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INTRODUCTION

THE usual mode of sexual reproduction in Metazoa is that in which both sexes are produced from fertilized eggs. In certain groups of invertebrate animals, however, there occurs a type of reproduction in which the males are normally *impaternate* (fatherless), being developed from unfertilized eggs. These eggs have undergone reduction in chromosone number as if in preparation for fertilization, but since fertilization is lacking, the males developing from them have the reduced or haploid set of hereditary factors. The eggs will, if fertilized, normally develop into females. Hence the females are biparental in inheritance, the males uniparental. The Silesian bee breeder Johannes Dzierzon set forth this principle in 1845 with respect to the honey-bee, stating that drones, the males, come from unfertilized eggs, while workers and queens, the females, come from fertilized eggs.

The production of animals from fertilized eggs has been called *zygogenesis* in distinction to *parthenogenesis*, which refers to the development of an egg without fertilization. There are other types of parthenogenesis besides that described by Dzierzon. Unfertilized eggs may start as haploids and subsequently acquire the diploid number of chromosomes in some stage of cleavage, or they may start as diploids. The end result, in either case, is a fatherless (*impaternate*) but diploid animal. The evolution of such animals, interesting as it is, does not present the difficulties involved in explaining how the regular production of haploid adults has come about. In the case of impaternate diploids the chief problem is one of origin. In the case of impaternate haploids there are added, among other problems, those of survival with reduced chromosome number, of sex determination, and of spermatogenesis in the haploid male. Aside from the haploid males regularly produced in six or seven groups of invertebrates,

there have been, with one or two exceptions, no known haploid adult animals. In contrast, diploid and polyploid impaternates are known to occur with more or less frequency and as independent events in many, if not most, of the larger groups of Metazoa. The origin of these will be discussed because of its possible bearing on the origin of male haploidy. Their method of sex determination is entirely orthodox, while that of haploid males involves a genetic mechanism essentially different.

Many of the hazards involved in the origin and survival of male haploidy which must have been overcome by evolution were stated by Schrader and Hughes-Schrader in 1931, in a discussion of the subject based on data available at that time. During the last decade, considerably more data have been accumulated, especially bearing upon sex determination in haploid animals, the problem which has been most difficult to explain, and it is for this reason that a review of the matter is now timely.

Different groups and species of animals combine different types of parthenogenesis with bisexual reproduction in their life cycles in various complicated ways. An excellent review of the subject has been given by Vandel (1931a), and no attempt will be made here to summarize what he has presented or to review more recent literature in detail. References given in this paper are selected, for the most part, from recent publications which show the extent and diversity of parthenogenesis, and thus have a bearing directly or indirectly upon the evolution of male haploidy, or in other words, the evolution of reproduction according to Dzierzon's Law.

Definitions

A considerable terminology has been developed in connection with the subject of parthenogenesis in which ambiguities are present, unfortunate, but certainly unavoidable in a science developed in

many lands and published in many languages. In order to orient the reader and to assist in expressing ideas more briefly, some definitions are given of terms to be used repeatedly.

The author follows Ray Lankester in using the term *impaternate* rather than parthenogenetic for the fatherless offspring developed from the unfertilized egg. Parthenogenesis may be *natural* (*spontaneous*) or it may be *artificial* (induced by some artificial stimulus). It may be *incomplete* (rudimentary), the embryo dying before maturity, or it may be complete, involving viability to the adult stage. It may be *obligatory*, occurring from a type of egg that cannot normally be fertilized, or it may be *facultative*, if the egg may develop whether fertilized or not. With reference to the sex of the impaternate offspring, parthenogenesis includes *arrhenotoky*, production of impaternate males, *thelytoky*, production of impaternate females, and *deuterotoky*, production of both sexes parthenogenetically.

The term *tychoparthenogenesis* (the prefix is derived from the Greek τύχη meaning chance, luck, or the favor of the gods) has been used for irregular cases occurring occasionally in zygogenetic species, either in nature or in experimental breeding (*Lymantria dispar* of Goldschmidt, 1917). The word may be extended to include a condition which may be regularly induced merely by preventing the female from mating (Tettigidae of Nabours, 1929, 1930) and which thus indicates a natural genetic tendency toward parthenogenesis. While the latter is, in a sense, induced tychoparthenogenesis, it is, of course, natural and facultative (spontaneous under the circumstances) rather than artificial (induced by artificial stimulus). With respect to sex of offspring, tychoparthenogenesis includes *tychothelytoky* and *tychodeuterotoky*. *Tychoarrhenotoky* has not been demonstrated. The possibility of its occurrence and the significance of the other two will be discussed in connection with sex determination.

Parthenogenesis may be *constant*, occurring in each successive generation, or it may be *cyclic*, in which case one or more parthenogenetic generations alternates with a bisexual. In cyclic parthenogenesis (*heterogony*) the parthenogenetic or agamic generation, the generation reproducing parthenogenetically, consists entirely or almost entirely, of females. The individuals of the bisexual generation, both males and (*gamic*) females, are impaternate. Parthenogenesis may

occur as a *general* condition throughout the range of the species, or it may be *geographic*, in which case the parthenogenetic race occupies a different area from the bisexual. Males may be absent or very rare (*spanandry*) within the range of the parthenogenetic race.

With reference to meiotic phenomena in the egg, parthenogenesis may be *haploid* or *diploid*. In diploid parthenogenesis meiosis may be omitted altogether, there may be but a single oocyte division or, if both divisions occur, there may be fusion of two of the resulting haploid nuclei (*parthenogamy*). Diploid parthenogenesis may also be brought about by doubling of chromosome number in oogonial mitosis (*endomitosis*) to form the tetraploid number. Subsequent synapsis and two oocyte divisions give rise to a diploid egg which undergoes cleavage. The result, in any case, is a diploid individual which has been diploid from its beginning. Diploid parthenogensis may be said to result in a *zygote*, which in some cases is heterozygous, in others homozygous for genes that were heterozygous in the mother.

In triploid and polyploid parthenogentic races or species oogenesis takes place according to various methods as in diploid parthenogenesis.

In haploid parthenogenesis, meiotic phenomena in the egg are normal, with two oocyte divisions resulting in a haploid nucleus. The offspring is not, however, necessarily haploid, although starting as such, since chromosome doubling by endomitosis or by fusion of nuclei may occur during cleavage. Higher multiples of the haploid set are reported for some tissues than for others. Whatever the ultimate cytological conditions may be, the individual may be designated an *azygote* and, barring mutation, will breed true, all sperms or eggs produced by it being of identical genetic composition, since it originates from a haploid cell.

The term diploid parthenogenesis has often been used to include all cases in which the impaternate offspring have been judged on purely morphological grounds to be diploid, even though this diploidy results from "regulation" after meiotic reduction. This usage, developed before application of the genetic point of view, has caused much confusion and useless discussion, since chromosome number sometimes fluctuates in different tissues, and the criteria for haploidy are frequently very uncertain. In azygotes resulting from tychoparthenogenesis or from artificial parthenogenesis, this fluctuation is often very great. I believe that the extension of the term haploid parthenogenesis

to include all cases of origin from a single reduced maternal nucleus in animals should be helpful, by emphasizing a distinction of fundamental genetic significance between azygotes, whether haploid or not, and impaternate zygotes, which are diploid (or polyploid) in origin.

I have used the terms haploid or diploid as applied to azygotes just as I have used the terms diploid or polyploid for zygotes. These terms must be understood to be relative. Actually we do not know that any "diploid" animal is diploid in all of its tissues, and we do know that polyploid cells and tissues occur in many diploids. Similarly, we cannot say that any "haploid" animal resulting from haploid parthenogenesis is haploid throughout. The azygotes resulting from tychoparthenogenesis are, at least for the most part, diploid and possess the type of gametogenesis characteristic of normal diploid zygotes. The azygotes, males, produced by haploid arrhenotoky in the regularly established parthenogensis of Dzierzon's Law and the subject of discussion of this paper, are only more-or-less haploid, the drone bee being less, in fact apparently diploid with some polyploid tissues. Whatever the chromosome count may be in "male haploidy," meiosis is peculiarly modified or eliminated in the males so that spermatogenesis is of the haploid type.

While tychoparthenogenesis and the parthenogenesis involved in male haploidy are both facultative, they differ in that the former is poorly adapted, with many inviable cases of rudimentary parthenogenesis, while the latter is highly perfected, reproductively economical, facultative in the highest degree.

The parthenogenesis of male haploidy is to be contrasted with obligate arrhenotoky occurring in the male-producing females of the parthenogenetic generation preceding the bisexual in some of the groups with cyclic parthenogenesis. Other parthenogenetic females of these groups may be obligately thelytokous or deuterotokous.

In groups with constant parthenogenesis facultative arrhenotoky may be combined with deuterotoky. Fertilized eggs will then produce females, unfertilized will produce either males or females.

Many of the terms defined above are applied in various ways to individuals, fraternities, generations, races, species, or groups of higher taxonomic order, and this diversity of usage by different authors makes it difficult to clarify the subject. An individual of either sex may be either bi-

parental or impaternate. A fraternity, generation, race, species, etc., may be either bisexual, consisting of males and females, or unisexual, made up of a single sex. The occurrence of induced parthenogenesis or of facultative parthenogenesis in a female, a race, a species, or a generation does not make it "parthenogenetic," for this term is used *sensu stricto* to indicate that the female or group is obligately parthenogenetic, that *all* offspring are impaternate. Thus a frog whose eggs are pricked and thereby stimulated to develop parthenogenetically does not become, through this process, different from any other frog, and is not said to be parthenogenetic. In the literature on artificial parthenogenesis the impaternate offspring are frequently designated as parthenogenetic, but this ambiguous usage is here avoided in accordance with the suggestion of Ray Lankester mentioned above.

