points still obscure, the Lepidoptera thus show a close

¹ Wilson, '09.

general agreement between the genetic facts and the cytological. The case is different with the birds, which still offer a puzzle but incompletely solved. All observers are agreed that genetically the female bird is the sex-heterozygote, but Guyer¹ has brought forward evidence to show that in the common fowl and the guinea hen the sperms are of two classes, distinguished by the presence or absence of an unpaired X-element or accessory chromosome. This element is a large curved body which in many cases passes to one pole in the first spermatocyte division in advance of the other chromosomes, thus producing two classes of second spermatocytes, one with nine and one with eight chromosomes. The second spermatocytes show, as a rule, either four or five chromosomes (the autosomes having secondarily coupled two by two),² all of which divide equally. Half the sperms receive eight chromosomes (apparently four) and half nine (apparently five). Guyer believes, however, that the 8-chromosome or no-X class degenerate; so that all the functional sperms are of the X-class, as in aphids or phylloxerans (p. 792).

In view of these facts it is very remarkable that the diploid groups seem to show in the female but one large curved chromosome (X), while in the male two such elements are present.³ The diploid groups thus seem to show the expected relation, the female being heterozygous, the male homozygous; but, *per contra*, the gamete-formation of the male seems to show this sex to be cytologically digametic, with one class of gametes non-functional. It is stated, further, that the X-chromosome of the spermatocyte-divisions is a bivalent body (representing the large pair in the spermatogonia) which passes as such to one pole.

If these facts be correctly determined they offer a cytological puzzle with which it is not possible to deal without additional data. This material, evidently, is very unfavorable for an accurate determination and it is greatly to be hoped that other species of birds may prove less difficult. A formal solution of the problem is offered by the hypothesis that the X-element of the male is a true bivalent (or pair of synaptic mates) which, after passing together to one pole in the first mitosis separates into its two components in the second, the equational-division being omitted. The sexes would then be produced according to the formulas: Egg X + Sperm X = XX (♂) and Egg O + Sperm X = XO (♀);⁴ but this involves a constant process of non-disjunction in spermatogenesis, a condition contradictory of all that is elsewhere known of synapsis and reduction.

¹ 'oga, 'ogb, '12, etc.

² As in the Hymenoptera (p. 797).

³ The total diploid number could not be determined exactly. In the male it is said to be 16-18.

⁴ This suggestion is due to T. H. Morgan.

III. SEX-CHROMOSOMES AND PARTHENOGENESIS

1. General Relations of Parthenogenesis to Sex

The fact that eggs which develop without fertilization may produce either males or females seems at first sight almost a nullification of the conclusions based on the study of fertilized eggs. The truth is far otherwise; the history of the chromosomes in parthenogenesis offers, indeed, a conclusive confirmation of those conclusions and forms one of the most interesting chapters in the whole subject of sex-production. In considering the subject it is necessary to distinguish clearly between parthenogenesis in female homogamety (as in the aphids, rotifers or Hymenoptera) and those cases in which this sex is digametic (Lepidoptera); but as will later be shown, the two cases are in principle in agreement.

a. Parthenogenesis with Female Homogamety. The facts in this case are most fully known in the aphids and phylloxerans; but those presented by the rotifers and Hymenoptera appear to conform to the same type and the same is probably true also of the daphnids and ostracodes. The main facts, earlier briefly outlined (p. 228), are as follows:

In the aphids (Fig. 379) the fertilized eggs produce only females which are strictly parthenogenetic and are the first of a series of similar females multiplying only by diploid parthenogenesis. Later in the summer appear parthenogenetic "stem-mothers," the offspring of which are also parthenogenetic but in most cases are of two physiological types, one producing only sexual females, the other only males. The fertilized eggs initiate a new cycle, producing (in the following spring) a new line of non-sexual parthenogenetic females, as before. A similar life-history is shown in the phylloxerans, the daphnids, and the ostracodes; and in all of these cases parthenogenesis (with the exception of one all-important point) is of the diploid type. Among phylloxerans some species have an "open life-cycle" like that of the aphids, *i. e.*, an indefinite number of parthenogenetic generations before the sexual forms appear. More commonly (*P. fallax*, *P. caryæcaulis*) the life-cycle is "closed," the stem-mother arising directly from the zygote (also the case in the gall-flies, p. 799). The offspring of the stem-mother are of two kinds, some producing only large eggs from which females develop, others only small eggs from which males develop, and as before, the cycle ends with fertilization (Fig. 379).

In the bees, wasps, and ants, on the other hand (Fig. 380), parthenogenesis appears to be exclusively of the haploid type, and no alternation takes place. Here all the fertilized sexual eggs produce females, the unfertilized exclusively males. The females, accordingly, are of diploid nuclear constitution, the males of haploid.

In the rotifers both types occur. The earlier part of the life-cycle agrees broadly with that of the aphid; a series of diploid female-producing parthenogenetic generations is followed by a generation the eggs of which may develop either sexually (*i. e.*, after fertilization), or by haploid parthenogenesis. This generation is exactly analogous to the bee or ant in the fact that if the egg be fertilized it produces a female of diploid constitution;

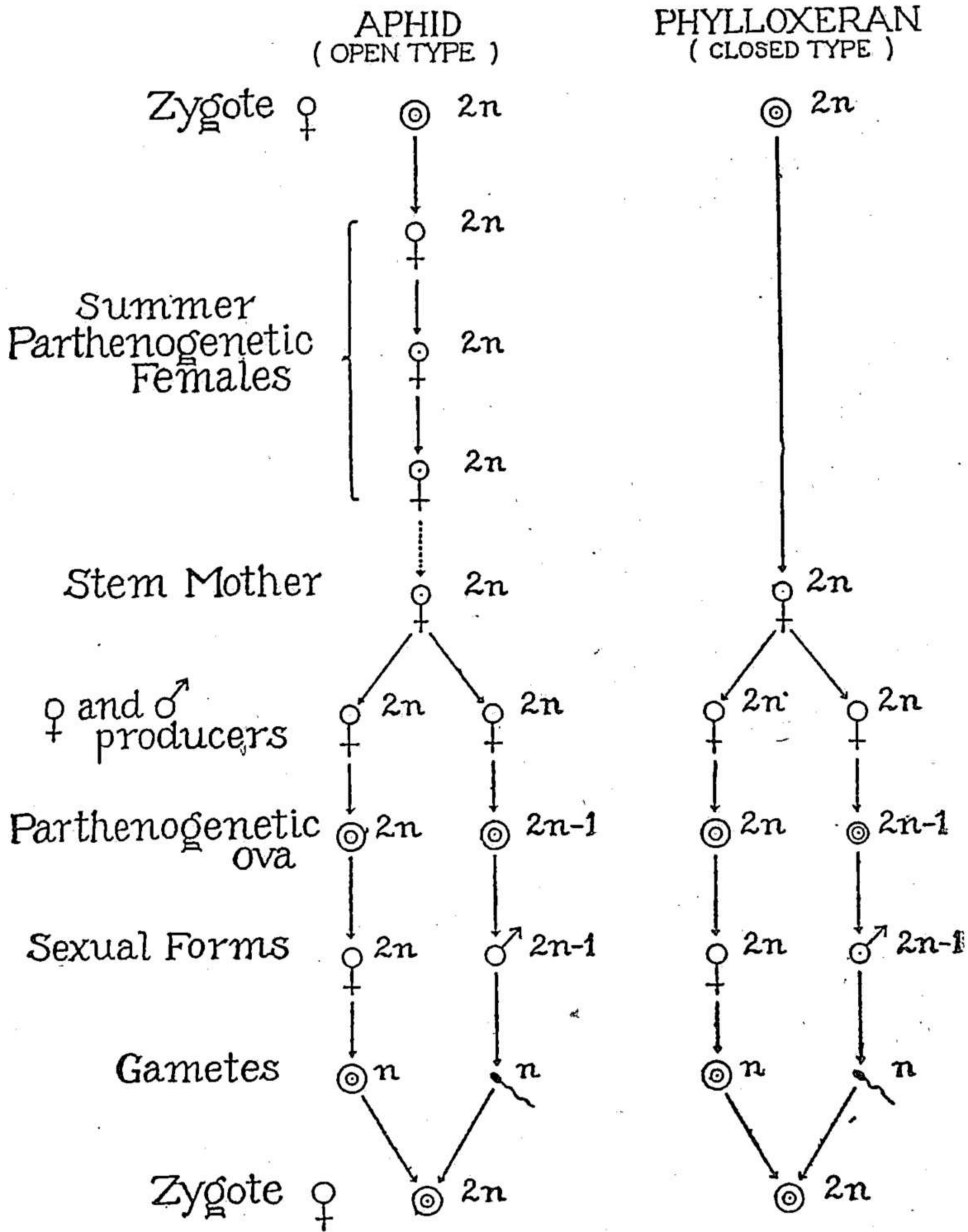


Fig. 379.—Diagram of diploid parthenogenetic life-cycles. Each cycle starts with the fertilized egg and ends with fertilization. The aphid shows a series of parthenogenetic female-producing generations before appearance of the sexual forms, the phylloxeran two such generations.

if it develops parthenogenetically, without fertilization, it produces a male which is of haploid constitution. In the gall-fly (*Neuroterus*) still a different combination appears (Fig. 380). Here, as usual, all the fertilized eggs produce parthenogenetic females, but some of these females produce only sexual females, by diploid parthenogenesis, while others give rise only to males by haploid parthenogenesis, as in rotifers or in the Hymenoptera.

Summing up these various cases we find that in all of them the fertilized eggs give rise exclusively to diploid females; that in diploid parthenogenesis the offspring may be either male or female (gall-flies, aphids, daphnids) whereas in haploid parthenogenesis only males are produced (rotifers, bees). In the latter case, obviously, the result is what we should expect; for if the egg develops with only the haploid group of chromosomes it contains but a single X and hence is *ipso facto* of male constitution. On the other hand,

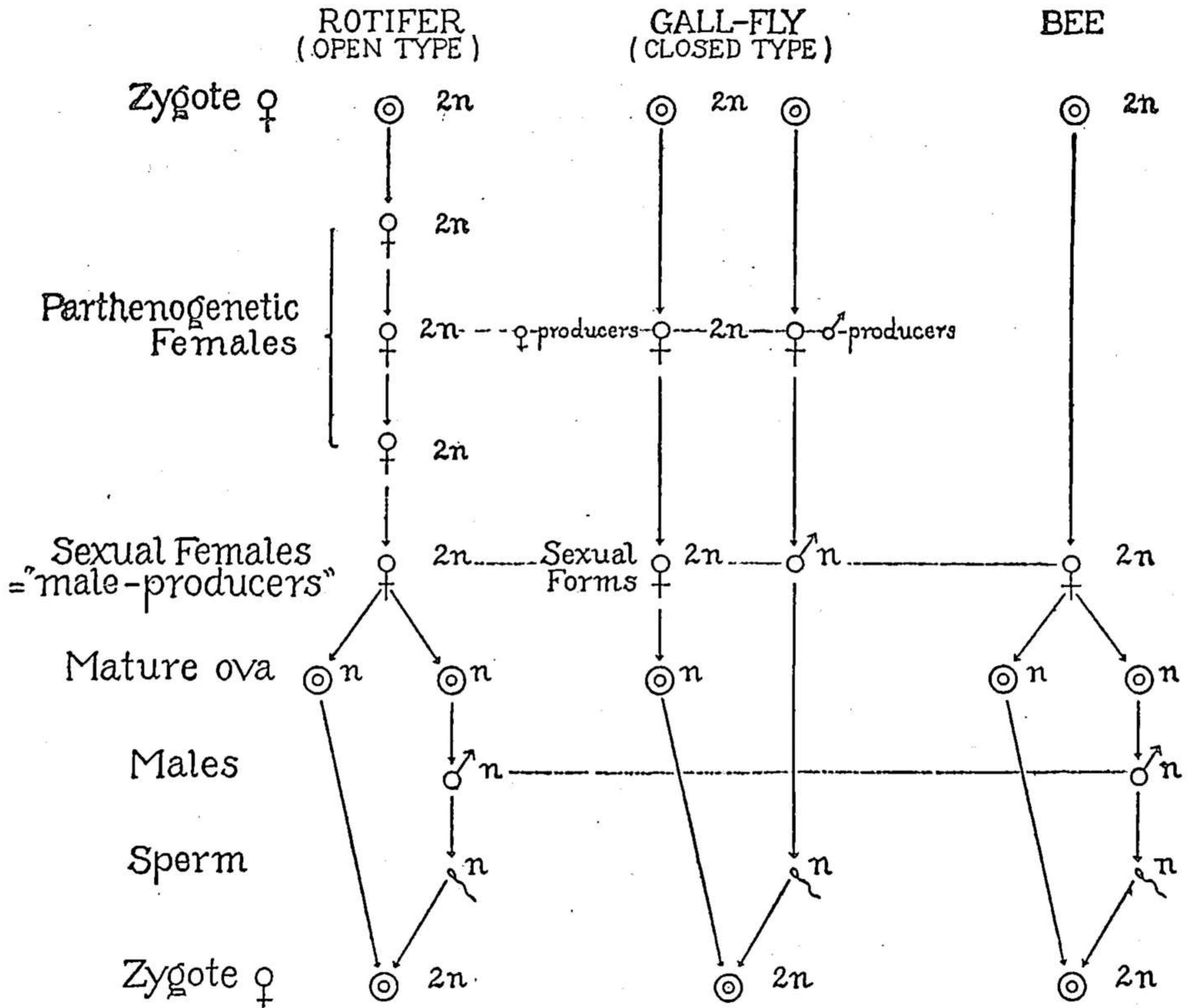


Fig. 380.—Diagram of mixed and of haploid parthenogenetic life-cycles. Each cycle starts with the fertilized egg or zygote and ends with fertilization. The rotifer shows a series of diploid female-producing parthenogenetic generations before appearance of the sexual forms, the gall-fly one such generation, the bee none. In all three cases males are produced from unfertilized mature eggs by haploid parthenogenesis.

the production of males in diploid parthenogenesis is by no means so evident, and its recent complete explanation by Morgan, Stevens, and De Baehr is one of the most interesting discoveries in this field.

2. The Sex-chromosomes in Diploid Parthenogenesis

In typical examples of this form of parthenogenesis the facts are now perfectly clear, though only a few cases have as yet been fully worked out.

In these cases, as earlier stated, but one polocyte is formed, the diploid number of chromosomes appears in the single maturation division (Fig. 223), and no general reduction of the chromosomes takes place. It was at first generally assumed that in this type no reduction of any kind takes place; and such is indeed the case in the production of females (e. g., in the aphids, phylloxerans, ostracodes or rotifers). Without exception so far as known, female-producing parthenogenetic eggs always develop with the diploid number of chromosomes.

In male-producing parthenogenetic eggs of this type the case is somewhat different. The important discovery was made independently by Morgan

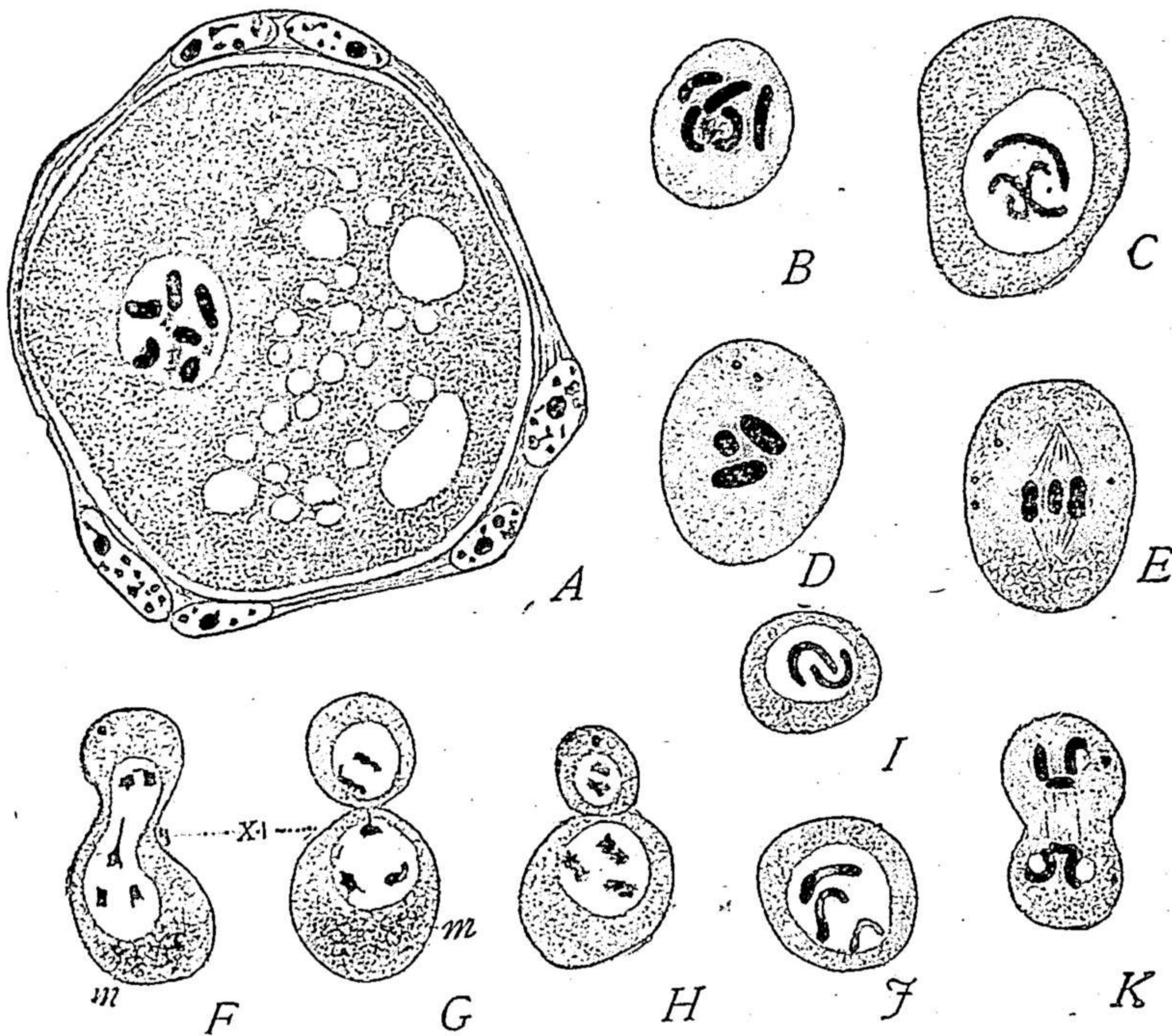


Fig. 381.—Sex-chromosomes in the aphid *Aphis saliceti* (BAEHR).

A, polar spindle of the parthenogenetic egg in polar view, with 6 chromosomes (the diploid number); *B*, spermatogonial metaphase, 5 chromosomes; *C*, spermatocyte-prophase; *D*, 1st spermatocyte-metaphase; *E*, the same in side-view; *F-H*, the first division, in side-view; *I* and *J*, the two resulting classes of second spermatocytes; *K*, second division of large second spermatocytes (*X*-class).

('08, '09) and Baehr ('08, '09) that the males of certain aphids and phylloxerans, though having no other mode of origin than by diploid parthenogenesis, nevertheless have one or two chromosomes fewer than the female. Thus, in *Aphis saliceti* (the simplest case) the females, according to Baehr, always have six chromosomes, the males five (Fig. 381). In like manner Morgan found in *Phylloxera fallax* 12 chromosomes in the female and but ten in the male; while the corresponding gametic numbers are 6 and 4, the *X*-element

consisting of two separate components, of which the female contains four and the male two.

It is clear from this that the production of the male must involve the elimination of one or two chromosomes; in other words, a reduction does occur *in the case of one or two chromosome-pairs*. This process, earlier suggested as a theoretical possibility,¹ was found actually to occur, in aphids

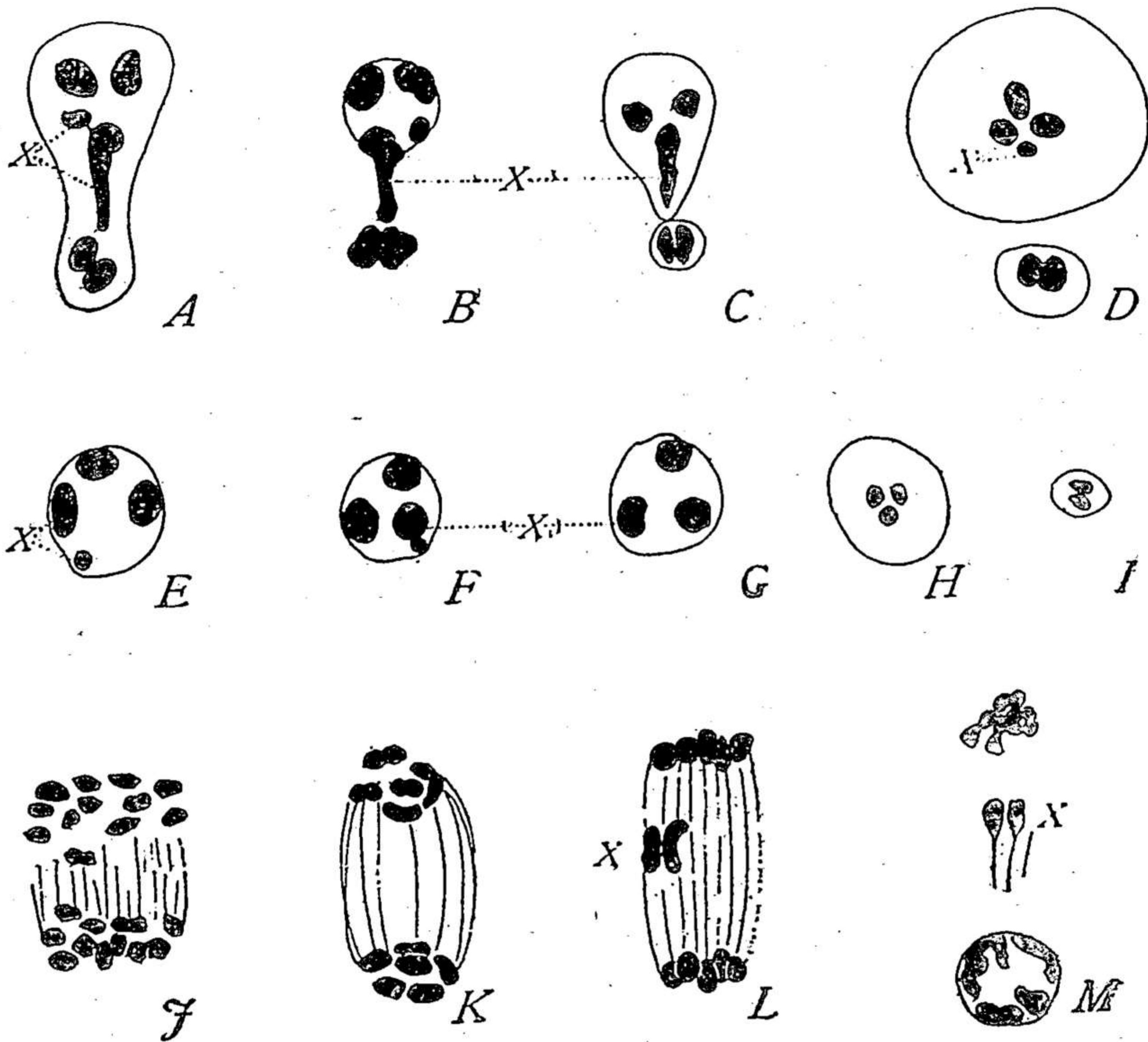


Fig. 382.—Sex-chromosomes in the parthenogenetic hemipter *Phylloxera* (MORGAN).

A, B, C, first spermatocyte-division in *P. caryacaulis*; *D* (more enlarged); the two resulting classes of second spermatocytes, one with 4 (or apparently 3) chromosomes, one with 2; *E, F*, 4-chromosome type (2 X-components) of second spermatocytes; *G*, 3-chromosome class (with single X); *H*, polar view of second spermatocyte-metaphase (3-chromosome type); *I*, 2-chromosome class of second spermatocyte (rudimentary, non-functional); *J*, *P. fallax*, polar spindle of stem-mother egg 12 chromosomes; *K*, *P. caryacaulis*, polar spindle of female-producing egg, six chromosomes to each pole; *L, M*, the same, polar spindles of male-producing eggs, elimination of lagging double X, showing five chromosomes left in the egg (the male number).

by Stevens ('10) and, especially by the work of Morgan ('12, '15), in two species of *Phylloxera* in which the X-element consists of two components, usually separate (p. 773). Morgan clearly showed, in these cases, that during the maturation of the smaller (male-producing) parthenogenetic eggs two chromosomes lag behind the others on the spindle during the anaphases, fail to enter the egg-nucleus, and are probably cast out in the polar body (Fig. 382). All is thus made clear; for we can hardly be mistaken

¹ Wilson ('07), Stevens ('09), Baehr ('09).

in the conclusion that the two extruded chromosomes (often closely coupled in *P. caryæcaulis*) represent a double X-element, comparable to that of *Syromastes* or *Fitchia* (p. 772) the mate of which remains in the egg. It thus comes to pass that the parthenogenetic eggs, though of diploid constitution in respect to the autosomes, are of two classes with respect to the X-chromosome, the female-producing egg having the constitution XX, the male-producing, X—obviously the same result which in the sexual process of so many other animals is effected by fertilization.

This is in itself a striking confirmation of the conclusions based on the ordinary sexual forms; but still more conclusive is the evidence given by the sexual reproduction of these same parthenogenetic species. Why should these animals differ from non-parthenogenetic species in the fact that fertilized eggs give rise exclusively to females? This question found a complete and simple answer, in the discovery that *only the X-class of sperms (i. e., the female-producing ones) come to complete development*. This fact, too, was independently discovered by Morgan in phylloxerans and by Baehr in aphids. In both forms the X-element, as usual, passes to one pole in one spermatocyte division (the first), but the division is markedly unequal. Thus are produced two visibly different classes of second spermatocytes, an X-bearing class of large size, and a no-X class of small size (Fig. 382). The former undergo an equal, equational-division and give rise to two functional sperms of the X-class. The small spermatocytes of the no-X class usually fail to divide and degenerate without giving rise to sperms. The only surviving sperms, therefore, are the X- or female-producing class. Nature here performs daily the precise crucial experiment needed to demonstrate the sex-producing capacities of the two classes of sperms. We may confidently expect that in the daphnids and ostracodes, likewise, the male-producing sperms will be found to be degenerate or non-functional; and also that in the parthenogenetic production of males one X-element is eliminated or rendered ineffective. In all these cases, however, one important point remains undetermined, namely, the mode in which the male-producing and female-producing mothers are differentiated. We look naturally to the origin of these mothers from the stem-mother in the hope of finding evidence of some kind of differential division in the maturation of the eggs from which they arise. Morgan ('12b) has in fact found certain peculiarities of the chromosomes in the male-producing eggs of *Phylloxera caryæcaulis* which suggest that a small component of the X-chromosome is eliminated during the maturation of the stem-mother's egg from which the male-producer arises; but the demonstration of this is still incomplete.

Since parthenogenesis of this type involves no general reduction we might expect to find no evidence of synapsis or the associated phenomena in the

oocytes, and such seems indeed sometimes to be the fact; but there are some notable exceptions. In some cases of diploid parthenogenesis the oocytes pass through a stage of synizesis indistinguishable from the same stage in the sexual egg, and this may even be followed by a process of pseudo-reduction and the formation of tetrads. Woltereck ('98), confirmed by Schleip ('09), found the former condition in the parthenogenetic oocytes of ostracodes (*Cypris*) but observed no process of pseudo-reduction. This was at first supposed to mean that synizesis has no necessary connection with the process of reduction.¹ Further observation, however, showed that this conclusion was unfounded. Strasburger ('04, '07, '09) found in *Marsilia* that diploid apogamy is preceded by a process of synizesis and pseudo-reduction, but that during the diakinesis the diploid number is restored by a disjunction of the synaptic mates of each bivalent; and indications of a similar process, though less complete, were found in *Alchemilla*. In *Wikströmia* the synaptic phase seems to be entirely absent, and the chromosome-number is diploid from the beginning. Similar variations seem to exist among animals. It was found by Fries ('09) that the sexual eggs of *Branchipus* pass through a typical synaptic stage involving a (probably) parasynaptic conjugation of chromosomes, but in the diploid parthenogenetic eggs of *Artemia* these appearances are wanting and the egg-nucleus gives rise directly to the diploid number of chromosomes. Morgan ('15) likewise found typical synizesis in the sexual eggs of the "bearberry aphid" but never in the parthenogenetic ones, the contrast being so great that ovaries producing the two respective types of eggs can thus readily be distinguished. On the other hand, Baehr ('20) found that the parthenogenetic eggs of *Aphis palmæ* undergo a marked synizesis and give rise to four bivalent chromosomes (the diploid number is eight); but in the diakinesis these are disjoined or "deconjugated" to form eight single chromosomes which undergo a simple longitudinal splitting during the single polar mitosis.

It thus seems to be well determined, as Strasburger ('09) indicated, that parthenogenetic eggs of the diploid type show different degrees of adaption to parthenogenesis. Some of them prepare for complete reduction by the usual process, but this is never fully carried out, the conjugation being undone in the diakinesis so as to restore the diploid number. In others the "deconjugation" is effected earlier (*Alchemilla*), and in still others the synaptic phase seems to have been lost entirely (*Wikströmia*). An indication of how such a series of stages may have had its beginning is possibly seen in the diakinetik deconjugation and reconjugation that takes place in the sexual eggs of *Lepidosiren* as described by Agar (p. 563),

¹ Hence also Woltereck's conclusion that synizesis and the associated changes represent an abortive mitosis, a view afterwards advocated by R. Hertwig and a number of others.

or in those of certain Hymenoptera (*Rhodites*, *Cynips*, etc.) which may undergo complete reduction and may either be fertilized or develop by diploid parthenogenesis (p. 803). All these facts point to the conclusion that the diploid parthenogenetic egg has been derived from a sexual egg which was originally capable of complete reduction (and perhaps also of haploid parthenogenesis), by the progressive restriction and final loss of the synaptic phenomena and their consequences.

3. Sex in Haploid Parthenogenesis

The second or haploid type of natural parthenogenesis is at present known only in Rotifera, Hymenoptera, Thysanoptera, Hemiptera and Arachnida.

In Hemiptera and Arachnida. Though only a single case is known in each of these groups the cytological facts seem to be so clear as to form a desirable introduction to more debatable cases. In the homopter *Trialeurodes vaporariorum*, as earlier indicated (p. 232), virgin females of the English race produce only females (presumably by diploid parthenogenesis) while those of the American race produce only males. Schrader ('20) found that in the latter case the females, produced sexually, are diploid (22 chromosomes) and the males produced parthenogenetically, are haploid, clearly showing 11 chromosomes. These numbers were found in all stages of development from cleavage up to late pupæ with gonads in an advanced stage of development. The egg undergoes a typical meiosis with reduction to the haploid number (11), and in fertilization receives 11 chromosomes from the sperm. In the male, on the other hand, no reduction occurs and the heterotypic division seems to be entirely suppressed, a result borne out by the numerical relations of the spermatids and spermatocytes. This case will bear further examination, but the main result seems to be well established. It is noteworthy that mated females produce offspring of both sexes, which suggests that the actual fertilization of the egg may be controlled by the female spermatheca, as in the bee.