A male should not be described as parthenogenetic, arrhenotokous, deuterotokous, thelytokous, or zygogenetic, but may belong to a race, a species, or a heterogonic generation characterized by any one of these terms. Exceptional or spanandric males occur in parthenogenetic (thelytokous) groups, but, except for these males, a parthenogenetic generation, race, or species consists of females only. Races or entire species are either parthenogenetic (female), arrhenotokous, deuterotokous, or zygogenetic. Parthenogenetic groups of taxonomic order higher than species do not occur, but such groups may be arrhenotokous, deuterotokous, or zygogenetic. A group (generation, race, species, etc.) reproducing according to Dzierzon's Law is said to be arrhenotokous. Thus the honey-bee *Apis mellifica* s an arrhenotokous, not a parthenogenetic or a zygogenetic, species. There are, however, races of the honey-bee that may produce females as well as males from unfertilized eggs. Such races are deuterotokous. The females of many species of grasshoppers are described as facultatively thelytokous because they produce females if they are unmated. The females of several species of moths are facultatively deuterotokous, producing impaternate offspring of both sexes. A certain parasitic wasp, *Nemeritis canescens*, although belonging to the arrhenotokous insect order Hymenoptera, is obligately thelytokous, a parthenogenetic species with males unknown. The European race of a certain stick insect, *Carausius morosus*, although belonging to the zygogenetic insect order Orthoptera, is obligately thelytokous,

a parthenogenetic race with rare, spanandric, males. The ancestral Asiatic type of the same species is bisexual and zygogenetic. This species therefore exhibits geographic parthenogenesis.

Use of the expressions arrhenotokous, deuterotokous, or thelytokous parthenogenesis is grammatically incorrect, redundant, because these adjectives imply parthenogenesis.

Extent of Occurrence of Male Haploidy

Production of males by haploid arrhenotoky is a stable mode of bisexual reproduction functioning quite as successfully as the more frequent method of zygogenesis of both sexes. It occurs in rotifers (Miller, 1931; Shull, 1929; Tauson, 1927; Wesenberg-Lund, 1923, 1930; Whitney, 1929), certain groups of mites (André, 1935; Cooper, 1937, 1939; Pätau, 1934, 1936; Putnam, 1939; Schrader, 1923), thrips (Davidson and Bald, 1931; Shull, 1917), white-flies (Morrill and Back, 1911; Schrader, 1920, 1926; Stoll and Shull, 1919; Thomsen, 1927), a certain tribe of scale-insects (Hughes-Schrader, 1927, 1930; Schrader and Hughes-Schrader, 1926), the beetle *Micromalthus* (Scott, 1936, 1938, 1941) and insects of the order Hymenoptera.

Most insects of this last-named order are much larger and more conspicuous than insects in the other orders and have, accordingly, received more attention from entomologists, cytologist, and students of heredity. For this reason, the Hymenoptera have contributed more than any other group to our understanding of the problems connected with male haploidy. Since reference will be made frequently to various members of the different subgroups of this order, they will now be very briefly characterized.

The order Hymenoptera is popularly said to include wasps, ants, and bees, but these divisions are by no means correlative. The great majority of species and major divisions are often called wasps. It is also often supposed that the order is characteristically made up of social insects. This is a misconception. Of the two large suborders, the Chalastogastra includes the more primitive species, plant feeders with caterpillar-like larvae, the horn-tails and saw-flies. Under the suborder Clistogastra, with maggot-like larvae, there are seven superfamilies. Four of these, Ichneumonoidea, Proctotrupoidea, Chalcidoidea and Evanioidea, include the vast majority of described species of the order, wasps which are largely

parasitic on other insects and hence of great value economically. The gall-forming wasps and their relatives, Cynipoidea, make up the fifth superfamily. The members of the two remaining superfamilies, the aculeates or stinging Hymenoptera, are for the most part, wasps and solitary, as are all those previously mentioned. Of the fourteen families of the aculeate Vespoidea, only two show social development, the Formicidae or ants, which are all social, and the Vespidae or hornets, yellow jackets, etc., with some species solitary, some social in varying degrees, and with social organization polyphyletic within the group.

The seventh superfamily of the Clistogastra the aculeate Sphecoidea, includes three families of digger wasps, all solitary, and five families of bees, largely solitary but showing polyphyletic evolution of social life.

The entire order, irrespective of social organization, from lowest to highest in all of its divisions is characterized by parthenogenesis mixed with sexual reproduction (Peacock and Gresson, 1931; Sanderson, 1932; S. G. Smith, 1941). Biparental males (diploid) have not been reported from nature in any species, and meiotic phenomena in the male, as well as spermatogonial and somatic mitoses, indicate male haploidy. Dzierzon's Law applies as the rule. The sterile biparental males regularly occurring in the parasitic wasp *Habrobracon*, under conditions of inbreeding and "domestication" which will be discussed later, are not considered here. Oogenesis in all male-producing eggs is regular, with two oocyte divisions giving rise to the haploid nucleus. Naturally occurring exceptions to Dzierzon's Law are all in the direction of thelytoky, and in this case the oocyte divisions are variously modified. Even in the honey-bee, the species studied by Dzierzon and on which he based his principle, thelytokous races occur in which workers (females) produce workers without mating.

Many species in diverse groups are entirely thelytokous, females producing females indefinitely by diploid parthenogenesis with males entirely unknown (B. R. Speicher, 1937). In other species thelytoky is geographic, the female race occupying a newer region than the bisexual (arrhenotokous) (Brues, 1928; S. G. Smith, 1941). This condition is supposed to aid in the rapid spread of the species. Bisexual reproduction may be resumed later in the new territory.

In several gall-making wasps among the

Cynipoidea, alternation of a bisexual with an agamic female generation takes place (heterogony). The sexual females may be very different in appearance from the agamic, so that some have been described under generic names different from their own offspring. In the more highly evolved species of this group, a single agamic female produces either males or females but not both, and Doncaster (1916) has shown that from a single mating of a sexual female there are obtained only male-producers or only female-producers. Among the less specialized species a single agamic female may produce both males and females, and the tendency to produce one sex only appears to have evolved gradually within the group (Patterson, 1928a). In the agamic female generation parthenogenesis is obligatory, and the females, if introduced to males, refuse to mate. A few functionless males with weak mating instincts occur in this generation, probably from unfertilized eggs of the sexual females. They have been shown to be haploid, as are the normal males of the sexual generation (Patterson, 1928b).

In many species, among the minute egg parasites Chalcidoidea and Proctotrupoidea, polyembryony takes place, a single egg giving rise to more than one embryo, with numbers ranging from a few to many hundreds. Dzierzon's Law applies here, so that males only are produced if the egg is unfertilized, while a fertilized egg gives rise to a female brood. However, it has been shown that a few males, haploid, may sometimes appear in a female brood, indicating probable somatic reduction of chromosome number in the germ mass (Patterson and Hamlett, 1925).

Since parthenogenesis and male haploidy characterize the entire order from the relatively primitive horn-tails and saw-flies to the highly specialized parasites and the social wasps, ants, and bees, it must have appeared very early in evolution.

Taxonomically, the Hymenoptera are singularly isolated, with highly specialized wing venation even in the most primitive members, which show no relationship with any other orders. In the paleontological record there is also no evidence of relationship to other groups. The earliest forms occur in the Upper Jurassic strata and include both the plant-feeding Chalastogastra and primitive members of the parasitic groups in the Clistogastra,—Ichneumonoidea, Proctotrupoidea, and Evanioidea. Since several groups under

both suborders are found in the Jurassic and since all known living Hymenoptera reproduce parthenogenetically, these extinct species must also have done so, unless we are to assume that parthenogenesis originated independently several times and spread through the entire order, which is highly improbable.

Fossil Hymenoptera are lacking in the Cretaceous period. The earliest aculeates date from the Eocene, at which time all the parasitic groups are also abundant. Among the ants, sexual females were distinct from the workers in the Tertiary, but polymorphism was absent among the latter, and differences separating the true workers from the soldiers were not evident until the Pleistocene.

PROBLEMS INVOLVED

Before an hypothesis is suggested to explain the steps in development of male haploidy, it will be necessary to consider certain problems concerning parthenogenesis, and some of the known facts which may throw light upon them. These problems may be discussed under five headings, as follows: (1) induction of parthenogenetic development in eggs; (2) viability of the azygote; (3) meiosis in the haploid male; (4) sex determination; (5) haploidy of the azygous male. The first two of these may be regarded as initial steps in the attainment of male haploidy. The remaining three problems will be considered before additional steps are presented.

Induction of Parthenogenetic Development in Eggs

Plants, with their normal alternation of an azygotic (gametophytic) with a zygotic (sporophytic) generation, have no block to post-meiotic mitosis. In animals this block is regularly established, with insurance thus added to syngamy but frequent lapses occur, initiating parthenogenesis. There is no need to discuss the causes of these lapses, which are the subject of innumerable experiments by physiologists and which fill volumes of research publications. Effective factors are chemical constituents of the water, temperature changes, and mechanical stimuli such as shaking or pricking the eggs, in addition to hereditary constitution. Lack of the block or its breakdown, as exemplified by the spore of a fern or the egg of a bee, is no greater problem than establishment of the block, as it occurs in the egg of a fly, for example.

In addition to experiments on artificial partheno-

genesis, the wide scattering of tychoparthenogenesis in different groups indicates the frequency of independent occurrence of this breakdown. Moreover, the presence of tychoparthenogenesis in some groups and in certain species, contrasted with its absence from others, demonstrates a racial or genetic basis.