In the mite *Tetranychus bimaculatus*, a case also made known by Schrader ('23), the facts are even more demonstrative, since the haploid number is but 3 and the diploid 6. In this case, also, as shown by several earlier observers, virgin females produce exclusively male offspring, while mated females produce offspring of both sexes. Schrader's work proves that all the eggs subsequent to meiosis have 3 chromosomes; that fertilized eggs divide with 6 chromosomes, unfertilized with 3; that in the blastoderm stages and up to the larval stages, some embryos show 6 chromosomes, others 3; that the spermatogonial divisions show 3 chromosomes and the oögonial 6; and that in the male the heterotypic division is suppressed.

while in the oöcytes the meiotic divisions take place normally, with 3 tetrads. All doubt thus seems to be removed that in this species, as in the foregoing case, males arise from unfertilized eggs and undergo complete development by haploid parthenogenesis, while females arise from fertilized eggs, and are diploid.

In *Hymenoptera*. The classical case of haploid parthenogenesis is offered by the honey-bee where the celebrated theory of Dzierzon (1845) long formed a center of controversy. Dzierzon's observations, supplemented by those of Siebold, Leuckart and many later investigators, proved that females alone (queens or workers) are produced from fertilized eggs, males alone (drones) from unfertilized. This condition is now known to be widespread among the Hymenoptera (bees, ants, wasps, chalcids) and so far as the production of males is concerned may be universal in this group. Some doubt, however, still hangs over the cytological side of the subject, since the phenomena are here in a measure confused by the frequent occurrence of double or multiple chromosome-groups in the somatic divisions (p. 803) and also by the frequent secondary coupling of the chromosomes two by two in both the spermatocytes and the oöcytes. This has led to uncertainty as to the number of chromosomes in the diploid and haploid groups, and as to the sexual chromosomal differences. Nevertheless, it may now be stated with considerable confidence that among the Hymenoptera thus far investigated the females, produced from fertilized eggs, develop with the diploid number of chromosomes (or a multiple of it) while the males, produced from unfertilized eggs, develop with the haploid number. The sex-chromosomes have not yet been identified as such. Nevertheless, it is highly probable from the general constitution of the chromosome-groups that the females have the sexual constitution XX, the males X; for the unfertilized eggs, having undergone reduction, should contain one X, and this number is not doubled in the course of development.¹ It must, however, be borne in mind that in case of both bees and ants virgin workers are asserted to have produced female offspring (workers, queens).² The workers and queens thus produced should, of course, be diploid; but how this result is produced is unknown. It might be due to a failure of reduction and the formation of but one polocyte in such eggs or to a secondary doubling (*cf.* p. 803). The cytological investigation of such cases should give a crucial test of the XO-XX quantitative theory of sex (p. 816).

We need not here review *in extenso* the rather complicated history of the researches on which this conclusion concerning sex-production in Hymenop-

¹ Wilson ('09), Baehr ('09), R. Hertwig ('12), Nachtsheim ('13), Patterson ('17), Whiting ('21), etc.

² See Wheeler ('03), on ants. Onions ('12, '14), on bees.

tera is based.¹ A first key to the problem was found by Blochmann ('86) with the discovery that not only the fertilized but also the unfertilized eggs produce both polocytes and hence presumably undergo complete reduction. The possibility was opened that in the bee the parthenogenetic egg (male-producing) might develop with the haploid number of chromosomes. Opposed to this were the observations of Petrunkevitch ('01, '13) who found that both fertilized and unfertilized eggs developed with 16 chromosomes, though higher numbers (32, 64) were also observed; he concluded, therefore, that 16 is the fundamental diploid number characteristic of both

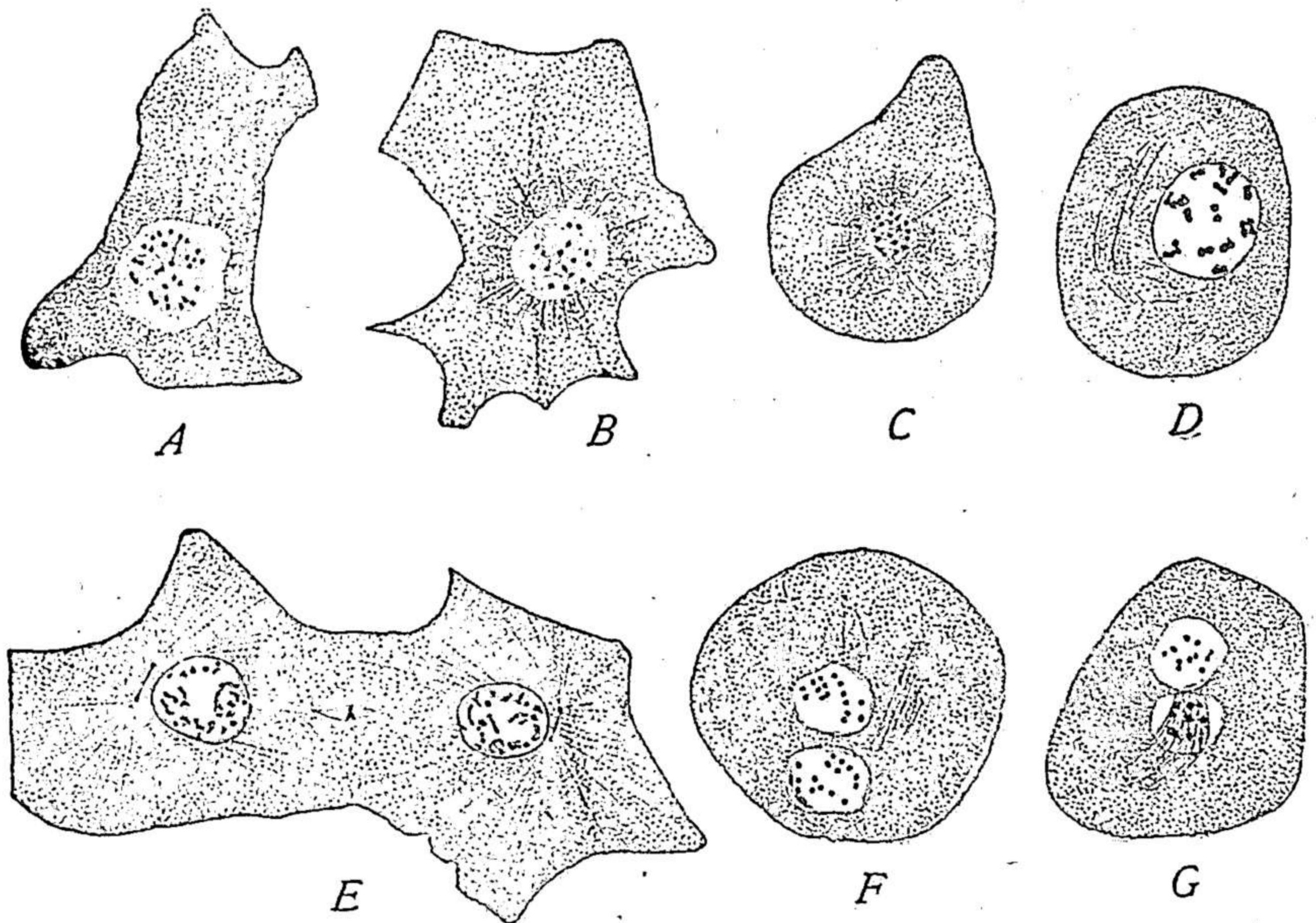


Fig. 383.—Chromosome-groups in the honeybee (NACHTSHEIM).

A, cleavage-cell (anaphase-group) from female (worker) embryo, 32 chromosomes; B, C, similar views, from male (drone) embryos, 16 chromosomes; D, first spermatocyte, diakinesis, 16 dyads; E, telophase, cleavage-cell, drone-embryo; F, G, second spermatocyte telophases, in F about 16 chromosomes, in G about 8.

sexes and 8 the haploid. This result seemed to be supported by the behavior of the chromosomes during maturation; for the polar spindle shows in fact eight tetrads, and the nucleus of the mature egg receives the same number of chromosomes. Petrunkevitch's conclusion was, however, insecurely based. The studies of Meves ('04, '07) on the spermatogenesis of both the bee and the hornet (*Vespa*), confirmed by those of Mark and Copeland ('06, '07) and other observers, proved that the spermatogonial number in the bee is 16, but also proved that each sperm-nucleus receives the same number. Meves therefore concluded that not 8 but 16 is the fundament

¹ A good review is given by Nachtsheim ('13). See also Schleip ('12), who gives an excellent view of the entire subject of sex-determination.

haploid number, and that the egg must have developed by haploid parthenogenesis. Substantially the same result is reached by Mark and Copeland, and by Doncaster ('07), and especially by Nachtsheim ('13), who made an extended reëxamination of the subject.

Nachtsheim's work clearly shows that the unfertilized egg (male) develops with 16 chromosomes, the fertilized egg (worker) with 32, these numbers occurring both in the cleavage and in later stages (Fig. 383). His observations also show that Petrunkevitch failed to reckon with a secondary linkage or coupling of the chromosomes first seen in the anaphases of the spermatocyte-division, the 16 chromosomes showing a tendency to unite two by two, so that the spermatid-nuclei often seem to receive only eight chromosomes.¹ In the female the same tendency to couple is seen at still earlier stages. In the female blastoderm 32 chromosomes are present; but in the oögonia the number seems reduced to 16, the chromosomes having already united two by two (p. 869). In the polar spindles appear eight tetrads, and after meiosis the egg seems to receive eight single chromosomes as Petrunkevitch correctly described. It now seems clear, however, that these chromosomes are bivalent, corresponding exactly to the eight chromosome-couples in the sperm-nucleus; and since the unfertilized egg segments with 16 chromosomes the fertilized with 32 the linkage must be dissolved as soon as development begins.

The foregoing results find a remarkable confirmation in the fact that no reduction of the chromosomes takes place, the sperms receiving 16 chromosomes, the same number shown in the cleavage, and in the spermatogonia. It is, however, a significant fact, discovered by Meves in the bee and hornet, that a kind of vestigial reduction-division takes place, the primary spermatocyte making an abortive attempt to divide, in the course of which an incomplete spindle is formed, and the chromosomes appear, but no nuclear division occurs. The result is the extrusion of a non-nucleated mass of protoplasm or "polar body" (Fig. 384), and this is followed by one complete mitosis in which both nucleus and protoplasm divide normally. A similar condition has been found in many other Hymenoptera.²

In these cases, evidently, the formation of a non-nucleated "polar body" is a vestigial process which represents the remnant of a formerly complete reduction-division. The second or homeotypic division is always a complete normal mitosis, involving the division of both nucleus and cytosome. A

¹ Earlier observed by Doncaster ('07). Such a secondary coupling in the second meiotic division has been observed in a considerable number of other cases, for instance, in birds (Guyer, '00, '09, G. Smith, '12), man (Guyer, '10) and other mammals (Jordan, '11, Wodsdalek, '13). It is not certain, however, that this may not in some cases be due to an artificial clumping.

² In the hornet and bumblebee (Meves and Duesberg, '07, '08; Mark and Copeland, '07); the ant *Camponotus* (Lams, '08); the solitary bees *Xylocopa* (Granata, '07, '13) and *Osmia* (Armbruster, '13); and the gall-flies *Neuroterus* (Doncaster, '10); *Paracopidosomopsis* (Patterson and Porter, '17).

curious and hitherto unexplained fact is that while in some cases this division is equal, and produces two normal sperms (wasps, ants, gall-flies), in others it is markedly unequal, the larger cell alone producing a normal sperm (bees).

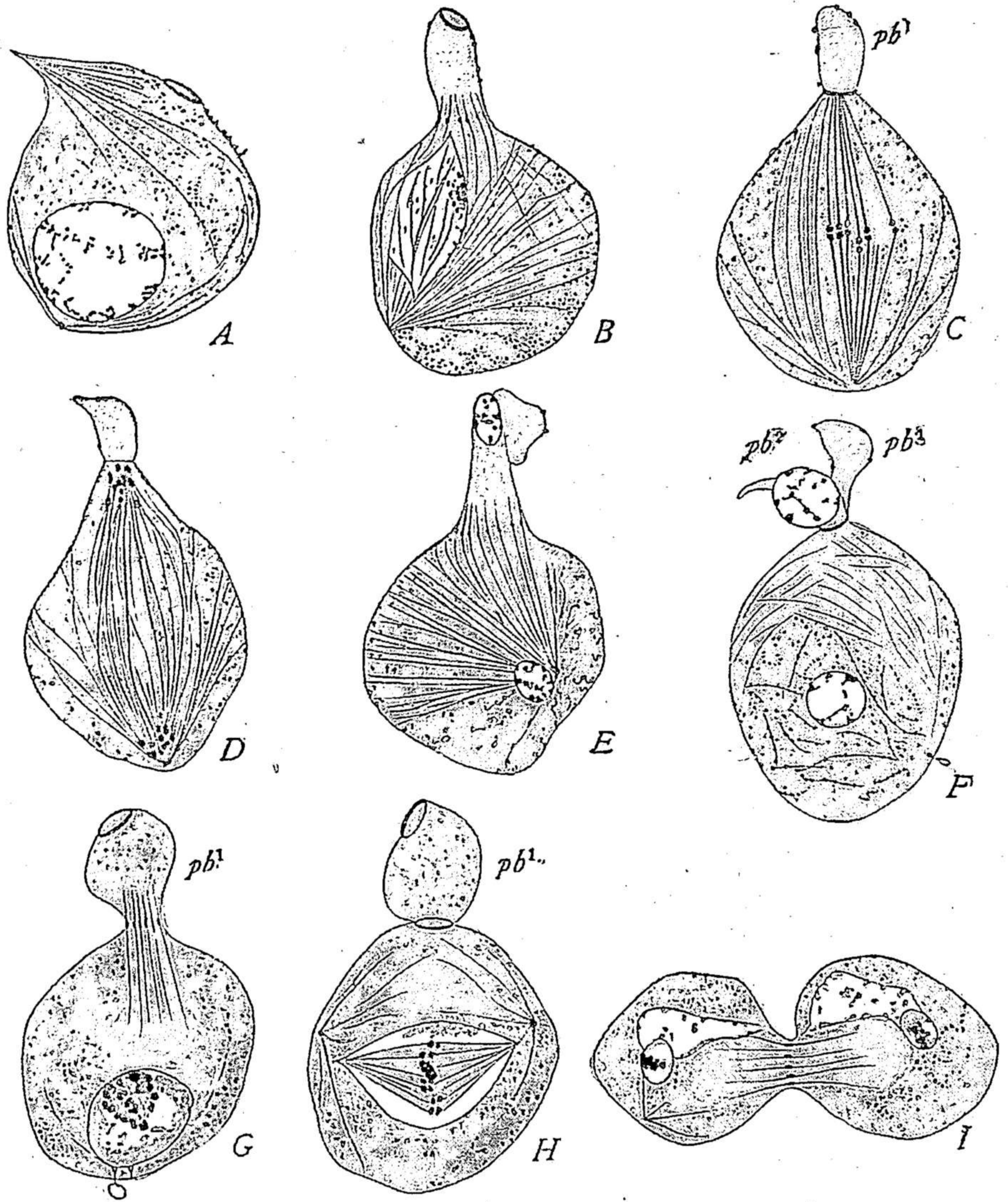


Fig. 384.—Spermatocyte-divisions in *Hymenoptera* (MEVES).

A, first spermatocyte of the honeybee (*Apis*); B, C, the first (abortive) division, producing a non-nucleated "polar body" (pb^1); D, E, F, the second division, producing a nucleated "polar body" (pb^2); G, H, corresponding first division in the hornet (*Vespa crabo*); I, second, equal division, producing two spermatids.

The meaning of this is unknown; but it is obvious that the unequal division of the bee must be of wholly different nature from that seen in the spermatogenesis of the aphid or phylloxeran (p. 792). This is proved by the wasps, in which the equal division is obviously identical with the unequal one of

the bee, yet both products are female-producing (*i. e.*, of the X-class). In the aphid, on the other hand, the unequal division produces one spermatocyte of the X-class and one (degenerate) of the no-X class.

The general result reached in case of the bee is probably of wide application among the Hymenoptera. Schleip ('08) demonstrated that it holds true for the ant (*Formica*) showing that fertilized eggs develop with 48 chromosomes, unfertilized (male-producing) with 24. Granata (*op. cit.*) found that in *Xylocopa*, a solitary bee, the sperms receive the spermatogonial number (16) without reduction, as in the honeybee or the ant.¹ In the gall-flies, where both diploid and haploid parthenogenesis occur, we may take as a type *Neuroterus* (*Spathogaster*) *lenticularis*, which has

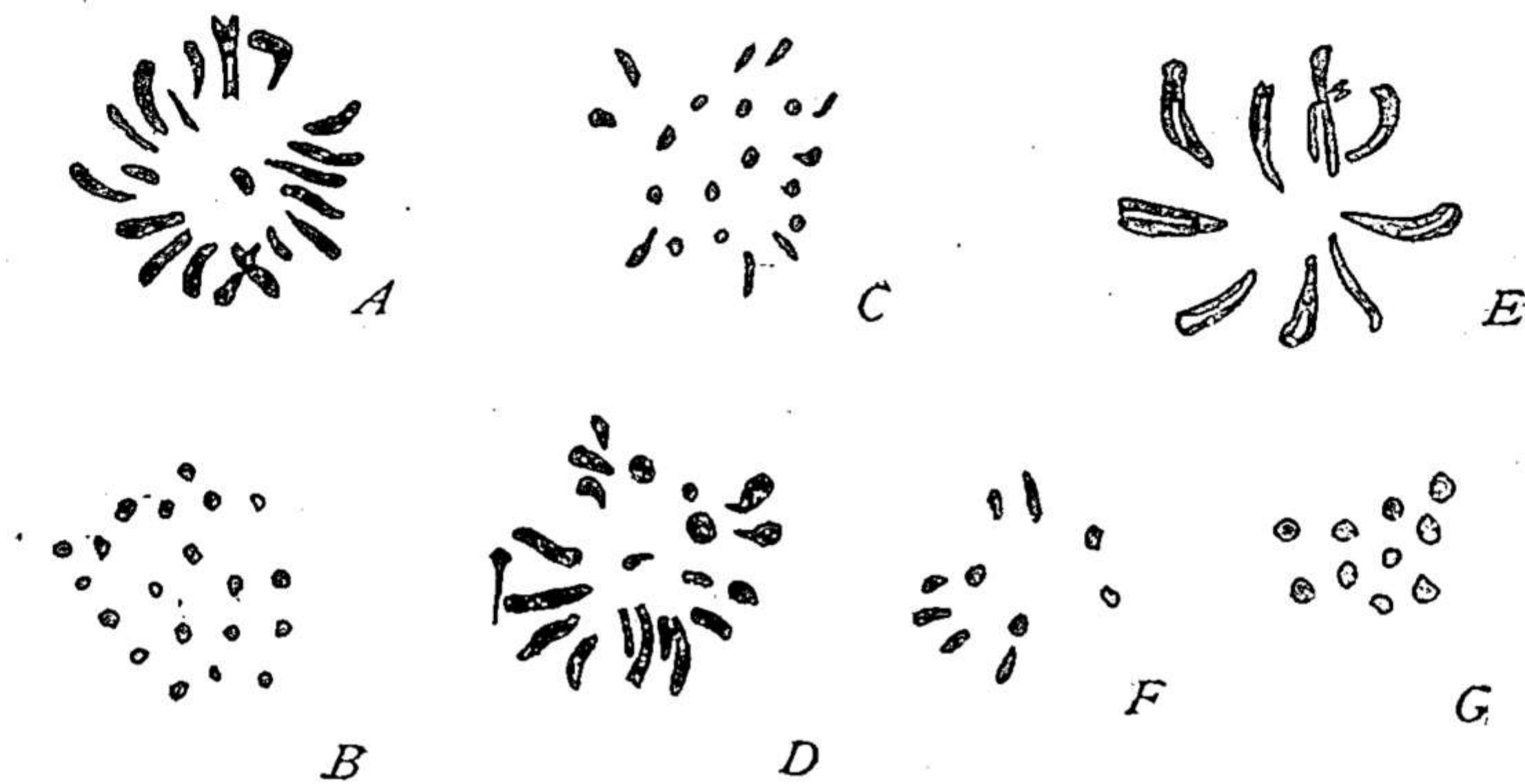


Fig. 385.—Sexual differences of the chromosome-groups in the gall-fly *Neuroterus* (DONCASTER).

A-D, female groups (20 chromosomes); E-G, male groups (10 chromosomes).

A, ovarian cell, metaphase; B, same, anaphase; C, anaphase, larval nervous system; D, cleavage-stage, metaphase; E, metaphase, larval nervous system; F, spermatogonial anaphase; G, cleavage-stage, anaphase.

been carefully studied by Doncaster ('10, '11, '16). In this species the diploid number is 20, the haploid 10, the former number characteristic of the females, the latter of the males (Fig. 385). The sexual egg forms two polar bodies, with a reduction of chromosome-number from 20 to 10. The spermatogonia show 10 chromosomes and undergo no reduction, the reduction-division being abortive, while the equational-division produces (as in *Vespa*) two equal spermatids and two functional sperms. The fertilized eggs develop within galls formed on the oak and hatch in the spring to produce exclusively parthenogenetic females, having 20 chromosomes, and constituting the asexual or agamic generation. Their eggs, without fertilization, produce either sexual females or males, in the former case de-

¹ Armbruster ('13) believed that in *Osmia* (also a solitary bee) the spermatogonial number was reduced from 16 to 8; but this, as Nachtsheim shows, is no doubt due to a secondary coupling as above described.

veloping with 20 chromosomes (*i. e.*, without undergoing reduction) in the latter case with 10.¹

Doncaster showed that each individual female produced by the agamic spring generation produces either male or female offspring but not both. These parthenogenetic mothers are therefore exactly comparable to the male-producers or female-producers of the phylloxeran, and the first agamic generation (the product of fertilization) corresponds to the stem-mother generation (p. 787). Doncaster has experimentally ('16) arrived at the further conclusion that each sexual female gives rise exclusively either to male-producing or to female-producing stem-mothers.² No explanation of this has thus far been found; it may be due to the existence of two kinds of males, or to differences in the maturation-process of eggs laid by two kinds of sexual females. Until this question (like the analogous one in case of the phylloxerans) has been settled the question of sex-determination in these forms will remain but incompletely solved. Concerning the main point, it seems highly probable, though only a small number of cases are yet known, that the haploid condition of the male is characteristic of Hymenoptera generally; for it is known that males are produced from unfertilized eggs in many Hymenoptera besides those that have been mentioned,³ and the cytological conclusions are fully borne out by the genetic facts.

The current cytological interpretation of the foregoing cases has already been indicated (p. 795). Since the males are haploid they contain but one X-chromosome, while the diploid females should contain two such chromosomes. There is, however, another possibility, namely, that the haploid group of the male represents a compound X-element, all the chromosomes containing "X-chromatin," while two such groups are present in the female.⁴ In case of the bee this seems improbable; but Schrader's remarkable observations on *Pseudococcus* seem to show that such a condition is actually realized, except that a compound Y-element is also present (p. 778).

¹ Doncaster states that the female-producing egg undergoes no maturation-division, the male-producing two divisions, the number of chromosomes remaining 20 in the first case, and in the second being reduced to 10. This suggests the need of further study of the female-producing eggs; but the final result seems to be well determined.

² Out of a total of 9574 offspring reared from over 80 galls, produced by 12 isolated females, only 2.09% of exceptions were found and there is good reason to suspect that these were due to accidental contamination.

³ For a recent discussion of this question see Nachtsheim ('21). An interesting exception to the above statement is found by Whiting ('21) in the parasitic wasp *Hadrobracon*. The genetic evidence (p. 929) proves that males are of haploid constitution but also proves that exceptionally they may arise from *fertilized* eggs. This is demonstrated in crosses between black-eyed males (dominant) and pure-bred orange-eyed females, in which a few of the sons show the black-eyed character of the father. This may mean that the anomalous males are sex-mosaics, or that some of the maternal chromosomes are cast out (*e. g.*, by non-disjunction or the like). See A. R. Whiting, *Genetics*, X, Jan. 1925.

⁴ Schrader ('20); see also Gutherz ('23).

3. In Rotifera

In the rotifers, as in the gall-flies or aphids, all the fertilized eggs produce parthenogenetic females, the eggs of which form but a single polocyte and develop by diploid parthenogenesis. This generation may be followed by a long series of others of the same type which in some cases (*Hydatina*) are known to be of diploid constitution (Whitney). Sooner or later appear the sexual forms, characterized by the production of small eggs which, unlike the ordinary parthenogenetic eggs, produce both polocytes and are capable of haploid parthenogenesis but, as in case of the bee are also capable of fertilization. If unfertilized these eggs remain small and develop by haploid parthenogenesis (Whitney) into males. If fertilized, the egg enlarges, secretes a thick membrane about itself, and is thus converted into a "resting" or "winter egg" (Fig. 386). Such eggs contain of course the diploid number of chromosomes; and after a long period of rest, produce parthenogenetic females with which the diploid parthenogenetic cycle begins.

This life-history, evidently, is closely similar to that of the bee, save that a series of diploid parthenogenetic generations precedes the appearance of the sexual forms. The gall-fly (*Neuroterus*) may be considered as intermediate in type, since only one generation of diploid parthenogenetic forms exists, *i. e.*, that produced by the zygotes. In all these cases, obviously, there is but one class of sperm, the female-producing. In case of the rotifer we naturally look for an explanation like that which applies to the bee; but in so doing find ourselves involved in certain difficulties that can only be cleared up by further work. Whitney ('17, '18) has found that there are in rotifers two kinds of sperms, both nucleated, but one much larger than the other and twice as numerous. A solution of the puzzle here offered has not yet been found.

The most interesting point in the life history of the rotifer is the proof that it affords of the fact that *fertilization changes the sex of the egg*. That such is the case in the bee has long seemed nearly certain; nevertheless it might be held that only eggs predestined as female-producing are capable of fertilization. In the rotifer, however, this possibility has now been excluded. Maupas ('90), Nusbaum ('97) and other of the earlier observers found that each individual female rotifer lays but one kind of egg, namely, (1) parthenogenetic (diploid) female-producing eggs or (2) parthenogenetic (haploid) male-producing, or (3) sexual "resting" or "winter" eggs, which develop only when fertilized. Of these three classes of eggs (Fig. 386) the second and third are now known to be identical. Maupas showed that winter eggs are never produced by females that have been isolated from the males, though a certain proportion of males may appear; that females that

have had free access to males produce winter eggs in almost exactly the same proportion as that of the males produced by control cultures of females that have been isolated from males. He therefore concluded that

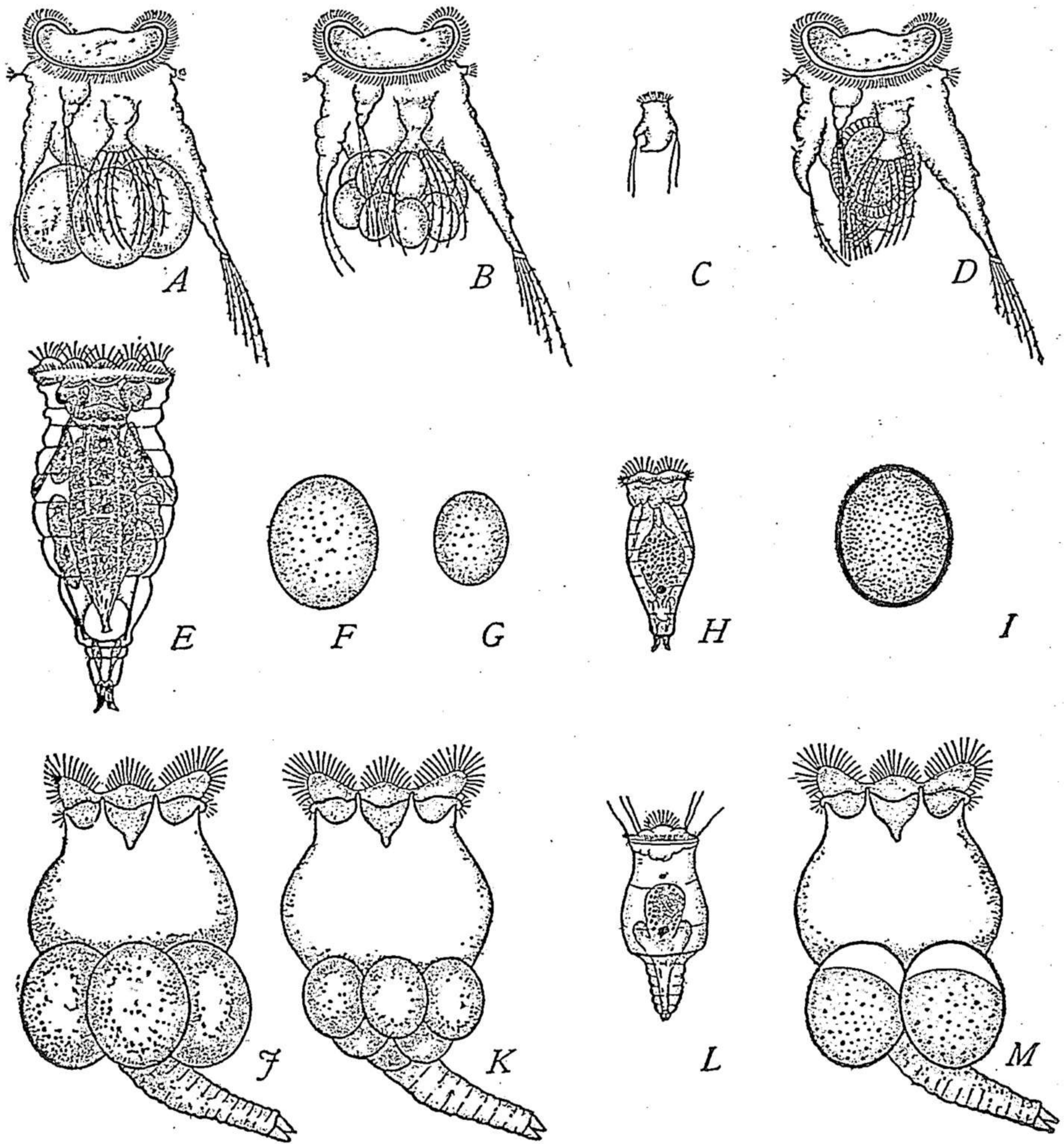


Fig. 386.—Sexual dimegaly of the eggs in Rotifers (WHITNEY).

A, *Pedalion mirum*, parthenogenetic female with female-producing eggs; B, female with "small male-producing" eggs; C, mature male; D, sexual female or fertilized "male-producer" bearing female-producing fertilized egg (the latter originally like those of B).

E, *Hydatina senta*, parthenogenetic female-producer; F, egg of same; G, male-producing egg; H, mature male; I, fertilized egg (originally like G).