Viability of the Azygotes

In presenting definitions concerning parthenogenesis, the distinction was made between haploid and diploid parthenogenesis, and it was pointed out that the former leads, not necessarily to a haploid animal, but often to a diploid azygote. In fact, tychoparthenogenesis is haploid, at least in the majority of cases, but in all cases the end result is a diploid. Most diploid zygous animals appear to carry recessive lethal genes which tend to be retained in the species because of their recessiveness. With the occasional development, in a normally zygogenetic species, of an unfertilized haploid egg such lethal genes disclose their presence, even though the egg develops into a diploid (homozygous) azygote. A high mortality of these azygotes (incomplete parthenogenesis) takes place, so that selection against recessive lethal genes must be very severe in tychoparthenogenesis. Many cases of incomplete parthenogenesis may be expected to occur in a zygogenetic species before an adult azygote appears. Having appeared, it is free from recessive lethals and ready to carry on should other conditions be conducive to that end.

The occurrence of such an azygote in the first place, together with its survival to maturity, indicates that it has certain genes required for successful parthenogenetic development. If it can reproduce, its offspring should, on the average, carry more genes tending toward parthenogenesis than the average of sexually produced individuals. Hence we might expect parthenogenetic races to appear by natural selection among the descendents of sporadically occurring diploid azygotes arising from haploid parthenogenesis, as well as of impaternates produced by diploid parthenogenesis in which recessive lethals would have no effect.

One definite condition which must be fulfilled (and which is undoubtedly accomplished by natural selection) if azygotes are to be viable, is a satisfactory surface-volume relationship in cells. Viable haploid sporophytes have been obtained in many species of plants without difficulty, whereas in normally diploid animals survival of a haploid is very infrequent. Fankhauser (1938) has been able by cold treatment to initiate haploid parthenogenesis in salamanders, but only one survived to a stage beyond sex differentiation. Surface-volume relationships in animal cells may be such that they place a much greater hazard on deviations from normal chromatin quantity than occurs in plants.

One method of regulation of the surface-volume relationship is by a doubling of chromosome number in the cleavage of an egg originally haploid, resulting in a restored but azygous diploid. Artificial parthenogenesis in frogs illustrates the problem of attainment of viability by chromosome doubling after parthenogenesis. Development is initiated by pricking the eggs (Kawamura, 1939; Parmenter, 1940). A small proportion of these gives off two polar bodies and undergoes cleavage. Embryos are highly inviable, but some have formed tadpoles, and a very few have metamorphosed. Of those not completing development, some are haploids, some diploids, and others are haplo-diploid or diplo-triploid mosaics, and even tetraploid tissue has been found. The increases in chromosome number come about before the first cleavage, during cleavage, or in later embryonic stages.

Because a large proportion of the impaternate tadpoles have been haploid and because others have had tissue in part haploid, it is certain that a majority, and perhaps all, were azygotes. The possibility is not excluded, however, that meiotic regulatory processes or parthenogamy from a polar body may have occurred in some, retaining maternal heterozygosis, and bringing about diploid parthenogenesis. It has not in all cases been noted that two polar bodies were extruded.

The cytological conditions of tychoparthenogenesis as it occurs in many invertebrates appear to be very similar to those in experimental parthenogenesis of frogs. There is a high mortality of developing embryos, and the survivors are diploid.

Before the remaining problems involved in attainment of male haploidy are discussed, certain types of diploidy in male Hymenoptera may be considered. This matter is taken up here because of its bearing on the viability of azygotes.

Chromosome number in the honey-bee has been a moot question for many decades. Nachtsheim (1913) summarized and discussed the various

views and was able to dispose of many of the cruder and less adequately supported hypotheses. His cytological study appears to be of the highest order. He regards sixteen as the haploid number of chromosomes and thirty-two as the diploid. Because there is reduction to eight in the primary oocyte, I prefer to regard eight as the haploid, and sixteen as the diploid chromosome number, and I consider his higher numbers as due to regulative splitting. Nachtsheim calls the first oocyte division reductional. By this he may mean either that the number of chromosomes is halved or that paternal elements are segregated from maternal. Presumably genes may segregate in either division, as in other forms.

In the following account I am disregarding Nachstsheim's terminology and his diagrams and am basing my statements on his excellent drawings of the actual material. Oogenesis is regular. There are sixteen chromosomes in the oogonia. Oocyte I metaphase is not shown. Eight dyads go to each pole in oocyte I anaphase. These dyads appear in both metaphase II spindles and divide into monads, eight of which pass to each pole in anaphase II.

Cleavage of the unfertilized male-producing egg shows that most of the chromosomes have already split in a regulative process, so that the number becomes sixteen, and this number is also seen in the blastoderm. It may be further increased in later stages. The chromosomes tend to lie in sister pairs because of their origin through regulative splitting.

Spermatogonia are not shown. There are sixteen dyads in the nucleus of the abortive spermatocyte I division. The spermatocyte II nucleus is divided equally, eight dyads going to each pole in anaphase. The chromatids may be separated so that they already appear as eight pairs of monads.

Cleavage in the fertilized egg shows thirty-two chromosomes, and approximately this number may be seen in the blastoderm. There is much discussion about the somatic chromosome numbers, some authors finding up to sixty-four (octoploid) in certain tissues of both sexes. It may well be that, due to regulation, the drone bee has, in general, the same chromosome numbers as the female, although it originates from a haploid egg. Nuclei of the male approximate in size those of the female (Oehninger, 1913; Nachtsheim, 1913).

The fact that all the chromosomes are duplicated keeps the genic balance similar in all male tissues.

The number sixteen in spermatocyte I and in cleavage of the unfertilized egg is undoubtedly regulative. Reduction to eight in spermatocyte II is perhaps the last echo of ancestral male haploidy. This type of polyploidy, seen also in many tissues of other animals, may be called somatic polyploidy. It has no bearing on genetic ratios, so that the male bee should breed as a haploid, the female as a diploid. The number of linkage groups should be eight.

A second method of regulation for surface-volume relationships might be by increase in chromosome size. Size of nuclei and size of cells might thus be increased in the haploid male to approximate conditions in the female. Somatic haploidy has been demonstrated for certain tissues in certain species, but it is possible that regulation by doubling may take place in other tissues. Cleavage and gonial nuclei of males have been shown to have half as many chromosomes as those of females in several forms. This proves to be the case in the Ichneumonoid wasp *Habrobracon* in which wing cell size of "haploid" males approximates that of females (B. R. Speicher, 1935). The chromosome number in wing cells is, however, not known.

At present, many workers in this field of study take for granted haploidy of the males produced according to Dzierzon's Law, but considerable doubt has been expressed at various times in the past as to whether haploid organisms could be viable. In view of the fact that gametophytes of plants are normally haploid, this doubt was restricted to viability of haploid forms of organisms that are normally diploid. Subsequently, after the demonstration of occasional haploidy in sporophytes of plants, the doubt was still expressed as to whether animals might survive as haploids. Cytological studies indicating somatic polyploidy of the drone honey-bee seemed to strengthen skepticism as to the viability of haploid Metazoa.

In order to "explain" the viability of males in the Hymenoptera despite their presumed or apparent haploidy, and also in order to account for certain cytological phenomena, the suggestion has been advanced that the "haploid" set of the males is fundamentally diploid. Since females have been shown to possess twice the male chromosome number, in certain tissues at least, it follows that females would be tetraploid.

In several of the lower Hymenoptera there is pairing, to some extent, among the chromosomes of the haploid set in the male. Sanderson (1932) calls attention to this in the saw-fly *Pteronidea ribesii*, in which the eight haploid chromosomes appear as three pairs and two odd chromosomes, and Dodds (1938) shows secondary pairing of the ten metaphase chromosomes in spermatocyte II in the gall-wasp *Neuroterus baccarum*, in which the female may have five groups of four "homologues" each. Greenshields (1936a) discusses this situation, arguing that in the Hymenoptera there may be a tetraploid female-diploid male relationship instead of a diploid-haploid. No such pairing is evident in chromosomes of the Ichneumonoid *Habrobracon*, and Speicher (1936) points out that genetic data show *Habrobracon* to breed as a haploid. Greenshields (1936b) says that there is conflict in the use of terms by cytologists and geneticists, and that the genetic "facts are by no means fatal to a theory of derived tetraploidydiploidy based on cytological findings." He regards the phenomena of pairing as vestiges in the evolutionary sense.

In the evolution of cytogenetic systems, duplication plays an important rôle. The entire complex of chromosomes of a normal diploid form may be doubled, resulting in an *autotetraploid*. These show irregular types of pairing, multiple synaptic complexes, etc. Sterile species hybrids may double their chromosome number, resulting in fertile *allotetraploids*. These tend to have more regular meiotic phenomena than autotetraploids and are, consequently, more fertile. Duplication of single chromosomes or of parts of chromosomes may occur, thus increasing the number or size of these structures. Genetic duplication is often evidenced by irregular types of segregation, but this condition may later be masked by selective elimination of certain types, by further chromosomal rearrangement, and by genic mutation, so that "normal" conditions reappear.

Genetic polyploidy, or more generally, genetic duplication, must be regarded as relative. It is impossible to determine how much duplication or how much deletion may have occurred in the past history of the chromosome set normal to any species. In polyploid series in several groups of plants, the gametic number of chromosomes has been called haploid. This haploid number may be various multiples of a more fundamental *monoploid* number which, presumably, acted as the haploid

number of some ancestral type. The term haploid is, therefore, a relative term. It is not improbable that there may be remnants of genetic polyploidy in the lower Hymenoptera or in certain higher groups, but this has disappeared or does not exist at all in others. In any case, the somatic regulative polyploidy of the bee appears to be a very different phenomenon.

Meiosis in the Haploid Male

In addition to cleavage of the unfertilized egg and survival of the azygote to maturity, the species with haploid arrhenotoky have attained some sort of regulation or omission of meiosis in spermatogenesis, so that the sperm cells have the full haploid set. Irregular distribution of chromosomes, such as occurs in haploid sporophytes (Bleier, 1933), has been avoided. This may involve a certain amount of telescoping of premeiotic processes with postmeiotic. If meiosis be deleted altogether, what appears to be a spermatogonial cell must enter directly upon spermiogenesis. The condition is here analogous to that obtaining in the formation of antherozoids in moss or fern gametophytes, in which there is, of course, no heritage of meiosis.