J-M, *Brachionus pala* (series exactly corresponding to A-D); J, female-producing female; K, male-producer; L, male; M, sexual female or fertilized "male-producer."

the sexual or winter egg is simply a "male-producing" egg that has been fertilized. This has been fully confirmed by Shull ('10), who added the decisive observation that the same female may produce both winter eggs and male-producing eggs, provided she be fertilized by old or spent males that

contain very few sperms. Since all observers are agreed that all parthenogenetic eggs from one individual are always of the same sex, this observation makes it in high degree probable that the winter eggs are male-producing eggs that have been fertilized. A curious corollary to this conclusion is that the sexual female always appears one generation earlier than the male; for she is, necessarily, the mother of the male (Shull, *op. cit.*).

4. Problematical Cases

Thus far all the facts are in general accord with the principle earlier emphasized (p. 505) that in the course of the two meiotic divisions each chromosome of the original diploid (gonial) groups divides but once (equationally), the reduction "division" being only the separation of two closely associated synaptic mates. The cases now to be considered seem at present explicable only under the assumption either that both divisions are equational or that two such divisions follow the heterotypic. Such cases, obviously, call for the closest scrutiny; but unluckily none of them has as yet been sufficiently worked out to justify more than tentative conclusions. In most of these cases the egg seems to undergo a complete process of meiosis, with the production of both polocytes and reduction of the chromosomes to the haploid number, yet it develops without fertilization with the full *diploid* number of chromosomes.¹ Such eggs, so far as known, always produce females. They have been adequately investigated only in certain of the Hymenoptera (gall-flies and their allies); but the analogous phenomena in female digamety (Lepidoptera) have been more carefully examined (p. 805).

The earliest and best-known of these cases is that of the rose gall-fly, *Rhodites rosæ*, in which males are almost unknown, reproduction being uniformly parthenogenetic and producing almost always females. Henking ('92) found in this case that both polocytes are formed; and that during this process the number of chromosomes is 9; nevertheless the egg segments with double this number (18-20). He therefore concluded that at some time subsequent to maturation the haploid number is doubled by a secondary splitting. The same result is reached in more extended recent studies on the same species² by Hogben ('20a), who shows that the somatic number is 18 and that the oöcyte undergoes a typical process of pseudoreduction to form 9 bivalents. The process of doubling subsequent to reduction has not yet actually been observed but would seem to involve an additional

¹ For the similar difficulty concerning the occasionally parthenogenetic production of females in bees, see p. 795.

² Schleip ('09) confirmed Henking in regard to the number of polocytes and also adopted the conception of a second equational split, but was apparently in error concerning the number of chromosomes.

equational division though possibly some other interpretation of the facts may be found.¹

A very noteworthy feature in this case is the fact, carefully studied by Hogben, that synapsis takes place (parasynaptically) in the usual manner and place but its effect is temporarily undone at a later period (subsequent to the confused period), when *the chromosomes reappear in the diploid number, 18*. This is followed by a *telosynaptic* reunion of the univalents to form again 9 bivalents which pass upon the first polar spindle. A similar phenomenon is described in *Cynips* and in the ichneumonid *Orthopelma* and is believed to be of wider occurrence in the parasitic Hymenoptera, since Hegner also described a late telosynaptic process in the chalcid *Copidosoma* and many other more or less isolated observations fit with the more complete ones on *Rhodites*. A curious additional fact seen in these forms is a clumping together and condensation of the chromosomes of the first polar spindle to form an almost solid mass or "chromatin-nucleus." This has been described by a considerable number of observers,² but the relations of this stage to the later stages of maturation have not yet been clearly worked out.

Similar in type to the foregoing is the parthenogenetic phasmid, *Bacillus rossii*, where males are of extreme rarity. Baehr ('07) here found two maturation-divisions, apparently preceded by true tetrad-formation, which makes it very probable that a complete reduction occurs, yet the eggs, with extremely rare exceptions are female-producing, and apparently must restore the diploid number. This case may perhaps be explained, like that of *Rhodites* by assuming the occurrence of an extra equation-division; but it seems at least equally possible that the number may be doubled by reunion of the second polar nucleus with the egg-nucleus or a process of similar type (p. 471). In respect to all these cases, however, we are still on hypothetical ground. The strongest cases for the occurrence of two equation-divisions (here accompanying a partial or complete failure of the reduction-division) is offered by the moth-hybrids of Federley and of Doncaster, and by certain plant-hybrids (p. 852). Further interesting suggestions are offered by the recent work of Seiler ('23) on the cytological phenomena of parthenogenesis in female digamety (Lepidoptera) a brief account of which follows:

a. Parthenogenesis and Sex with Female Digamety. The occasional parthenogenetic development of unfertilized sexual eggs in Lepidoptera (the so-

¹ Hogben ('20a) suggests (1) that both polar mitoses may be equational and that the subsequent doubling may be due to a disjunction of the bivalents; but this seems to differ little in substance from the earlier suggestions of Henking and of Schleip.

² E. g., by Hegner ('14) in *Copidosoma*, *Andricus*, and *Apanteles*; by Martin ('14) in *Ageniaspis*, *Silvestri* ('14) in *Copidosoma*; by Gatenby ('18) in *Trichogramma*, and Hogben ('20) in *Neuroterus*, *Cynips* and *Rhodites*.

called "facultative" parthenogenesis) has been recorded by several observers;¹ and it has long been known that in the family of Psychidæ there are some forms in which parthenogenesis is of regular or even of almost exclusive occurrence (p. 231). The studies of Seiler on *Solenobia*, including both the obligatory or regular parthenogenesis and the facultative or occasional parthenogenesis of the sexual forms, shows that in the former case parthenogenesis, as in the summer generations of aphids, is strictly female-producing, and the parthenogenetic race was never found to produce males. In the rare facultative parthenogenesis of sexual eggs development is seldom complete and rarely proceeds as far as the adult or even the pupal stage. In these cases both males and females may be produced.² Cytologically a striking contrast appears between the two cases. In the facultative process both polar divisions take place, leading to reduction, and the egg begins its development with the haploid number; but in later stages this number is doubled in most of the cells (as often occurs also in the bee, p. 870). The obligatory process, on the other hand, resembles that occurring in the aphids, rotifers or gall-flies (p. 468) in the fact that but one polar division takes place, without reduction. The remarkable fact is, however, that here too the number is doubled, in this case producing the *tetraploid* number, which appears in most if not all of the embryonic cells. It is an interesting fact that in both cases alike the early stages show the typical leptotene, synizesis and diplotene stages leading to the formation of typical tetrads of the haploid number (in *Solenobia triquetrella* and *pineti* approximately 30). In some other respects the two species seem to differ remarkably, in particular in respect to the manner in which the doubling of number takes place.

In *triquetrella* the 30 tetrads first divide equationally giving 30 dyads, which are said *again to divide equationally* in the second mitosis, the 30 dyads thus produced then separating to form at each pole 60 single chromosomes (the diploid number); and this number appears also in the first two cleavages. In later cleavage the number is almost invariably tetraploid ($120\pm$) a result attributed to a fusion of nuclei two by two.³ In *S. pineti* the early stages are similar; but the tetraploid condition is differently produced, the dyads separating already in the anaphases of the heterotypic division to form 60 single chromosomes which are then doubled in number (to 120) in later anaphases of the same spindle.⁴ In the facultative

¹ E. g., Platner ('88) in *Liparis dispar*, Henking ('92) in *Bombus mori*, Hartmann ('12) in the first named species and others. See also Goldschmidt ('17).

² See Hartmann ('12), Goldschmidt ('17).

³ This conclusion seems insufficiently based, though such a fusion is actually figured.

⁴ The cytoplasmic changes accompanying this doubling are considered by Seiler to represent an abortive second mitosis, the doubling in number at this time being compared to the formation and reunion of the second polocyte in *Artemia* (p. 471).

type (preceded by complete reduction) the mode of doubling to produce the diploid number was not determined.

There are some points in this account that evidently call for further examination; nevertheless the main facts seem clear and contribute in an important way to our understanding of sex-production in parthenogenesis. So far as the obligatory type is concerned the results offer no difficulty; for in the absence of a reduction-division the constitution of the mature ovum does not differ from that of the female that produces it; and since the doubling of the whole group does not affect the balance between the sex-chromosomes and autosomes (p. 817) all such parthenogenetic eggs should be female-producing, as is actually the case. The facultative type with complete reduction is by no means so clear. Seiler's interpretation is as follows. Since complete reduction occurs the eggs should be of the two classes, $A + X$, and A , which being doubled give the two classes of embryos, $AA + XX = \sigma$ and $AA = \varphi$. The first class obviously should be males and the second are assumed to be females containing no X like those supposed to arise by non-disjunction (p. 877). The difficulties here involved can only be cleared up by further research.

5. Sex and Chromosomes in Artificial Parthenogenesis

The relations of the chromosomes to sex in artificial parthenogenesis (*cf.* p. 472) are still incompletely known owing to the fact that in very few cases have such parthenogenetic larvæ been reared to a point at which sex could be positively determined. Yves Delage ('12), succeeded in rearing through the metamorphosis six sea-urchin larvæ from parthenogenetic eggs, of which two lived long enough to be identified as males. The chromosome-numbers were not determined; but since the female is homogametic in these animals the sex of such larvæ might be expected to be male if they were haploid (*i. e.*, X -containing), and to be female if of diploid constitution (XX -containing).¹ The second available case is that of the frog, in which out of twenty larvæ reared through the metamorphosis 15 were males, 3 females, and 2 doubtful Loeb ('18). Parmenter ('20) examined 14 individuals out of 65 parthenogenetically produced larvæ reared by Loeb, including one male frog and 13 tadpoles of undetermined sex. In all of these, *the male frog included*, the number was diploid (26) or nearly so; hence it is probable that this number is characteristic of both sexes. (See also Hovasse, p. 479.) Without further cytological examination this result cannot be certainly explained.

6. Sexual Dimegaly of the Ova in Relation to the Chromosomes

We may here conveniently consider with reference to the foregoing account, the sexual dimegaly of the ova earlier referred to (pp. 277, 787).

¹ *Cf.* Shearer and Lloyd, Q. J., '13.

This condition was long since observed in the parthenogenetic eggs of rotifers of several genera (Fig. 386)¹ and also in those of phylloxerans² where they have been more recently studied with care by Morgan ('09). An even more marked sexual dimegaly in sexual eggs (Fig. 117) exists in *Dinophilus apatris* (Korschelt, '82); and sexual dimegaly has also been described in the sexual eggs of mites (Reuter, '07) and spiders (Montgomery, '07). In case of the insects it was likewise supposed by earlier observers that males arise from smaller eggs and females from larger ones; but this result was contradicted by the later careful work of Cuénot ('99, '05). In case of the vertebrates Beard ('02) inferred the preëxistence of male-producing and female-producing eggs in elasmobranchs from the fact that at an early stage there are two sizes of blastodisks, the larger containing a number of primordial germ-cells (≈ 512) about twice that found in the smaller. The former he assumed to be female-producing, the latter male-producing. More recently Riddle ('11, '14, '17, etc.) has maintained in the case of fowls and pigeons that eggs of smaller size, higher water-content and lower energy-content (measured by amount of fat and of phosphorus) are male-producing, while those showing the opposite characters are female-producing.

In all the pronounced cases (rotifers, phylloxerans, *Dinophilus*) the size-dimorphism of the eggs is correlated with a corresponding size-difference between the adult sexes, an extreme case being offered by *Dinophilus apatris*, where the males are stated to be not more than $1/27$ the volume of the females and the male-producing eggs are of correspondingly smaller size (Fig. 117). The sexual dimegaly of the eggs is therefore a true case of promorphology.

It is a very noteworthy and, at first sight, puzzling fact that in many of the foregoing cases (rotifers, phylloxerans) the sexual dimegaly exists in forms where with respect to the *chromosomes* it is the male and not the female that is digametic. This apparent anomaly disappears, however, upon further consideration. In the rotifer, for example, the size of the sexual egg depends upon whether the egg is fertilized or not; in the latter case it remains small and produces a male by haploid parthenogenesis, while if fertilized it enlarges to form a female-producing egg (p. 802). In the phylloxerans the case is different since both the large and the small eggs are parthenogenetic. Here, however, the egg acquires the appropriate chromosome-combination during maturation, the larger eggs retaining the full diploid number, including XX (hence females like their parthenogenetic mothers), while the smaller eliminate one X-element, thus establishing the male combination, AAXO (p. 791). In this instructive case the

¹ Dalrymple ('49), Leydig ('54), Cohen ('55), Hudson ('72), Levander ('94), etc.

² Balbiani ('73), Lichstein ('76, '78, '79), Buckton ('83), etc.

eggs are *predestined* as male-producing or female-producing irrespective of the chromosome-number; but it is plain that sex is not determined in the egg until the establishment of the chromosome-combination characteristic of the sex in question. There could not be a clearer illustration of the fact that the sex-chromosomes should not be regarded as the sole determiners of sex but only as differential factors in a complex reaction-system¹ (p. 916).¹

Still a different case is offered by *Dinophilus apatris*. Shearer ('13) endeavored to show that this form is essentially of the rotifer type, *i. e.*, that the size-difference between the eggs results from fertilization, unfertilized eggs remaining very small and producing males, the fertilized ones becoming larger and producing females. The subsequent work of Nachtsheim ('19) proved, however, that this was an error; for virgin females, raised from the egg in complete isolation from the males, produce eggs of both kinds, and unfertilized eggs do not divide at all. Both kinds of eggs, form two polocytes and undergo complete reduction (from 20 to 10-chromosomes), and both are fertilized in normal fashion (Fig. 117).

The explanation of this case is still problematical. The most natural one would seem to be (as in the case of the bird's egg) that the female is here the digametic sex and that the mode of maturation of the egg is determined by its size—as certainly occurs in the parthenogenetic eggs of *Phylloxera*, different as the two cases otherwise are. It is possible that the female is homogametic and that selective fertilization occurs; but this seems less probable. In any case we may probably assume without error that in one way or another these eggs, too, ultimately acquire the chromosome-combination appropriate to their sex.

IV. THE CHROMOSOMES IN HERMAPHRODITES, INTERSEXES, AND GYNANDROMORPHS

1. Hermaphrodites and Intersexes

Important light will no doubt be thrown on the sex-producing mechanism by the further study of the group of related phenomena enumerated in the above heading. Unfortunately our actual cytological knowledge in this subject is extremely limited. In hermaphrodites of the usual type, *e. g.*, in oligochætes, leeches, pulmonates or ascidians, there is still no sufficient evidence of the existence of sex-chromosomes or of any connection between the chromosomes and sex-production. There is, however, one case among the hermaphroditic nematodes in which the existence of sex-chromosomes is definitely established by the independent work of Boveri ('11) and of Schleip ('11).

¹ For further discussion of this point, see p. 815.

This case is offered by the nematode *Angiostomum (Rhabditis) nigrovirenosum*, a form characterized by an alternation of generation between a free-living dioecious form and a parasitic hermaphroditic form that lives in the lungs of the frog.¹ In the dioecious generation males and females occur in nearly equal numbers. The fertilized eggs of this generation develop into the parasitic, hermaphrodite form which has the general morphology of a female, possessing an "ovary" which first produces oögonia and somewhat later also spermatogonia, the two being formed in irregularly alternating zones. From the spermatogonia arise spermatocytes which undergo two divisions as usual, and produce functional sperms. The eggs are fertilized by sperms of the same individual (the hermaphrodite is strictly self-fertilizing) and produce the free-living males and females in approximately equal numbers.

Cytological examination shows that in the parasitic (hermaphroditic) generation the diploid number of chromosomes is 12 which in the maturation of the egg is reduced to one-half, each egg receiving six chromosomes (Fig. 387). During the spermatogenesis of this generation, on the other hand, but half the sperms receive six chromosomes, the other half only five owing to the fact that in the second division one of the X-chromosomes remains near the equator, fails to enter the daughter-nucleus and degenerates. It thus comes to pass that one spermatid of each pair receives a complete haploid group of six chromosomes, the other but five.