Among the mites this condition is approximated. Schrader (1923) indicates no distinction in *Tetranychus bimaculatus* between spermatogonia and spermatids, each with three chromosomes, the haploid number. There is no growth stage, and meiosis is omitted. Pätau (1934, 1936), showing that the male of *Pediculoides ventricosus* is haploid with three chromosomes, did not follow spermatogenesis because he considered the cells too small. Presumably there is also no appreciable growth stage in the haploid "spermatocytes" of this mite.

In the homopteran insects of the family Aleurodidae or white-flies, the males are haploid. Schrader (1920) states that in the males of *Trialeurodes vaporariorum*, with eleven chromosomes, the "reduction" division is omitted, and the "equation" division is not differentiated from the last spermatogonial. Thomsen (1927), however, states that in *Aleurodes proletella* the spermatocytes have a clear growth stage, but there is only one meiotic division.

Most haploid males make some compromise with meiosis. This is effected in various ways in different groups.

In the one beetle shown to have haploid arrhenotoky, *Micromalthus debilis*, Scott (1936)

studied spermatogenesis. The ten chromosomes of the abortive first spermatocyte anaphase move away from the single pole, with the attachment fibres lengthening. The second division is normal giving rise to two normal spermatids.

In the rotifer, *Asplanchna amphora*, Whitney (1929) showed thirteen chromosomes dividing in the first spermatocyte. Two types of sperms were found. The larger motile functional type, with thirteen chromosomes, the haploid number, develops directly from the secondary spermatocytes. A few of the secondary spermatocytes, however, divide with irregular distribution of chromosomes, to form spermatids with a small amount of chromatin. These develop into small non-functional spermatozoa. Tauson (1927) found but a single spermatocyte division with the reduced number twelve in *Asplanchna intermedia*, the second division being lacking. In this species she failed to find any rudimentary spermatozoa.

In the scale insects, Coccidae, of the tribe Iceryini, the males are haploid with two chromosomes. There is a single meiotic division of the first spermatocyte nucleus. The cytoplasmic division is suppressed and binucleate spermatids are thus produced from each of which two sperms develop (Hughes-Schrader, 1930). In the cottony cushion scale, *Icerya purchasi*, the females are secondarily modified into hermaphrodites. These have four chromosomes (Hughes-Schrader, 1927). The males, which are infrequent, are similar in spermatogenesis to males of the related species having females. Spermatogenesis of the haploid cells in the hermaphrodite gonad tallies in every respect with that in the males. Diploid cells in the hermaphrodite have also shown spermatogenesis in limited regions. It is clear that two divisions occur and that each sperm receives the haploid number. In several cysts of large cells there were four chromatin threads in various phases of condensation. Early telophases were found with four rods at each pole, and a few binucleate cells with four chromosomes in each nucleus. In the second anaphase two chromosomes go to each pole. As in the haploid spermatocytes of the hermaphrodites and of the males, there is no cytoplasmic division. The secondary spermatocytes from the diploid cells are therefore binucleate, with four chromosomes in each nucleus, and the spermatids are quadrinucleate, with two chromosomes in each nucleus. Each spermatid from the haploid spermatocytes develops two

sperms and each spermatid from the diploid spermatocytes develops four sperms. In this form, apparently, normal meiosis with reduction can take place in spermatogenesis in diploid tissue.

With the exception of *Telenomus*, in which it is the second spermatocyte division that is abortive (Dreyfus and Breuer, 1944) the reported cases in the Hymenoptera show failure of nuclear division in the first spermatocyte, which usually gives off a small cytoplasmic bud. The second division is equal, and two sperm cells result, except that in the bees there is but one sperm cell which develops from the larger of the two very unequal spermatids. In the different hymenopterous species studied, details differ, as in degree of condensation of chromosomes during the first "division," in which also the cytoplasmic bud may be lacking.

That certain types of meiotic regulation become fixed in the heritage of different groups is shown also in the spermatogenesis of diploid males in *Habrobracon*. Here there is asynapsis; a cytoplasmic bud is given off, as in haploid males, and an equational division of the entire set of twenty chromosomes ensues, giving rise to two diploid sperms (Torvik-Greb, 1935). These may occasionally function in the production of triploid females. It is of interest to contrast the failure of reduction in the spermatogenesis of the diploid males of *Habrobracon* with its presence in the diploid spermatogenesis of the hermaphrodite *Icerya purchasi*. Possibly the general pattern of spermatogenesis in the Hymenoptera is more definitely fixed genetically, or it may be that since the hermaphrodite coccid is but little removed from the female, its diploid spermatogenesis takes on something of the character of oogenesis.

Regulation of meiosis in haploid males has, as we have just seen, been accomplished in a variety of ways. One or another of these methods must have been selected in the attainment of male haploidy from an assortment of diverse conditions depending in part, at least, upon the normal mode of the ancestral diploid stock.

Sex Determination
Zygogenetic back-cross sex determination

With the development of the Mendelian principles of heredity, it has been shown that sex determination, as a rule, is comparable to the "back-cross" of the heterozygous dominant to the recessive. Two general categories may be recog-

nized,—the XY-male type and the WZ-female type.

Most animals and many dioecious plants belong to the XY-male type. In these one-half of the sperm cells receives the recessive factor X, the other half receives the dominant factor Y. All eggs receive the factor X from the homozygous recessive female, XX, in which crossing-over takes place. Cytological conditions corresponding to these factors are very diverse, especially in the male. The entire X-chromosome may segregate as a unit from the Y in meiosis, as in the fly *Drosophila*, or there may be crossing-over between portions of the X- and Y-chromosomes, as in man and in some fishes. In the latter case the factors X and Y correspond, not with entire chromosomes, but with those parts only that fail to cross over. The Y-chromosome may be larger than the X, it may be the same size and indistinguishable cytologically, or it may be smaller. There may be several small Y-chromosomes which segregate as a group from the X, or there may be no Y-chromosome. The factor Y then corresponds to the small chromosomes or to the absence of the X-chromosome.

The WZ-female type of sex determination is found in birds, in moths, and in some fishes. What has been said about the chromosomes in the XY-male type may be applied here also, but just in reverse as regards the sexes. The male has two Z-factors and is, therefore, recessive in a Mendelian sense. The female is heterozygous dominant, with W dominant over Z.

The sex of an individual is determined by the ratio existing between male-producing and female-producing genes. These sex genes may occur in the autosomes as well as in the sex chromosomes. They may be absent from one or the other of the sex chromosomes. In *Drosophila*, with sex genes absent from the Y, and X is predominantly female-producing and the autosomes predominantly male-producing. In the dioecious plant *Melandrium*, the Y is highly male-potent in genic content, the X is female-potent and very little if any sex potency has been located in the autosomes (Warmke and Blakeslee, 1940).

A single set of autosomes is designated A. In XY-male sex determination, the complete male formula is $XY + 2A$, the female formula $2X + 2A$. However the sex genes may be arranged, there are more female-producing genes in the female, more male-producing genes in the male, and the difference in the ratio determines the sex. Since the autosomes are normally the same in the two sexes, they may be left out of the formula. Sex differentiation depends upon the type of sperm cell which fertilizes the egg.

In WZ-female sex determination, the male formula is $2Z + 2A$, the female formula $WZ + 2A$, and the same principles outlined above apply, but in reverse as to the sexes.

"Protection" from natural selection exists in the heterozygote, so that one chromosome may degenerate, losing most of its genes, as has the Y in *Drosophila*, or becoming small in size or disappearing. Muller (1918) expressed this idea, stating that lethal changes and deleterious mutations as well as visible recessives "should be found to have arisen in any chromosome region that has been protected for a long time from the action of natural selection. . . . The Y chromosome is so protected by the X."

Geneticists often use the formulae of the cytologists, distinguishing XO males from XY males. These two formulae are, of course, inadequate to express the great variety of cytological conditions that exist in the XY-male type. Since it is usually unnecessary to express these differences in genetic formulae, I am, for the sake of simplicity, proposing to use the terms X- and W-factors as female differentiators, Y- and Z-factors as male differentiators. Linkage and crossing-over may then be expressed with the alleles X vs. Y and W vs. Z.

Chromosome constitution and, therefore, the sex of the individual, is usually determined at fertilization of the egg, but this may occur at other times, as, for example, during cleavage in certain zygogenetic animals. In the fly *Sciara* all zygotes begin as $3X + 2A$ but subsequent elimination of X's occurs so that the soma of the male becomes $X + 2A$ and that of the female $2X + 2A$ (Metz, 1938). *Sciara* therefore belongs to the XY-male category.

In parthenogenesis, the chromosome constitution of the offspring is usually decided during meiosis. In the agamic generations of aphids, both X-chromosomes are, in general, retained in the egg so that females, $2X + 2A$, are produced. However, one X-chromosome is regularly extruded from the male-producing parthenogenetic egg, leaving $X + 2A$.

Tychoparthenogenesis is usually haploid, with restoration of the diploid number by endomitotic doubling. The offspring, starting as haploids, are therefore homozygous both for sex and for other factors. With XY-male sex determination the

offspring are, in general, females, 2X + 2A, from the X + A eggs laid by the 2X + 2A mothers. The rare exceptional males occurring here may be explained by failure of the X to double at the first cleavage. With WZ-female sex determination the offspring are males, 2Z + 2A from the Z + A eggs, and females, 2W + 2A from W + A eggs, in equal numbers. The exceptional composition of the females, WW instead of the usual WZ, will be discussed later.

Origin of parthenogenetic races and species

Parthenogenesis, as it exists in thelytokous races, rarely if ever is haploid. Parthenogamy from a polar body may occur as in *Lecanium* (Thomsen, 1929), but the more usual condition appears to be an advance of cleavage into meiosis so that an oocyte nucleus becomes the first cleavage nucleus. This advance may result in omission of synapsis, so that the nuclei resulting from the last oogonial division enter immediately upon cleavage. The diploid (or polyploid) group may then accumulate by mutation a considerable amount of heterozygosis. Obvious variation will then be limited to dominant changes, and different lines, lacking the possibility of crossing (amphimixis), will differ in many unseen (recessive) traits.

Vandel (1931a, 1936, 1937, 1940) regards tychoparthenogenesis (haploid) as the primitive type from which there has developed the normal and regular (diploid or polyploid) parthenogenesis of thelytokous races. Doubling of chromosome numbers, which occurs somatically in tychoparthenogenesis, is extended in thelytokous races to involve the germ track. Vandel (1936) makes comparisons in nuclear phenomena between tychoparthenogenesis, which he calls genotypic, and experimental parthenogenesis which is phenotypic, initiated by artificial means. Either type may be incomplete (rudimentary) or may result in an animal viable to maturity. He traces the origin of polyploidy in parthenogenetic races to a persistence and an extension of endomitosis or parthenogamy. He omits discussion of male haploidy, which he regards as a specialized problem insoluble from the data available to him.

In the evolution from the usual bisexual zygogenetic type of reproduction to the thelytoky of parthenogenetic races, there is elimination of the male and a tendency toward polyploidy. In the evolution of male haploidy, progression is in the reverse direction. Parthenogenesis produces

males with reduced chromosomes. Since the race cannot consist entirely of males, a limit tends to be set to selection for this reduction, because the biparental females are necessarily diploid. There must also be established some genetic mechanism effecting physiological harmony of haploidy and diploidy in the same species. An answer to this problem is suggested in the nature of the sex differentiating factor which will be discussed below.

Thelytoky

Parthenogenetic races or species are, of course, female, thelytokous, except for the rare or spanandric males. The type of parthenogenesis is diploid (or polyploid), and the chromosome complement of the mother is passed on unchanged to the daughters.

Induced parthenogenesis may be either diploid or haploid. In the latter case mortality is very high, and the diploid number of chromosomes is usually restored in the few surviving individuals.

Let us first review parthenogenesis in some of the groups which are known to be of the XY-male type or are probably so. Here females are to be expected.

One impaternate rabbit, normal and presumably diploid, from induced parthenogenesis was raised to maturity by Pincus and Shapiro (1940), a female as expected from an XX mother.

Fankhauser's (1938) *Triton* from induced parthenogenesis, the only amphibian attaining the stage of sexual differentiation as a haploid, was female. It is not known whether salamanders are of the XY-male type.

The few impaternate frogs from experimental parthenogenesis reared to the stage of sexual differentiation were all diploid. They included individuals of both sexes and also a number of sex-intergrade types with considerable asymmetry. The frog is presumed to belong to the XY-male category, although there is no convincing cytological evidence, and genetic data are derived from race and species crosses and are not clear-cut. Kawamura (1939) who obtained only five frogs with testes among twenty-three impaternates, concludes that "the preponderance of females and the absence of typical males can be explained well by the theory of male digametism." The parthenogenetic origin of these frogs, with irregularities in chromosome regulation, may account for their tendency toward hermaphroditism, which

was to some extent effective although they belonged to the sexually "differentiated" race.

Parthenogenesis is very rare in the two-winged flies, the Diptera. A few parthenogenetic races and species have been reported, especially in the Chironomidae (Sturtevant, 1923; Thienemann and Strenzke, 1940a, 1940b). Nothing is known of their cytology. It is of interest to note that paedogenesis, a type of parthenogenetic reproduction by larvae, also occurs in this same family. In haplo-diploid mosaics of *Drosophila*, Bridges (1930) showed the haploid region as well as the diploid to be female, as was to be expected from the known fact that Diptera are XY-male in type.

Parthenogenetic species have been recently reported in the Embioptera (Ross, 1940), the first parthenogenesis for this small order of neuropteroid insects, and in the Psocoptera (Badonnel, 1938), the "book-louse" order. Both species are known only as females.

Induced tychothelytoky has been shown in crickets (Ohmachi, 1929) and in termites (Light, 1944). Crickets, and probably also termites, the socialized relatives of cockroaches, are of the XY-male type.

Phasmids are of the XY-male type. There is an extensive literature from field studies and from breeding experiments showing geographic and constant thelytoky in many species (Cappe de Baillon and de Vichet, 1939, 1940). It is also certain that tychothelytoky occurs.

In the Saltatoria (jumping Orthoptera), parthenogenetic species appear to be rare. In the Tettigoniidae, Cappe de Baillon (1939) and Matthey (1941) have reported parthenogenetic species, with polyploidy probable from comparison of chromosome numbers in related forms.

Induced tychothelytoky has been shown in four species of the grouse locusts, Tetrigidae, in the extensive genetic experiments carried out by Nabours (1929, 1930). In one of these, *Apotettix eurycephalus*, among more than 5,000 impaternates bred to maturity, only thirteen were males. All were homozygous for numerous traits for which their mothers were heterozygous, indicating haploid parthenogenesis (King and Slipher, 1933). The homologous (sister) chromosomes in these impaternates tend to be approximated in the metaphase plates of cleavage in unfertilized eggs, while in fertilized eggs the homologues (members of paternal and maternal pairs) are widely separated (Robertson, 1930). Induced tychothelyt-

oky also occurs in several Acrididae (Slifer and King, 1932; King and Slifer, 1934; Creighton, 1938). The meiotic process is normal, being unaffected by the absence of the sperm. The haploid set of early cleavage is doubled as development progresses, so that some, perhaps all, cells of the embryo become diploid. Development is successfully completed in few of the individuals, and these are females. The rare impaternate males in Nabours' grouse locusts may be readily accounted for by accidental loss of an X-chromosome or its failure to double along with the autosomes.

Insects of the order Lepidoptera, moths and butterflies, possess the WZ-female type of sex determination. Among moths of the family Psychidae and of the Lymantriid genus *Orgyia*, there are parthenogenetic species and geographic races which may be diploid or polyploid (Seiler and Schaeffer, 1941).

Astaurov (1940) has induced thelytoky by heat treatment in the silk-worm, *Bombyx mori*: The unfertilized eggs were immersed in water at 46.0° C. for eighteen minutes. About 500,000 caterpillars capable of transforming to adults were produced over the period from 1932–1937. Of 37,152 identified as to sex, 37,139 were females and only thirteen males. The great majority were of maternal phenotype and genotype. Cytological studies by Frolova showed that the eggs undergo a single division, presumably equational, and that the diploid number of chromosomes is retained. Eggs of impaternate females were subjected to treatment each generation for six successive generations. Tetraploid females also appeared, and these were perpetuated parthenogenetically by heat treatment. When tetraploid females were crossed with normal diploid males, there resulted sterile triploid males and females.

Deuterotoky

Several instances of tychodeuterotoky have been reported in different species of moths. The literature has been reviewed by Vandel (1931a) for these examples of infrequent facultative parthenogenesis, in which males and females are produced in approximately equal numbers.

T. L. Smith (1938), carrying out genetic experiments with x-ray mutant types in the wax moth *Galleria mellonella*, showed that while mated females lay from two hundred to one thousand

eggs, which hatch in ten days, about ten per cent of unmated females show facultative parthenogenesis, and hatching requires several weeks. The impaternate offspring from a single female number from one to ten only, but these are normal in every way. Only seventy-nine attained an age in which sex was identified. There were forty males and thirty-nine females. When the mothers were heterozygous for recessive autosomal traits, the impaternate offspring were nineteen wild type and nine recessive.

According to genetic evidence, Lepidoptera have the WZ-female type of sex determination. Cytologically, females may be ZO or ZW. In the moth *Phragmatobia* there is one large Z- which segregates against two small W-chromosomes. Many species have no visibly differentiated sex chromosomes, and here it is presumed that the W-chromosome is equal in size to the Z. Chromosome numbers tend to be rather high in the Lepidoptera, and there is probably a considerable amount of distant phyletic polyploidy, in addition to the more recent cases in closely related species or varieties, in which one has double the number present in the other.

Explanation of the 1:1 sex ratio obtaining in the tychodeuterotoky of Lepidoptera apparently lies in the fact that it is haploid with subsequent doubling of the chromosome complex, and that the WW females, as well as the ZZ males, are viable (Seiler, 1923). It might have been expected that WW, which may be a homozygous deficiency, would be inviable and that all-male broods would result. Such have not been found, however, and we must attribute the viability of the females to vestigial polyploidy, with Z-factors duplicated and acting as autosomes (females Z'Z' ZO, males Z'Z' ZZ).

Sex determination in male haploidy

In all types of parthenogenesis other than male haploidy the principle of genic balance applies, so that sex determination *sensu stricto* is orthodox, however irregular may be the determination of chromosome distribution. This is true because the ratio of male-producing to female-producing genes is higher in males than in females, just as it is in "back-cross" sexual reproduction.

In haploid arrhenotoky, however, as it exists in the Hymenoptera and in the other groups mentioned above, sex determination has appeared to be fundamentally irreconcilable with generally accepted principles. This has been clearly stated by Bridges (1925). "To me, sex determination in the bee is the outstanding unsolved puzzle, although before the development of the idea of genic balance it seemed one of the clearest and simplest of cases. If it is true that the male is a haploid individual, then we would suppose that the diploid individual should likewise be a male, since the ratios among the sex-determining genes are not different in the two cases."

Three hypotheses were suggested to meet this difficulty before adequate genetic experiments had been carried out. One resorted to the cytoplasm, haven of cytogenetic theoreticians unable to make a better known port. The cytoplasm was supposed to transmit indefinitely a male tendency strong enough to dominate a single set of female-producing chromosomes, but dominated by the diploid set. This hypothesis disregarded the fact of regulation, assuming that the ratio of genic material to cytoplasm in azygotes was only half that in zygotes.