Schleip demonstrated correspondingly that in fertilization the egg-nucleus contributes always six chromosomes, while the sperm-nucleus contributes in some cases six, in others five, and also found two kinds of embryos containing respectively 12 and 11 chromosomes. Boveri's observations, finally, prove that the males of the dioecious generation have 11 chromosomes, and that half the sperms receive 6 chromosomes and half 5, as we should expect.

A difficulty arises from the fact that we are thus led to expect the resulting zygotes to be likewise of two classes, *i. e.*, females (or hermaphrodites) with 12 chromosomes and males with 11, but in point of fact, all the fertilized eggs produce hermaphrodites (modified females) with 12 chromosomes. The explanation of this is unknown; but both Boveri and Schleip have suggested that the male-producing sperm (*i. e.*, the 5-chromosome or no-X class) of this generation may be non-functional and degenerate. The probability of this will readily be admitted when we recall the analogous phenomena in the aphids or phylloxerans. It is also possible that the 11-chromosome zygotes are not viable. This interesting case can hardly be taken as typical of hermaphrodites generally; for this species is hermaphro-

¹ For further facts concerning the sexual relations in nematodes, see p. 230.

ditic during only a portion of its life-cycle, and the hermaphroditic generation is obviously a modified female.

Another case of supposed sex-chromosomes in a hermaphrodite is described by Zarnik ('11) in the pteropod *Cressus*; but analysis of the results reveals a number of serious difficulties which Zarnik endeavors to meet by a number of rather complicated assumptions. These will here be passed over since the subsequent work of Schitz ('17) has raised serious doubts concern-

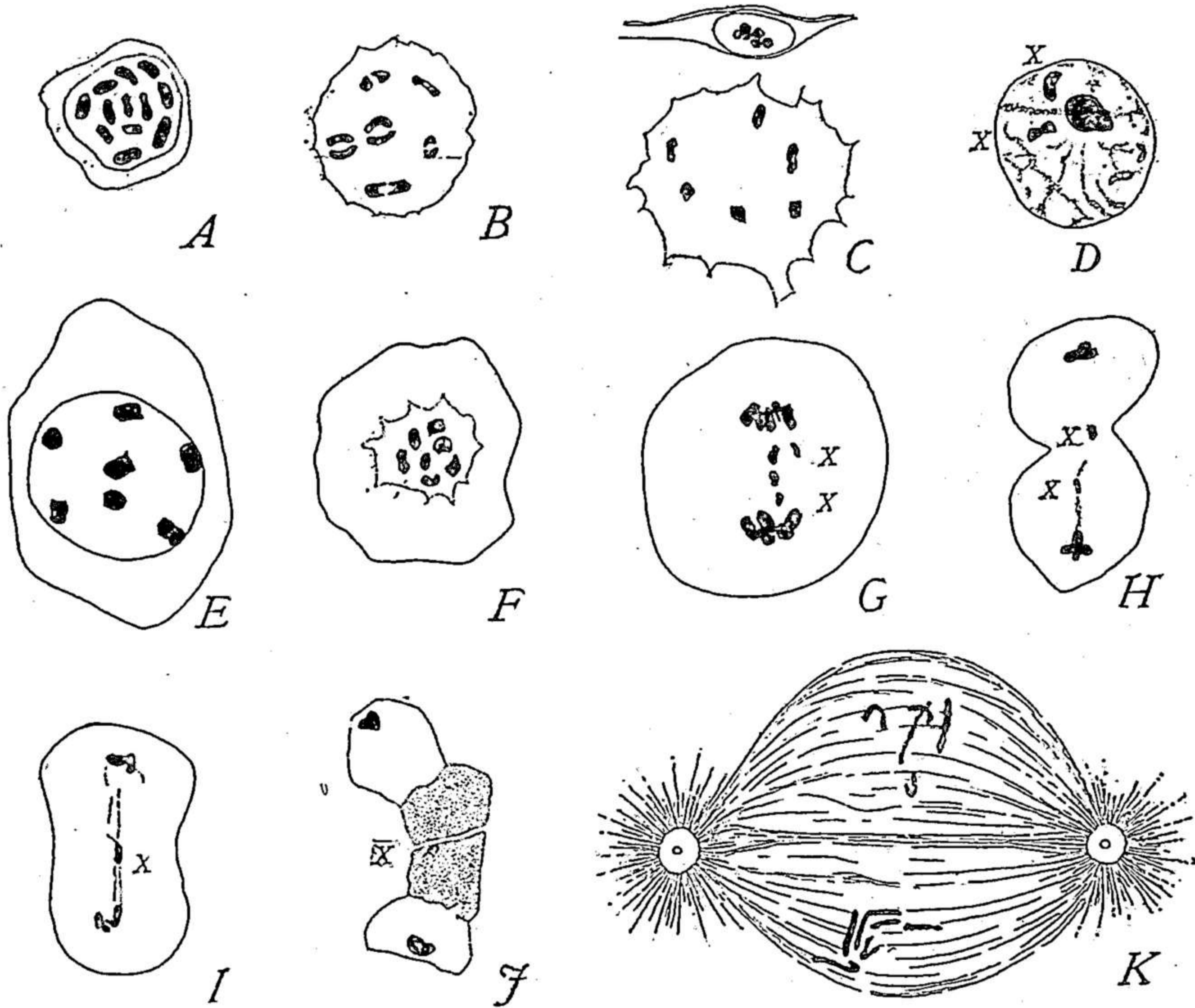


Fig. 387.—Sex-chromosomes in the hermaphroditic nematode *Angiostomum nigrovenosum* (SCHLEIP).

A, oögonial mitosis, 12 chromosomes; B, first polar mitosis of the egg, 6 tetrads; C, second polar mitosis; D, spermatocyte, growth-period, two chromosome-nucleoli (X-chromosomes); E, primary mitosis; F, polar view, and G, side-view of first anaphase, the two X-chromosomes (divided) lagging; H, second spermatocyte-telophase, two lagging X-chromosomes; I, later telophase, one X has passed to the pole, while one lags; J, two sister-spermatids, with lagging X in one; K, first cleavage-figure of fertilized egg, showing 6 egg-chromosomes below and 5 sperm-chromosomes above.

ing Zarnik's observations. The whole subject of the chromosomes of hermaphrodites evidently calls for further examination. In such an inquiry it will be important to bear in mind that the true hermaphrodite should not be thought of as merely a composite of male and female, but as the result of a definite genetic complex analogous to that which by the mosaic-like patterns of pigment ("spotting-factors," etc.) are determined in other organisms; and the same in principle is true of the closely related phenomena of intersexuality, as shown especially by Goldschmidt ('10). In both these

cases, therefore, it may very well be that the sex-producing mechanism is cytologically unrecognizable.

2. Gynandromorphs

A remarkable opportunity for testing the chromosome-theory of sex-production is offered by sex-mosaics or gynandromorphs, the genetics of which have been carefully examined in hybrid races of *Drosophila* by Morgan and Bridges ('19). Though the cytological phenomena are not yet directly known, important suggestions have been made concerning the underlying chromosome-conditions. One of these was based by Boveri on the facts of partial fertilization in which the sperm-nucleus does not conjugate with the egg-nucleus until the 2-cell stage or even later (p. 458). In such embryos some of the nuclei are of purely maternal origin and hence of haploid constitution containing but one X-chromosome, while those arising from the fusion-nucleus, are of biparental origin and of diploid constitution, and may contain XX. We should expect such diploid regions to show female sex-linked characters and the haploid regions male characters, the particular pattern of the sex-mosaic depending upon the period and place at which the fusion-nucleus is formed. This hypothesis may be tested genetically by the study of hybrid gynandromorphs derived from parents differing in respect to one or more sex-linked characters; and a large number of such gynandromorphs, some of them of most remarkable type, have been obtained in *Drosophila*. The study of these and other forms led to two new hypotheses. One of these assumed gynandromorphs to arise from dispermic eggs in which one sperm-nucleus unites with the egg-nucleus, while the other develops independently in the egg.¹ In the later work of Morgan and Bridges it is shown that a more probable explanation is found in the assumption of an elimination of one X-chromosome at an early division of a cleavage-nucleus of a female (XX) embryo by a lagging or dislocation on the spindle. The effect of this should be the production of larvæ and adults having two kinds of nuclei, some being of XX constitution, others of XO. This hypothesis was tested by the study of many hybrid gynandromorphs combining in each case two or more different sex-linked characters of the two parental races. Since the factors for such characters are known to be borne by the X-chromosomes alone it was thus possible to determine the presumable distribution of these chromosomes by the genetic evidence. A critical test of the hypothesis is given in these cases by non-sex-linked characters, *i. e.*, those borne by autosomes; for these are present throughout, while the sexual characters of the gynandromorph show only in certain regions. It is thus possible, for instance, to obtain gynandromorphs

¹ Morgan, '05.

that show a white eye or miniature wing on the male side, and a red eye or normal wing on the female, while both sides alike show dominant autosomal characters derived from one or both parents. The results seem to prove conclusively that the *Drosophila* cases cannot be explained by either partial fertilization or dispermy and only find an intelligible explanation on the elimination-hypothesis. Apart from the genetic evidence, the hypothesis of elimination has in its favor the somewhat analogous elimination of one X-chromosome in *Rhabditis nigrovenosa* above described (p. 809) or in the maturation of the male-producing eggs in the aphids and phylloxerans, through which the female or XX-condition is converted into the male.

V. THE SEX-CHROMOSOMES IN PLANTS

The problem of sex-determination in higher plants assumes a somewhat different aspect from that offered by animals, since in the former the true sexual generation or gametophyte is a haploid organism while the diploid generation is an asexual sporophyte. Obviously, therefore, the chromosomal relations of the true males and females (*i. e.*, the gametophytes) cannot be identical with those of animals; we cannot, for example, suppose the female to be XX and the male XY, since these conditions can only occur in a diploid organism. It is, however, important to bear in mind that in dioecious plants a sexual differentiation is clearly shown already in the diploid sporophyte, the sexual characters being as it were thrown back or impressed upon the asexual generation. In practice, therefore, it is found convenient to speak of the staminate (microspore- or pollen-producing) sporophytes as "male" and of the pistillate or megaspore-producing ones as "female."

If the sex-chromosomes of plants follow the same general scheme as in animals we should look for their segregation in the meiotic or spore-forming divisions; and the sexual predestination of the spores, earlier referred to (p. 746) leads to the same expectation. This expectation is borne out by the history of the sex-chromosomes in the three cases thus far definitely made known. The clearest of these is that of the liverwort *Sphaerocarpus*, where Allen ('17, '19) demonstrated the existence of an unequal pair of sex-chromosomes similar in a general way to the XY-pair of insects and by him designated by the same names.¹ The number of chromosomes in thalli of both sexes is eight (haploid) one of these being the large "X-chromosome" in the females while in the male its place is taken by the small "Y" (Fig. 388). The diploid groups (of the sporophyte) should, accordingly, include

¹ A few earlier observers have recorded in the sporogenesis either lagging chromosomes or such as pass precociously to the poles, Cardiff ('06) on *Salomonina*, Darling ('09) on *Acer*: but there is no evidence to show that these are sex-chromosomes.

16 chromosomes, including seven equal pairs and one unequal XY-pair; and this is clearly the case. The total number is about 16, including a single large X-chromosome. Unluckily the small Y-chromosome has not yet been identified, and does not appear in the figures; this, however, is probably due to an accident of the technique. We should expect that in the sporogenesis X and Y should couple to form an XY-bivalent and then disjoin. Though the proof of this is not complete, it is practically certain that such is the case, since Allen found that the second or homeotypic division is of two types, both showing eight chromosomes, one containing the "X-chromosome" and one the "Y," quite as in the meiosis of the Cole-

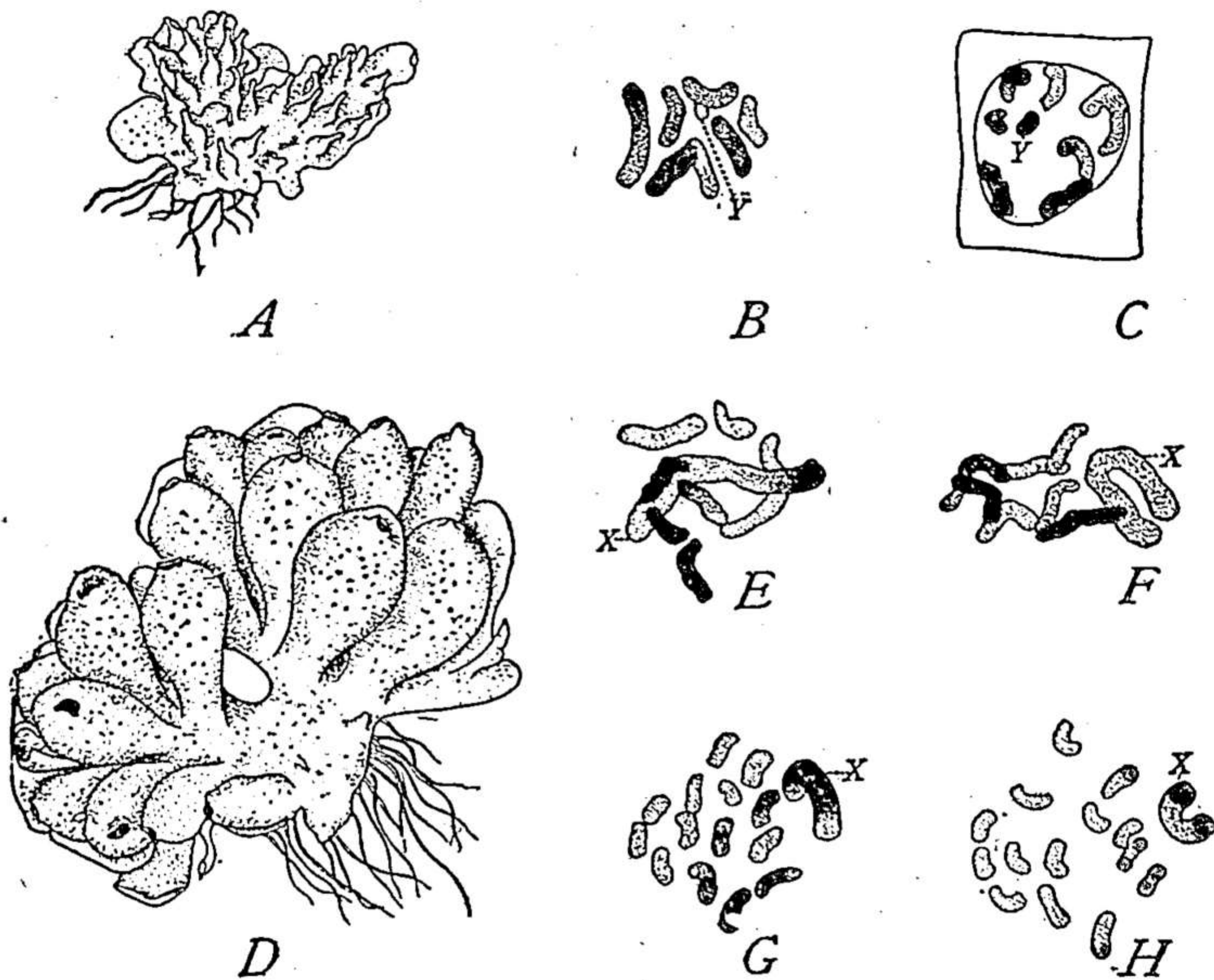


Fig. 388.—Sex-chromosomes in the liverwort *Spharocarpus* (ALLEN).