The second hypothesis placed sex differences in the Hymenoptera in the same category as those noted in different chromosomal types with multiples of the single complete set, in so-called euploid series. Such differences are seen in the rougher texture of eyes and larger size of triploid females of *Drosophila* and in the broader leaves of polyploid plants. However, the complicated sex differences found in insects are obviously of a very different order from these. This theory was elaborated into an algebraic sum hypothesis for male-determining and female-determining genes. When applies to the various sex and chromosomal types of *Drosophila*, it failed to fit the obvious relative intervals between them, as shown by Bridges (1925). This theory also ignored regulation and assumed a constant difference in quantity rather than in the rate of production of genic material, thus disregarding the factor of time.

According to the third hypothesis, it was supposed that the environment of the embryo might be different, that males were different because they had a different start in life than females, just as in a fern the gametophyte has the characters of a gametophyte because it develops from a spore, while the sporophyte is such because it begins in an archegonium. Thus, in the honey-bee there have been supposed to be two different types of eggs, a female-producing type which cannot develop unless fertilized (obligate zygogenesis)

and a male-producing type which cannot be fertilized (obligate parthenogenesis). It is now generally recognized that, as regards the honey-bee, there is but a single type of egg, facultatively parthenogenetic.

Schmieder (1938), however, suggests that there may be two types of eggs in the chalcidoid *Melittobia chalybii* because of the "fact that the ratio of males to females (3:97), produced by normally mated females, is approximately the same as the ratio of males to unhatchable eggs, produced by females not so mated." These eggs might be female-producing if they were fertilized. However, "unmated females deposit only a very few eggs and of these only a small percentage undergoes development. It is therefore more practicable to study haploid development in eggs obtained from females mated with another species of *Melittobia*, since after such mating oviposition occurs often at a rate comparable to that occurring in normally mated females. The foreign sperm is generally observed as having entered the egg but actual syngamy seems never to occur, or, at least, never to yield viable zygotes. The small percentage of eggs that eventually hatches always produces haploid males of the maternal type." The unhatchability of the eggs fertilized by foreign sperm may be explained by a lethal effect of the foreign sperm, without the necessity of postulating the existence of two different types of eggs. However, if the ratio of males to the few unhatchable eggs laid by unmated females is also only three per cent, then these eggs may be of a different type from those developing into males. They may be unhatchable because unfertilized, or for some other reason, defective yolk, for example. It is stated of *Melittobia acasta* that virgin females lay only a few eggs which invariably develop into males.

In the ichneumonoid *Habrobracon juglandis* it is obvious that at least two-thirds and presumably all eggs are facultatively parthenogenetic. Hatchability may be as high as 98 per cent and viability to the adult stage as high as 90 per cent, whether the females are mated or not. Since two-thirds or more of the offspring from mated females are females, at least this proportion of the eggs which produce males, if unfertilized, would produce females if fertilized.

Results from genetic experiments bearing upon the problem of male haploidy will now be presented.

In the ichneumonoid wasp *Habrobracon juglandis* (*Ashmead*), investigated by the writer and his co-workers, a large number of recessive mutant traits has been obtained, and crosses have been made in various ways to test the principles of heredity. Unmated females heterozygous for various traits produce haploid males segregating in azygotic (approximating gametic) ratios. Linkage tests thus made show that maps are very long in crossover units. On this account, despite much work extending over several years, there is as yet no approximation of linkage groups to the number ten, corresponding to the haploid set of chromosomes.

Recessive females crossed with dominant males produce recessive haploid sons and dominant heterozygous daughters, as expected according to Dzierzon's Law, but if the parents come from the same general stock, then there are also regularly produced diploid biparental males, which resemble their sisters in showing all the dominant traits inherited from both parents, but which are in no way intersexual. They are, however, of low viability and almost sterile. Their sperms are diploid, and consequently their few daughters are triploid. Diploid males are separable from their haploid brothers, not only in showing paternal traits, but also, with some difficulty, by slight differences in proportion of bodily structures and by the larger size of their cells. These are, in fact, much larger than the cells of diploid females. Triploid females, the daughters of diploid males, have cells even larger than diploid females, and haploid males average in cell size almost as large as diploid females (B. R. Speicher, 1935). It appears, then, that while increase in number of chromosome sets increases cell size, maleness as such is an even more effective factor.

Sex determination has been shown to depend upon a series of multiple alleles, of which nine have thus far been identified (Whiting, 1940a, 1943). These are designated *xa*, *xb*, etc., to *xi*. Any heterozygote (diploid), *xa/xb*, *xa/xc*, *xc/xd*, etc., is female; any azygote (haploid), *xa*, *xb*, *xc*, etc., or any homozygote (diploid), *xa/xa*, *xb/xb*, etc., is male. Each member of the allelic series is regarded, not as a single gene, but as a chromosome segment, perhaps very long (to speak in relative terms, because the chromosomes are all very small) and containing many different genes which do not cross over. Thus the allele or segment designated *xa* might have the genes + *Fa mb* + *mc* + etc., *xb* might have *ma* + + *Fb mc* + etc., and *xc* might have *ma* + *mb* + + *Fc* etc.

From these formulae it may be seen that any

heterozygote will show more of the dominant traits determined by the female-producing genes, *Fa*, *Fb*, *Fc*, etc., and that any homozygote or azygote will show more of the recessive traits determined by the male-producing genes, *ma*, *mb*, *mc*, etc. Sex determination is, therefore, complementary, with females of the different genotypes being heterozygous (diploid) dominants for many of the genes, while the males are homozygous (diploid) or azygous (haploid) recessives. Genes for secondary as well as for primary sex characters must be located within this segment. The longer antennae, the larger ocelli, the slightly larger eyes, and the weaker sclerotization of the abdomen of the male must be dependent upon such genes, which in the aggregate are also recessive.

The complementary character of sex determination is shown by certain males which are mosaic for various mutant traits (Whiting, Greb, and Speicher, 1934). Haploid mosaic males occur in a small but variable proportion, less than one per cent, of the offspring of heterozygous females. If a female (black-eyed double dominant) is heterozygous for two different white eye colors, called white, *wh*, and ivory, *oi*, respectively, a son may be produced having the eyes in part white, in part ivory. These two eye colors are normally indistinguishable, but ivory is non-autonomous in mosaics, so that a soaking-through effect takes place from the non-ivory tissue. The complementary action of the two dominant alleles, non-white and non-ivory, then causes a black line in the ivory region edging the white. This black region is "physiologically" double dominant, but genetically ivory. Similarly, in the region of the genitalia of a proportion of mosaic males there are developed small-sized "female" reproductive appendages, indicating a complementary action of dominant female genes in the different sex alleles characterizing the two different types of tissue of the mosaic male. The influence appears to be unidirectional, as if, for example, *xa* affected *xb* but not the reverse. This has, however, not been checked with the different alleles of the series. It was this complementary action in these "gynandroid" males (resembling gynanders) that first gave the hint of complementary sex factors that led to the formulation of complementary sex determination.

Sex determination is, in a sense, polygenic, but because of no crossing-over within the segment, the various groups of genes act as a single series of allelic factors. Just as the many sex-producing

genes distributed along the X-chromosome of *Drosophila* segregate as a unit from the Y without crossing-over, so the dominant female-producing genes and the recessive male-producing genes of the *x*-factor in *Habrobracon* segregate without crossing-over from their homologues. Males, as determined by the various alleles (whether azygous or homozygous), or females as determined by any of the heterozygous combinations, are always phenotypically similar.

Whether the sex-alleles ever mutate has not been established with certainty. They appear to be very stable. Extensive breeding within a two-allele stock has resulted in two-allele fraternities almost exclusively, as evidenced by the presence of diploid males. With certain very rare exceptions, the fraternities lacking diploid males are small, so that the lack is evidently due to error of sampling. The rare exceptions, which were not adequately tested, may have been due to contamination, though this is unlikely, or to some combination of factors reducing diploid male viability, or to mutation in a sex allele itself.

In linkage tests, the *x*-factor acts as a single gene, occupying a point on the linkage map. It has been shown to lie near the center of the left arm of a linkage group which is about five hundred crossover units in length. Since no interference occurs across a region approximately central, it may be supposed that the centromere is median.

The method of making a linkage test with the sex-factor may be illustrated by a single example. The mutant gene fused, *fu*, lies about ten units to the right of *x*. An orange-eyed, *o*, female heterozygous for fused, $\dfrac{o\ xa\ +}{o\ xb\ fu}$, is crossed with a black-eyed fused male, $+\ xb\ fu$. The orange-eyed sons are haploid from unfertilized eggs and are fused and non-fused in equal numbers. Sex linkage is not determinable among these because *xa* males and *xb* males are similar. The black-eyes zygous diploid or biparental offspring, *o*/+, are either fused or non-fused and either males or females. From the ratio of the different combinations, the percentage of crossovers may be determined. In the example given, the non-crossover offspring will be $\dfrac{xa\ +}{xb\ fu}$ or non-fused females, and $\dfrac{xb\ fu}{xb\ fu}$ or fused males; the crossovers, averaging in this case 10 per cent, will be $\dfrac{xb\ +}{xb\ fu}$ or non-fused males, and $\dfrac{xa\ fu}{xb\ fu}$ or fused females. This is called a two-allele cross.

In crosses involving three sex-alleles, sex-linkage cannot be determined, because all the zygous offspring are heterozygous for x and are therefore female. $xa/xb \times xc$ gives xa/xc, xb/xc. Fecundity is higher here, and the ratio of females to haploid males is doubled, because the poorly viable diploid males are replaced by females. In this case, if the cross is made between a female heterozygous for fused and a fused male, fused and non-fused females are in equal numbers.

Three kinds of fraternities from heterozygous females by fused males are therefore distinguishable as follows:—

	Females non-fused / fused	Diploid males non-fused / fused	Haploid males non-fused / fused
(1) two-allele........	9/1	1/9	1/1
(2) two-allele........	1/9	9/1	1/1
(3) three-allele......	1/1	0	1/1

Before the multiple allele principle was demonstrated, two different hypotheses, now discarded, were suggested to explain the lack of diploid males in three-allele fraternities. These were differential mutaration, and multiple independently segregating factors (Whiting, 1935).

Habrobracon is an arrhenotokous species, but in combinations of certain stocks unmated females produce a small proportion of diploid daughters in addition to their haploid sons. These impaternate daughters are either heterozygous or homozygous for genes for which their mothers were heterozygous. Female $+/a$ produces impaternate daughters in the ratio: $1 +/+$, $2 +/a$, $1 a/a$. It was at first supposed that suppression of meiosis, or parthenogamy from a polar nucleus, might cause their appearance (K. G. Speicher, 1934) but cytological work later showed twenty tetrads, the diploid number, in the first oocyte mitosis (Speicher and Speicher, 1938). Two meiotic divisions would then leave the diploid number of monads in the egg nucleus. If the homologues contained different sex-alleles, a female would result. The fact that the heterozygotes for a mutant gene are equal to the homozygotes rather than twice as numerous indicates that the genes, $A \, A \, a \, a$, assort as two pairs, Aa and Aa, rather than at random. This is to be interpreted as meaning that synapsis is initiated in two oocyte I groups of chromosomes which remain separate, and each of which contains both a haploid paternal and a haploid maternal set. The bivalents are therefore paternal-mater-

nal, none being paternal-paternal or maternal-maternal.

If the mother is heterozygous for a sex-linked gene, the 1:2:1 ratio of impaternate females does not hold. Thus when the mother is heterozygous for fused, most of her impaternate daughters are also heterozygous. Most of the homozygotes should be diploid males (Whiting and Speicher, 1935). This example of tychothelytoky in an arrhenotokous species is of interest as showing a possible step toward a thelytokous race.

It will now be of interest to examine forms with haploid arrhenotoky other than *Habrobracon juglandis*, and it will be pertinent to inquire whether there is positive evidence indicating that the *Habrobracon* scheme cannot be universally applied. We may have the possibility of some complementary scheme not involving multiple alleles. Reproductive economy might be low with wastage of fifty per cent of the fertilized eggs (diploid males), as in two-allele crosses of *Habrobracon juglandis*, or good reproductive economy might be attained by some sort of non-randomness in fertilization, by independent pairs of multiple factors, or by some other means to assure that all fertilized eggs should develop into females. Cytologic and breeding data are, unfortunately, indecisive, and genetic evidence is very meager.

We may first consider data from other Hymenoptera and later review the other groups that show haploid arrhenotoky. Two species of *Habrobracon* other than *H. juglandis* have been studied to some extent. In *H. brevicornis*, aberrant males were found (Whiting, and Whiting, 1927) similar to the gynandroid males in *H. juglandis* which gave the hint for complementary sex inheritance. No genetic data were available, but it is probable that these were also gynandroid sex mosaics. B. R. and K. G. Speicher (1940), using a recessive mutation in the same species (rough, similar to rough in *H. juglandis*), obtained from rough females by wild type males, 51 wild type females, 172 rough males, and 34 wild type males. The wild type sons were diploid, as shown by cytologic study, having twenty chromosomes in the spermatocytes instead of ten, the number found in haploid males. These observations may be taken to indicate complementary inheritance.

More extensive data are available for *H. pectinophorae* from the work of Inaba (1939). Diploid males were obtained, identified as in *H. juglandis*, by crossing recessive females with

white eyes or with curved wings to wild-type males. The ratio of females to haploid males was higher in fraternities without diploid males, suggesting three-alleles. Triploid females were obtained, sired by diploid males. Cytological study showed conditions, in general, similar to those in *H. juglandis*, but the chromosomes were evidently somewhat larger and had different spindle fiber positions. Chromosome numbers were as in *H. juglandis*, ten in haploid males, twenty in diploid males and in females, and thirty in triploid females.

These data indicate that cytogenetic conditions in the different *Habrobracon* species are very similar.

In the chalcidoid *Pteromalus puparum*, Dozorceva 1936a, b, c, d; Whiting, 1940b) found a sex-linked trait, red eyes. No fraternities were reported from red-eyes females by wild-type males, such tests for diploid males being lacking. Heterozygous females by red males produced three kinds of fraternities, those with a marked excess of red females, those with a marked deficiency, and those approximating equality. Presumably the first two are from two-allele crosses and the last from three-allele. It is claimed by Dozorceva that there are two types of males, in one of which the sex chromosome is much shorter than in the other, and that females are digamic. As noted above, however, her genetic evidence suggests triple allelels, *xa, xb, xc*, so that the conditions may be similar to those in *Habrobracon*. B. R. Speicher (unpublished), after examination of *Pteromalus puparum* collected on Long Island, N. Y., was unable to confirm the cytological conditions picture by Dozorceva in the Russian material.

The egg parasite *Telenomus fariai* (Lima), a scelionid wasp of the superfamily Proctotrypoidea, has been investigated cytologically by Dreyfus and Breuer (1944). Daughters and sons of the same mother copulate before leaving the host egg shell, so that there is normally very close inbreeding. Unmated females produce only males. Mated females produce bisexual broods, with females in excess of males. Females have twenty chromosomes, males ten. No diploid males were found. According to the authors, one of the large pairs of chromosomes consists of a V-shaped and a J-shaped member. Males are all haploid, and spermatogonia all show the V. However, the large chromosome that appears in the equal first spermatocyte division is a J. The last spermatogonial division is unequal cytoplasmically.

The smaller daughter cell degenerates, while the larger becomes the first spermatocyte. It is assumed that in this division one arm of the V breaks and that the spermatocyte therefore receives a J. The second spermatocyte division is abortive, with a cytoplasmic bud pinched off. Sperms are then all J-bearing. It is further assumed that maturation of the egg is differential, so that the V is always retained. All fertilized eggs then give rise to females, all unfertilized to males. It would be of much interest to have genetic work on *Telenomus* to check with the cytological findings.

Haploidy of the azygous male

The complementary principle of sex determination answers the question, "Why is the haploid a male?" We may now consider the problem, "Why is the male a haploid?" Somatic haploidy has been questioned with respect to the males in many of the arrhenotokous groups. Evidence based on cleavage nuclei is regarded as inadequate (Vandel, 1931a; Schrader and Hughes-Schrader, 1931). We have seen that the drone bee is somatically diploid (in part polyploid) and that this "somatic" diploidy involves most of the germ track.

The difference between the azygote of tychoparthenogenesis and the azygote of haploid arrhenotoky lies in the fact that the former has the diploid type of gametocytes while the latter has the haploid type. The haploid type has become so fixed genetically in the Hymenoptera that spermatogonial diploidy, whether determined by male biparentalism, as in the diploid males of *Habrobracon*, or by regulative doubling, as in the drone honey-bee, fails to result, in the spermatocytes, in the diploid type of mieosis that would produce haploid sperms. The sperms produced are therefore diploid. There is, however, a significant difference in the two cases. Diploid *Habrobracon* males have triploid daughters, because their diploid sperms unite with reduced haploid eggs. The diploidy of the biparental males is "genetic," since their offspring are different from the offspring of haploid males. Diploid drone bees have tetraploid daughters, because the reduced eggs are diploid. Nevertheless, in the bee, eight remains the gametic number because reduction to eight takes place in the oocytes. The diploid drone, therefore, breeds as a haploid although he produces diploid sperms, and the tetraploid queen breeds as a diploid, although she

produces diploid instead of haploid eggs. Eight dyads go to each pole in anaphase and oocyte I and there are eight "monads" in telophase of oocyte II. Whether these "monads" have already become dyads through regulative splitting, and just when the dyads divide to produce a diploid female pronucleus, is a problem for cytological technique and observation. Although somatic diploidy is here extended into the germ track, it does not produce genetic diploidy. If we had been studying genetics rather than cytology, we would not have been aware of this regulative splitting.

The "somatic" diploidy of the drone bee I regard as a secondary type of regulation, subsequent to and probably supplanting the regulation in size of the haploid chromosomes that are seen at least in cleavage and in spermatogenesis of most males in arrhenotokous groups. The drone bee has devised a mechanism extending diploidy into the germ track without surrendering the haploid type of spermatogenesis and his capacity to breed as a haploid. The honey-bee is thus admirably adapted through numerical regulation, so that chromosome numbers in corresponding tissues in males and females are the same. Biparental diploid males of *Habrobracon*, however, are a waste product, of low viability, probably because of their excessively large cells, and producing diploid sperms which are rarely able to fertilize the eggs.

The question asked at the beginning of this section, "Why is the male a haploid?" may be reformulated to read "Why have the males in the groups showing haploid arrhenotoky evolved a haploid type of spermatogenesis instead of retaining the diploid type of the ancestral zygogenetic groups from which they came?"

An answer to this question, which must necessarily be hypothetical, and even somewhat speculative, may be formulated as follows.

The diploid impaternates of tychoparthenogenesis undergo, at some point in their development, delay in cytokinesis relative to chromosome splitting, and thus they become diploid. This may involve a certain disharmony in rhythm between cell body and nucleus. The males of haploid arrhenotoky have had ample time, in the course of evolution, to acquire genes located in the sex differentiating segments, *xa, xb, xc*, etc., which retard chromosome division relative to chromosome growth. Since these genes are recessive, they do not affect the females (sex heterozygotes)

but only the males. Haploidy of the azygous males thus attains regulation of the nucleoplasmic ratio, without introducing disharmony between division of nucleus and of cell. Evolution may here have found a more satisfactory solution of the problem of regulation than occurs as an immediate solution in tychoparthenogenesis. Diploid impaternate female grasshoppers, produced by haploid thelytoky, if isolated for many generations, should be found to have advanced cleavage into meiosis so that the oocyte nuclei would become the first cleavage nuclei. Parthenogenesis would then become diploid. Continued endomitosis would result in polyploidy. This is the evolutionary course of azygosis in the female.