A, male gametophytes; B, haploid chromosome-group from the same (wall of antheridium); C, prophase nucleus from same; D, female gametophyte; E, haploid group from same (basal cell of archegonium); F, similar group (archegonial involucre); G, H, diploid chromosome-groups from young sporophyte (sister anaphase-groups from the same spindle).

optera or Diptera (p. 768). Apparently, therefore, no doubt can exist that the heterokinesis or disjunction of X and Y takes place in the first or heterotypic division as in Diptera or Coleoptera; this, however, has not yet actually been observed. In any case it is clear that half the spores receive the X-chromosome and half the Y, the former producing female gametophytes and the latter male.

This result is confirmed by the work of Santos ('23) on the dioecious seed-plant *Elodea*, the diploid (sporophytic) groups of which show about 48 chromosomes including one large equal pair and one smaller very unequal one (supposedly an XY-pair). In the heterotypic division X and Y dis-

join, so that half the pollen-grains receive X and half Y. Since this agrees closely with Allen's results on *Sphaerocarpus* and is in harmony with Correns' conclusions on the sexual predestination of the pollen-grains in *Bryonia dioica* (p. 743) a strong presumption is created that these chromosomes are in fact sex-chromosomes analogous to those observed in animals.

In *Rumex acetosa* Kihara and Ono ('23) report a condition that seems to differ from all other known cases in the presence of a double Y-element. The male diploid number is 15, the heterotypic division showing 6 bivalents and one trivalent element consisting of one large X-chromosome opposed to two Y's.¹ In the heterotypic division this disjoins so as to give second sporocytes with $6 + X = 7$ chromosomes, and $6 + 2Y = 8$, the resulting pollen-grains being correspondingly of two types. The diploid groups show either one large X ($=\sigma$) or two (presumably $=\phi$).²

The foregoing three cases, alike in principle, thus offer a situation hitherto not known in animals. On the one hand, both X and Y are present in the diploid sporophyte, which may nevertheless be either "male" or "female." On the other hand, the male gametophyte contains Y but no X, while the female contains one X. All of these conditions, obviously, are contrary to those observed in animals, and demonstrate that although the mechanism concerned is similar in a general way, the X and Y-chromosomes of the two groups must operate very differently. In *Sphaerocarpus* or *Elodea*, it would seem, we must either accept the sex-formulas $X = \phi$ and $Y = \sigma$, as in Allen's terminology, or (if Y be considered as a smaller X) large $X = \phi$ and small $X = \sigma$. The first alternative would lend plausibility to the suggestion of Castle ('09) considered at p. 821, that in female digamety in animals the female constitution may be XO, the male no-X. Under the second alternative the large X might stand for XX (*i. e.*, a double dose of the X-chromatin) and the small one for X (single dose). The sex-formulas for *Sphaerocarpus* would thus become identical with those in the Diptera or Coleoptera; but a new difficulty arises from the fact that the sporophyte formula now becomes XXX. At present, therefore, we cannot certainly state the relation between the condition seen in *Sphaerocarpus* and that in the XX-XY type of animals generally.³

¹ This element is closely similar to the XY-triad of the mantids (p. 778) though the X seems here to be single and the Y double.

² Winge ('23) reports several additional cases of supposed sex-chromosomes in seed-plants; but the evidence hardly seems adequate to establish their nature.

³ The segregation of sex in monœcious plants has an interesting bearing on this problem. In the monœcious moss *Funaria hygrometrica* the Marchals found that both male and female gametophytes may arise from the same protonema. Collins ('19, '20) found, however, in this species that gametophytes produced by regeneration from antheridia or the surrounding perigonal leaves of a "male flower" produce only antheridia, while those from the "female flower" produce only archegonia. These facts suggest that there is a kind of separation or "somatic segregation" of sex-factors in the haploid tissue of the gametophyte prior to the gamete-formation and their subsequent reunion in

VI GENERAL CONSIDERATIONS

The combined cytological and genetical investigation of sex has clearly revealed the underlying general mechanism of sex-production but still offers only an incomplete solution of many interesting further problems, both physiological and morphological, which can here only be outlined in a general way.

1. Physiological Problems

How the sex-chromosomes operate in sex-determination is still in large degree an unsolved puzzle which belongs to the larger problem of the determinative action of chromosomes generally. In its discussion we may for the present limit it to the more frequent case in which the male is the digametic sex and the female the homogametic. The problem may also be simplified by excluding the Y-chromosome, since it may be absent without affecting sex-determination. The proof of this is given in the genus *Metapodius*, where a Y-chromosome is usually present but may be absent from certain individuals of the species without in any visible way affecting either sex or the secondary sexual characters (Wilson, '09); and the same is possibly the case also in man (p. 766).¹

a. Sex-chromosomes and Sex-determination. It has often been urged that the sex-chromosomes may not be determiners of sex but only its cytological accompaniments or indicators ("index-hypothesis") which merely follow sex without playing any part in its causation; but this has not stood the test of critical analysis and has been decisively disproved by Bridges' crucial investigations on non-disjunction (p. 947), and also by those of L. V. Morgan on X-linkage (p. 946). In upholding the contrary view that the sex-chromosomes (X) are true sex-determining factors we must guard against the crude notion that they are such in any exclusive sense. In relation to sex, as to other hereditary traits, the chromosomes form only one part of a larger factorial complex in which are involved other chromosomes (autosomes) as well as cytoplasmic factors (pp. 667, 817). Since, however, they form the visible differentials between the sexes we may for the moment conveniently speak of them as "sex-determiners" or "sex-differentiators."

fertilization; but it seems more probable that this is not a true segregation in the Mendelian sense but only an inhibition of one or the other sex-character, such as often appears in hermaphrodites.

¹ The nature of the Y-chromosome is still an unsolved puzzle. As the synaptic mate of X it evidently belongs to a long established mechanism of synapsis and disjunction such as we see in other chromosome-pairs. Bridges' work on non-disjunction shows that in *Drosophila* the absence of Y causes sterility; but the case of *Metapodius* shows that this cannot be general. There are a few sex-linked characters which behave as if borne by the Y-chromosome, being confined to the male line and apparently non-transmissible through the female. One of these is a pigment-spot in a fish (Schmidt, '20), the other the web-toed character in man (Schofield, '21). See Winge ('22), Castle ('22).

It might be supposed that there are two kinds of X-chromosomes respectively male-determining and female-determining; but this involves us in numerous difficulties. To give but a single example: In the haploid parthenogenesis of the rotifer or bee the X-chromosome of the mature egg must by the hypothesis contain the σ -determining X-chromosome, since, if unfertilized, it always develops into a male. If fertilized it always produces a female; and by the hypothesis this must be due to the introduction of a dominant ♀ -determining X by the sperm; but since the male is haploid its single X must be σ -determining — a *reductio ad absurdum*. Many other difficulties of the same type exist.¹ All these difficulties disappear if we assume that in any particular species there is but one kind of X-chromosome, in itself neither male-determining nor female-determining but so adjusted to the general mechanism of development that when single it swings development towards the male side, when double towards the female. This view, essentially quantitative, ascribes to the egg the capacity to produce either the female or the male, according to the presence of more or less of X-substance.² Its correctness in principle is demonstrated by the above-mentioned observations of Bridges and of L. V. Morgan, which prove that the presence of two X-chromosomes in the zygote, however caused, determines such a zygote *ipso facto* as a female whatever be the situation in the gametes. Thus, a normal X-bearing egg gives rise to a male if fertilized by a no-X or Y-bearing sperm; if, however, as a result of non-disjunction or X-linkage the mature egg contain XX it produces a female even when fertilized by the no-X or "male-producing" sperm. The demonstrative proof of this, in which cytology and genetics unite, will be considered later (pp. 947, 948).

With these facts in mind we are in a position to look more closely into the relation of the X-chromosome to the remainder of the factorial complex. That other chromosomes (autosomes) play a part in sex-determination has recently been demonstrated in an interesting way by Bridges' observations on triploid mutants in *Drosophila*.³ Among various heteroploid forms obtained in certain strains of these flies, individuals were obtained with one, two or three X-chromosomes, variously combined with trisomic, disomic or monosomic conditions of the other chromosome-pairs. Individuals that are triploid throughout (including 3 X's) are females scarcely different from the normal diploid females; but those having two X's and

¹ See Castle ('03), Wilson ('06, '09).

² Wilson ('09, '11). This conclusion was a more specific development of Morgan's earlier suggestion ('03, '07) that sex might be determined by the relative quantity of nuclear substance. Both cytological and genetic evidence indicates that the X-substance forms but a part, and probably a small part, of the X-chromosomes.

³ Bridges ('21, '22). Morgan, Sturtevant and Bridges ('21).

otherwise triploid are *inter-sexes* and are also larger and different from the normal in some other definite respects. Here it is plain that the female character depends not alone on the presence of two X's but also on the autosome-combination; *i. e.*, sex must be determined by a certain balanced relation between sex-chromosomes and autosomes. Equally interesting is the fact that individuals with 3 X's but otherwise diploid are sterile females of low viability that differ decidedly in somatic characters from the normal; while one-X individuals otherwise triploid are males, also of peculiar and characteristic somatic type. These facts clearly indicate that the X-chromosome affects not only sex-production but also the somatic characters; while conversely the autosomes as a group, besides their somatic effects, also embody a tendency towards male-production. *The actual performance of the zygote, therefore, is a common effect of the whole group, and is turned this way or that as the result of a quantitative balance between X-chromosomes and autosomes.*¹ This shows specifically that the X-chromosomes should not be thought of as the sole determiners of sex but only as *differentiators*; and in this respect they are to be regarded precisely as we regard other kinds of chromosomes.

Even this conclusion does not go far enough; for it is also clear that the effect of chromosome-combinations during development can only be realized by coöperation with other, presumably cytoplasmic activities. In the hermaphroditic generation of *Angiostomum nigrovenosum*, for example (p. 809), the oögonia and oöcytes are characterized by the presence of XX (as in the females of the dioecious generation), while the males have X. In the hermaphroditic gonad, however, as both Boveri and Schleip have emphasized, the spermatocytes are clearly differentiated from the oöcytes at a time *when both X-chromosomes* are still present. This fact led Boveri and Schleip to the conclusion that the X-chromosomes cannot be primary determining causes of sex; and that they can at most be concerned only with the determination of secondary characters. Upon further consideration, however, the matter will appear in a different light.

The case of the phylloxerans is instructive in connection with this question. Here, as already described (p. 807), the eggs are visibly predestined as male and female before the elimination of one X-element to produce the characteristic male nuclear constitution (p. 791). Morgan concluded from these facts that sex is already determined in these eggs before they are laid, and before the polar spindle has developed; sex therefore is determined in the presence of all the chromosomes ('09, p. 271). This, however, is a question of definition. It seems preferable to say that sex is not actually determined until all the conditions necessary for its production have been

¹ Cf. p. 816.

fulfilled, one of these being the establishment of the appropriate nuclear constitution. A similar question is raised by the spermatogenesis of the aphids and phylloxerans. Here, as shown by Morgan, Stevens and Baehr, the first spermatocyte-division is unequal, and it is always the larger of the two products into which the X-element passes in the heterokinesis (p. 792). Baehr shows further that a mass of mitochondria passes into the larger cell, but apparently does not enter the smaller one (Fig. 381). Here, evidently, the pole to which X passes is already predestined as the female-producing or X-pole before heterokinesis takes place. This case clearly brings out the distinction between sex-predestination and sex-determination. Manifestly the X-class of spermatocytes, though normally *predestined* as female-producing, are not predetermined as females. On the contrary could these cells (like the X-bearing ova of rotifers or bees) undergo complete parthenogenetic development they would, presumably, give rise to males because their nuclear constitution is X, not XX.

The analysis enters upon a further stage when we consider hermaphroditism, intersexuality, and the sex of haploid organisms, in all of which cases the simple quantitative interpretation seems to require a more precise physiological formulation. In the Lepidoptera, for example, the chromosome-mechanism is identical with that seen in male digamety, yet its relation to sex-production is exactly the opposite; and so far as visible facts go, we might equally well maintain that in this group $XX = \sigma$ and $XO = \varphi$. In the haploid organism (e. g., *Sphaerocarpus*) neither set of formulas can be used. We might here assume a quantitative relation, of simpler type, one sex containing X and the other no-X or less X (p. 814); but this in its turn breaks down in the case of hermaphroditism or intersexuality. Here it is not easy to avoid the conception of more specific male-determining and female-determining factors (e. g., enzymes or hormones), which call forth corresponding reactions in the developing germ.¹ These hypothetical factors have conveniently been designated by Morgan as *M* or *F*, or, correspondingly, as *andrase* and *gynase*.² We here consider this hypothesis only in its relation to the chromosome-mechanism.

In the case of male digamety Morgan assumed the M-factor to be present equally in all the gametes, borne presumably by one or more of the autosome-pairs, while the F-factor is borne by the X-chromosome. All the mature eggs, therefore, are FM, while the sperms are either FM or OM (in which $F=X$). The observed results then follow under the assumption that FF (XX) dominates over MM, while MM dominates over F. Thus:

¹ The conception of such opposing sex-factors or sex-substances was suggested by Morgan ('11a, '11b, '13) and by Woltereck ('11), to whom is due the idea that they may be zymogens. It was further developed especially by Goldschmidt ('14, '17, '20) in its application to intersexes.

² Goldschmidt ('17), etc.

Egg XA (= FM) + Sperm XA (= FM) = XXAA = FF (MM) ♀.

Egg XA (= FM) + Sperm OA (or YA) = XOAA = (FO) MM ♂.

These formulas must not be taken too literally; they offer merely a convenient symbolism. The X-chromosome, for instance, here stands for the F-factor; but the genetic evidence, derived especially from non-disjunction, seems to prove that zygotes lacking X are non-viable (p. 948). The X-chromosome is therefore necessary for the production of males as well as females.¹

The conception of Goldschmidt is similar in principle, but suggests that M may be borne by the cytoplasm (or possibly by the Y-chromosome). In the case of female digamety the hypothesis is reversed, the X-chromosome being assumed to carry M, while F is borne by the cytoplasm of the ovum (or possibly by the Y-chromosome) Thus:

Egg XA (=MF) + Sperm XA (=MF) = XXAA = MM(FF) ♂.

Egg OA or YA (=OF) + Sperm XA (=MF) = XOAA or XYAA = (MO) FF ♀.

This hypothesis is ingeniously applied to the explanation of intersexuality in Lepidoptera by Goldschmidt ('16, '17, '20, etc.) by the additional assumption that in some races both sex-factors, M and F, vary quantitatively thus giving different combinations of male and female characters. In case of ordinary hermaphrodites the simplest assumption would be that the M and F factors are equally balanced, and that both are borne by all the gametes, the sexual formula thus becoming MMFF; and from such a starting-point we readily pass to the sex of haploid organisms and to the so-called determination of sex by external conditions.²

The foregoing conceptions are in harmony with numerous anatomical facts, such as the frequent presence in one sex of rudimentary structures that are fully developed and functional in the opposite sex, many of which were emphasized by Darwin and other earlier writers. From the cytological standpoint further questions of fundamental interest for the theory of sex-determination are raised by the fact that in some cases the ovary may produce spermatocytes and sperms as well as ova or, contrariwise, the testis may produce, in addition to spermatocytes and sperms, cells resembling oöcytes. An example of the former case is offered by the parasitic nematode *Angiostomum nigrovenosum*, earlier considered (p. 809), in which this condition undoubtedly represents a true hermaphroditism. On the other hand, it is doubtful whether the same can be said of the reverse case. The occasional

¹ Cf. Morgan, Sturtevant, Muller and Bridges ('23).

² For development of this conception see G. Hertwig ('21).

presence of oöcyte-like cells in the testis of adult dioecious animals has been noted by many observers; ¹ in some cases such cells are of regular occurrence in the earlier stages of the testis though they later disappear. A conspicuous case of this is offered in the frog, where the nature of these "ova" is a long debated question. Some observers have considered them as true oöcytes and have in consequence considered the larvæ (of frogs) to be at first hermaphroditic, afterwards developing into either males or females.² On the other hand, a different view has been taken by Levi ('15) and especially by Swingle ('20, '21, '22), who have urged that the so-called "oöcytes" are hypertrophied spermatocytes. Swingle has proved in case of the bullfrog *Rana catesbiana* (which has a very long larval period) that they undergo a regular heterotypic mitosis quite like that of the spermatocytes though rarely going further than the anaphase. These cells later degenerate, to be replaced by functional spermatocytes derived from the sex-cords.

In case of the toad (*Bufo*) a further step appears in the fact that the oöcyte-like cells of the testis of the larval male are massed at the anterior end of the testis to form a definite structure, "Bidder's organ"³ which persists in the adult male toad. The so-called oöcytes *do not, however, become functional ova* but degenerate, to be replaced by others periodically arising by fresh proliferations, but likewise in the end degenerating.

Closely similar to this in principle is the remarkable case of the stone-fly, *Perla*, in which the cytological conditions have been partially worked out. Some species of this genus are ordinary dioecious forms; but in *P. marginata* the upper region of the male gonad, common to both testes, is converted into a structure like that of an ovary and contains numerous large cells closely similar to oöcytes.⁴ The resemblance is heightened by the fact that these cells pass through a regular bouquet-stage and undergo synapsis, and form yolk-spherules. As in the case of Bidder's organ, however, the "oöcytes" all degenerate soon after the synaptic stage. The remarkable fact in this case, determined by Junker, is that the "oögonia," from which arise the oöcyte-like cells, divide with the chromosome-number *characteristic of the male*, 22, while the female number is 24.⁵ Here, therefore, oöcyte-like cells and a structure closely resembling an ovary, are produced *in the presence of the chromosome-number characteristic of the male*—a condition exactly the reverse of that seen in *Angiostomum nigrovenosum* (p. 809).

Junker himself (a pupil of Baltzer), concludes from this that "the chromo-

¹ For example in Crustacea, (Nebeski ('80), Ishikawa ('91) or in scorpions as observed by the writer.

² See especially Pflüger ('82), R. Hertwig ('04), Kuschakewitsch ('10), Witschi ('13, '14, '21).

³ See King ('08).

⁴ Schönemund, '12, Junker, '23.

⁵ In the male, half the sperms receive 10 chromosomes and half 12, the X-element consisting of two components as in *Syromastes* (p. 773).

osomes have nothing to do with the determination of the primary sex-cells" (cf. Boveri and Schleip, above) but this conclusion, to say the least, seems premature. It is a significant fact that neither in this case nor in that of Bidder's organ do the "oöcytes" become functional eggs. Even if they really are oöcytes their invariable degeneration suggests that something is lacking in their factorial complex, perhaps owing to a disturbance of the normal balance between the sex-factors. In view, therefore, of the demonstrative evidence of the determinative effect of the chromosome-combination offered by non-disjunction, triploids, X-linkage, and other phenomena, we may well suspend judgment concerning the case of *Perla* until its real meaning has become clearer.

b. The Relation between Male and Female Digamety. Whether sex-digamety in the male or in the female is the more primitive type is unknown; but for the sake of discussion we may assume it to be the former. The transition from one to the other seems to have taken place readily, and independently in different groups, but in what manner is still purely conjectural. It seems clear that both types employ the same general form of chromosome-mechanism, and one that automatically ensures the production of digamety in one sex in each generation. In order not to prejudice the question some writers have employed a different symbolism for the two types, employing in the one case $XX = \text{♀}$ and XY (or XO) = ♂, and in the other $ZZ = \text{♂}$ and $ZW = \text{♀}$; ¹ the observed genetic results then follow on the assumption that the factors for sex and sex-linked characters are borne by Z. The latter thus becomes in all respects the analogue of the X-chromosome save that when doubled it stands for the male instead of the female condition; and that such is actually the case seems to be fully established by Seiler's work on the *Psychidæ*. ²

Concerning the possible relation between these two types we have as yet only guesses. We might assume that the sex-factor and the chromosome-mechanism are identical in both, in which case the difference would have to be referred to a reversed reaction of the developing germ (*i. e.*, the remaining hereditary complex) to that factor; but, as Morgan has pointed out, ³ it seems simpler to assume that the difference somehow lies in the sex-chromosomes themselves. Castle ('09) showed that the genetic results in female digamety can be explained by the assumption that the female condition is represented by X, the male by no-X; and this led to the further suggestion that the cytological conditions might be expressed by the formulas XY (or XO) = ♀ and $YY = \text{♂}$, ⁴ which would agree with all the observed cytological conditions. More recently Castle ('21) has followed this up by

¹ See Morgan, Sturtevant, Müller and Bridges ('15), Morgan ('19).

² See p. 784 ff., Doncaster ('20).

³ '19, p. 174.

⁴ Wilson ('09b).

the suggestion that such a condition may have arisen through non-disjunction, giving various recombinations in the offspring of which two proved to be stable and self-perpetuating, namely, $YY\sigma$ and $XXY\phi$, of which the latter, by permanent union of X and X, becomes XY.

This hypothesis calls for an additional assumption concerning the production of males; for Bridges's work on non-disjunction (p. 948) in *Drosophila* proves that zygotes of the YY (or no-X) class are non-viable. Most attempts to conceive the relation between the two types have in fact assumed neither a change in the reaction-system as a whole nor in the chromosome-mechanism *per se*, but in the sex-factors borne by the chromosomes. This view is taken by Morgan ('19, p. 174), and by Doncaster ('20); it seems also to form the basis of Goldschmidt's assumption regarding the reversal of dominance in the two types, and of the more recent development of his views by G. Hertwig. Whether these various possibilities can be decisively tested by further observation and experiment remains to be seen.

2. Morphological Problems. Evolution of the Sex-chromosomes¹

The cytological evidence unmistakably indicates that the sex-chromosomes are fundamentally similar to other chromosomes and that they originally formed a pair of synaptic mates indistinguishable in appearance, behavior and visible structure; such a condition, indeed, seems still to exist in many animals (and plants) in which these chromosomes have not yet been identified as such. In this condition they still for the most part remain in the homogametic sex, their most striking peculiarities only appearing in the digametic sex. It is probable therefore that most of their special characteristics have resulted from their constantly heterozygous condition in one sex, which must have existed from a very ancient period. It is evident further that the X-chromosome is a body of complex constitution and that only a part of it, and probably only a very small part, forms the sex-differentiator. This is made plain, first, by the great differences in the size of this chromosome shown by different species, and even by rather closely related ones (p. 768). The complexity of organization of the X-chromosome is indicated in some cases by its visible structure (*e. g.*, in *Notonecta indica* or *Lygæus bicrucis*, p. 777); in others by its appearance as a group of components, constant in number and size-relations, which form separate chromosomes in the diploid groups and even in the meiotic divisions of the female, but are always associated to form a compound synaptic mate for the Y-chromosome in the corresponding divisions of the male. Such an extreme type of this as appears for instance in *Ascaris incurva* (p. 776), is connected by many interme-

¹ The conclusions here outlined were first indicated in Wilson, '11, though they were to some extent foreshadowed in earlier studies ('05 a, b, '06, etc.).

diate conditions with those in which X is always a single body or is linked with one of the autosomes. In all these cases it is probable that most of the X-material, whether in the form of chromosomes or of the separate components that appear in the compound types, has nothing to do directly with sex-determination but is only concerned with sex-linked heredity (p. 939).¹ For the sake of convenience, therefore, we may speak of the sex-differentiator as the "sex-chromatin," which we may think of as a factor or specific substance, perhaps borne by a very minute single body of the same nature as those which carry other Mendelian factors.

To picture the evolution of the sex-chromosomes in detail is not possible at present. There is some reason to suspect that primitively the "sex-chromatin" may have been widely distributed among the chromosomes, perhaps shared by the entire group.² All the facts indicate that this chromatin early became localized in one of the chromosome-pairs, originally homozygous in both sexes in respect to all the factors excepting the X-factor. Such a pair would correspond essentially to the XX- and XY-pairs as now generally understood. For our purpose it may be thought of as a YY-pair, one member of which (in the heterozygous sex) contains the X-chromatin.³ A condition more or less like this may have persisted in many cases with little or no modification; and to this perhaps may be ascribed the failure to find sex-chromosomes in many species. In such cases the heterozygous nature of the sex-pair would give no recognizable cytological sign, as is so often the case also in other heterozygous chromosome-pairs. In many cases, however, the heterozygous pair has become visibly heteromorphic in various ways, some of which are indicated in the diagram, Fig. 389. As this shows, the "X-chromosome," even in the more highly modified forms, may still be conceived as an "XY-chromosome" of which the synaptic mate is a Y-chromosome, the true nature of the pair being indicated in the male by the formula XY-Y and in the female by XY-XY. In one line of change (B) the no-X member of the original pair (the Y-chromosome) has become reduced step by step to final disappearance; in another (C) the no-X member or Y-chromosome has persisted. In either case the X-containing member may have progressively broken up into separate components one of which is assumed to contain the X-chromatin.

As the diagram also shows, linkage of the X-chromosome produces a condition closely similar to some of those seen in series A (for example in *Thyanta calceata*) and it seems possible that in some cases such linkage is not a secondary union (as has often been assumed) but a more or less direct survival of a more primitive association. In the curious case of *Blaps*, for

¹ Cf. Wilson ('11).

² See *Pseudococcus*, p. 778. Cf. Schrader ('20, '23), Gutherz ('23).

³ Cf. Stevens ('06), Wilson ('11).

example (Fig. 378), we might conceive the "X-complex" as a YY-pair of larger chromosomes with one member of which are associated one large and two small X-components, the whole forming an XY-complex.

Originally, we may assume, the YY-pair was itself homozygous, in which case no sex-linked heredity would appear. Sex-linkage, and perhaps certain forms of secondary sexual characters, would appear as soon as this pair became heterozygous in respect to factors borne by the Y-chromatin in either synaptic mate. One way in which this has occurred, evidently, has been by reduction and finally disappearance of the Y-chromosome; but even

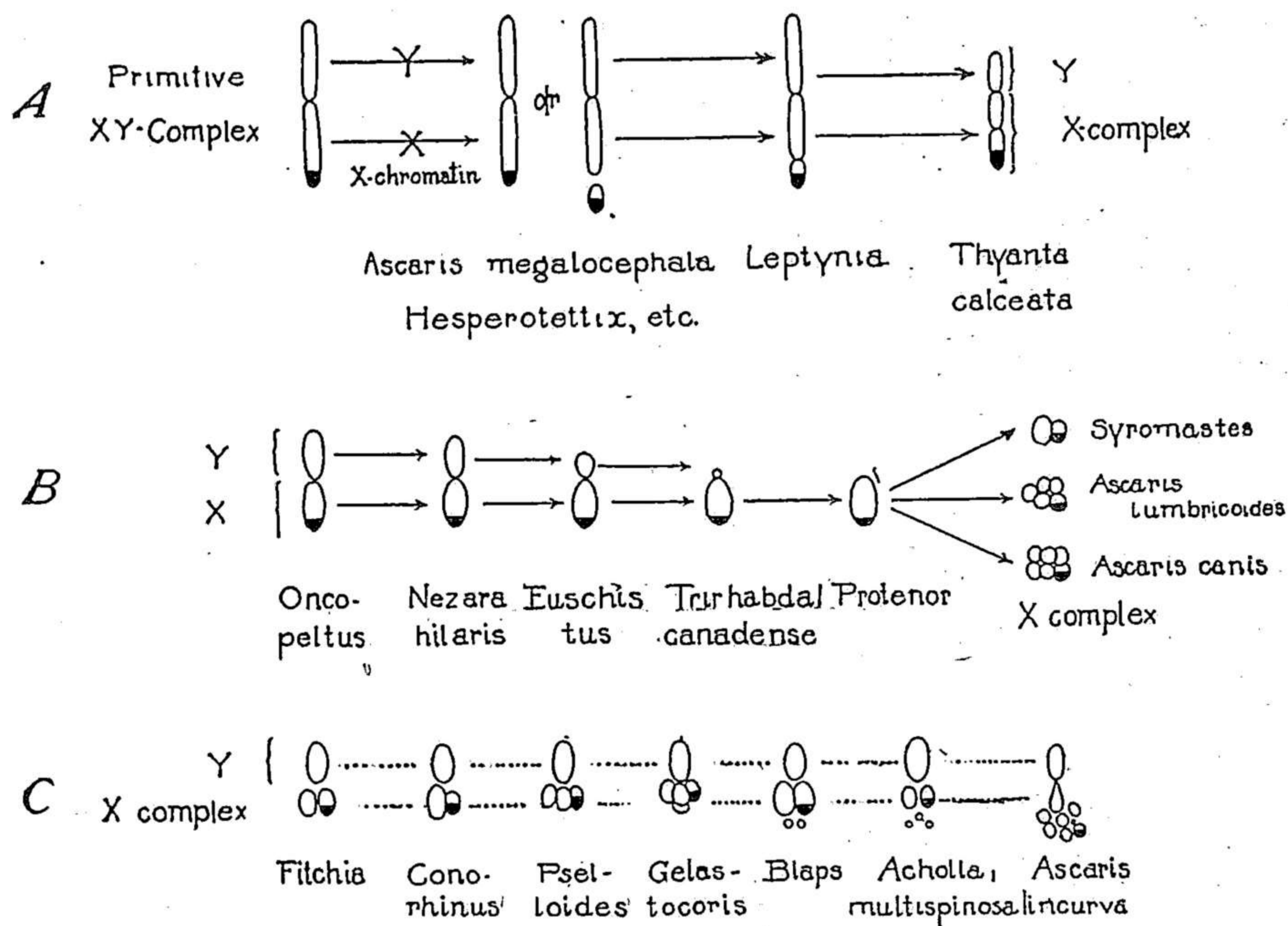


Fig. 389.—Diagram of the possible relations of the XY-complex.

A, relations of the primitive complex to linear aggregates; B, reduction and disappearance of Y, breaking up of X; C, persistence of Y, breaking up of X.

when it has persisted we may perhaps infer from its remarkable genetic emptiness, which genetic writers have emphasized, that it has lost many factors even though its main body still remains to play the part of a synaptic mate to the X-chromosome (*cf.* p. 815). The Y-chromosome may, however, have remained homozygous for many factors which have not yet been detected by genetic study.

3. Conclusion

To what extent sex may be determined by an automatically operating nuclear mechanism such as has here been described is unknown; but a mechanism that exists in the same general form in organisms as diverse as

bryophytes, nematodes, echinoderms, arthropods and vertebrates is beyond a doubt one of far-reaching significance, and may be as widely distributed as Mendelian heredity generally. The nature of the X-chromatin, its origin and mode of action, are alike unknown, the questions here raised merging into the larger one of the physiological relations of nucleus and cytosome (p. 653). In some manner, no doubt, this chromatin affects the metabolism of the cell; and since one sex differs from the other by a relative excess of this substance we are led to suspect a characteristic and fundamental difference of metabolism between the sexes, and one that is either itself quantitative or has a quantitative basis. This is not to be escaped by the assumption of specific male-determining and female-determining factors (M and F); for, as has been indicated, this assumption can only be worked out under the additional postulate that a quantitative factor plays the decisive rôle in throwing these factors into action. Beyond this we enter a region of pure speculation; but we cannot wholly put aside the thought that sex may be rooted in a simple principle of plus and minus that holds true of all sexual organisms from the lowest to the highest¹ and may perhaps in some manner fit with Bütschli's hypothesis concerning the origin of syngamy (p. 616).

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(See also II, IV, V, VI, VII, XII. For abbreviations, see General Literature List.)

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¹ Wilson ('10a, p. 591).

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