The evolutionary course of azygosis in the male must necessarily be different. The azygotic males of haploid arrhenotoky are selected to breed as haploids. This fact sets a limit to their somatic polyploidy.

ORIGIN AND DISTRIBUTION OF MALE HAPLOIDY

Having discussed the various problems involved in the attainment of male haploidy, we may now consider theoretical possibilities concerning the manner in which this mode of reproduction may have arisen. We have seen that parthenogenetic (female) races and species occur with greater or less frequency in diverse groups. This type of constant parthenogenesis has evidently arisen independently many times. It tends toward polyploidy and, as Vandel (1936) suggests, it probably originates from tychothelytoky. Male haploidy, on the other hand, has evidently become established very infrequently, despite the fact that it is a highly successful mode of reproduction possessing the advantages of amphimixis and involving very large taxonomic groups.

The Chromosome Degeneration Hypothesis

Schrader and Hughes-Schrader (1931) have presented a theory of the attainment of male haploidy based on the gradual inactivation or degeneration of one of the haploid groups of chromosomes. This theory attempts to answer the problems of the acquisition of viability in the haploid state and of the regulation of meiosis in the haploid male.

The theory is based largely on work with the homopteran family Coccidae, the scale insects. In this family there exist diverse cytogenetic conditions which, it is suggested, represent "both

beginning and end stages in the establishment of haploidy." In the genera *Llaveia* and *Protortonia* both sexes are invariably diploid, while in *Icerya* and related genera the females are diploid from fertilized eggs, the males haploid from unfertilized eggs. Intermediate stages may therefore be expected, but in no case has a haploid individual been found within the diploid species. However, there is a series of chromosomal conditions of the diploid males themselves which is supposed to represent intermediate stages in the acquisition of haploid male viability. "The basic phenomenon is a gradual degeneration of one haploid set of chromosomes in the male; the process is reflected chiefly in the behavior of the chromosomes during meiosis, but in its late stages the soma also is affected."

The "degeneration" begins in *Llaveia bouvari*, in which about five per cent of the spermatocytes show asynapsis of one autosome pair, while in the remainder pairing is normal. In *Protortonia primitiva*, no pairing of the ordinary sort occurs; asynapsis affects both autosome pairs. There is no evidence for any selective assortment in segregation.

In *Gossyparia spuria*, one haploid set shows marked heteropycnosis, condensing prior to the other set, segregating selectively together and forming a non-functional sperm. The somatic cells, as well, show clumping of this set which appears first during the late blastula stage of the males. There are no heterochromosomes, but males and females are produced by each mother from zygotes which are not morphologically separable in chromosome content. Conditions are apparently similar in the genera *Pseudococcus*, *Lecanium*, and *Phenococcus*. In *Phenococcus aceri-cola* (Hughes-Schrader, 1935) the later stages, showing disintegration of the condensed group, are especially clear. It is concluded that "a physiological haploidy seems to be in progress of evolution through the inactivation of one of the haploid sets of chromosomes in the male line."

Finally, in the iceryine species, the morphological haploidy of the males is completely established.

In the females of all species studied meiosis is of the orthodox type with normal synapsis, with no heterochromosomes, and with two divisions resulting in haploid nuclei.

It is stated that "this scheme attempts no expression of the phylogenetic relations of the various coccid species involved" but "is rather to be interpreted to the effect that some such development as we have traced is taking place in different groups of coccids, but evidently at different rates, and probably in different ways, in different groups.'

The writer doubts that the three cytological departures from orthodox conditions demonstrated in the male coccids-asynapsis, heteropycnotic clumping, and haploid parthenogenesis—are related phenomena.

Asynapsis, involving failure of crossing-over, is of frequent occurrence in other forms. There may later be contact of homologues, a "touch-and-go pairing," so that normal segregation occurs and inviable zygotic combinations are thus avoided, or, as in the asynaptic mutant type in maize (Beadle, 1930), even this brief approxima-tion of homologues may be lacking and chromo-somes may be assorted irregularly, so that few gametes contain the haploid set. In none of these cases does there appear to be any association between asynapsis and chromosome degeneration.

There likewise appears to be no association between haploid parthenogenesis and chromosome degeneration. No specific set of chromosomes is "lost" in the formation of haploid males, since any of the possible combinations of chromosomes (or of genes) present in the diploid mother may be transmitted to her haploid sons.

The degenerative processes noted in the male coccids of the Gossyparia type may be compared with conditions in the fly *Sciara* (Metz, 1938). Here a complete and perfectly normal chromosome set received by a male from his mother will, if transmitted to his son, be lost in the monocentric mitosis of the spermatocytes of his son. Just what chromosomes, whether paternal or maternal, are lost in *Gossyparia* is not known, for no genetic factors have been followed to tag them as has been done in *Sciara*.

In *Sciara* all zygotes are similar at the beginning, and sex is determined by differential loss of sex chromosomes in cleavage. This loss depends upon the genetic constitution of the mother which may be a male-producer or a female producer; or, in certain races, both sexes may occur in the same brood. Comparison may further be made with conditions in the isopod crustacean *Trichoniscus provisorius* (Vandel, 1938), in which, as in *Sciara*, there are (monogenic) races with unisexual broods having female-producing (thelygenic) females and male-producing (arrhenogenic) females, and there are (deuterogenic) races with bisexual broods.

(The terms used here indicating sex of offspring imply a special type of zygogenetic reproduction rather than parthenogenetic). Whether in *Trichoniscus* there is chromosome elimination or clumping in cleavage is not indicated, but the breeding data here suggest interesting comparisons with the cytological and breeding data on *Gossyparia* and with the cytogenetic conditions in *Sciara*. Evidence suggests that certain other invertebrates may likewise possess a comparable mode of zygogenetic reproduction showing aberrant sex ratios.

Review of Groups Showing Male Haploidy

In the introductory part of this paper there are listed seven groups of animals with haploid males. The Hymenoptera have already been discussed in some detail, and it is now in order to review the others because of their implications for the evolution of male haploidy.

Iceryini

In the iceryine coccids cytological conditions are very clear. The females have four chromosomes, the males two (Hughes-Schrader, 1930). No diploid males have been found. Unmated females produce males only, mated females produce both males and females. In the cottony cushion scale *Icerya purchasi* (Hughes-Schrader, 1927) true females are lacking, but their place is taken by hermaphrodites which presumably evolved from females. These hermaphrodites may produce further hermaphrodites, either by self-fertilization or by mating with males, but since males are infrequent and the eggs are developed in such a way that they are surrounded by sperms from the same individual, self-fertilization is the rule. According to the complementary hypothesis, only two sex alleles would be involved, and the alternatives are presented of considerable reproductive wastage or some type of non-randomness in distribution of sex factors. "Coincident with or slightly before the first appearance of haploid nuclei in the hermaphrodite gonad, degeneration of certain germ cell nuclei occurs" (Hughes-Schrader, 1927). Whether this is in any way selective is not clear. There is apparently no marked mortality of eggs subsequent to fertilization, but the possibility is not excluded that death of the homozygotes, diploid males, may occur at some postembryonic stage. This highly successful species may be tending, through hermaphroditism and

self-fertilization, toward the eventual complete elimination of males and may be getting on very well in spite of a possible wastage of fifty percent of its eggs.

Haploid males have not been found in other groups of coccids, among which the species are either zygogenetic or parthenogenetic (female). Sex determination in some groups (*Gossyparia*, etc.) may be of the *Sciara* type. In others (*Llaveia*, etc.) it is of the usual XY-male backcross type (Schrader and Hughes-Schrader, 1931).

Aleurodidae

"White-flies" of the homopteran family Aleurodidae are pests in greenhouses and in fruit orchards. The group has been much neglected by taxonomists, and it is probable that the majority of the species is as yet undescribed. In many species males are not known. Zygogenetic species have not been found. *Aleurotulus nephrolepidis* (Thomsen, 1927) is purely thelytokous. Morrill and Back (1911) state that virgin females of *Dialeurodes citri*, the citrus white-fly of the southern United States, produce males only. Thomsen (1927) reports that in *Aleurodes proletella* there is arrhenotoky, and that mated females produce both males and females. All eggs give off two polar bodies, and the unfertilized remain haploid.

In *Trialeurodes vaporariorum* (Schrader, 1920, 1926; Thomsen, 1927) there are two races. An arrhenotokous race occurs in America, in England, and in Denmark. A race reproducing by indefinite thelytoky and with spanandric males occurs in England and in Denmark. Thelytokous females may be mated with males of the arrhenotokous race or with the spanandric males, but it is supposed that the eggs are not fertilized. Maturation is apparently the same in the eggs of both races, with two polar bodies given off and chromosome number reduced from twenty-two to eleven. In the thelytokous race the eleven chromosomes of the reduced egg nucleus probably divide before the first cleavage giving the diploid number, for in the two-nucleus stage of cleavage the chromosome number is twenty-two. Regulation of this type is theoretically reconcilable with the *Habrobracon* principles of sex determination, if it be assumed that the thelytokous race differs from the bisexual due to a chromosomal rearrangement. As I have stated in a previous publication (Whiting, 1943), "homozygous females might be produced if x were duplicated either by translocation or by unequal

crossing-over so that $xa/xb + 2A$ would become $xa\ xb/xa\ xb + 2A$. Theoretically, haploid females $xa\ xb + 1A$ would then be possible. That such have not been found is not surprising, however, since thelytokous forms tend to become polyploid rather than haploid."

Micromalthus

Among the beetles there are several thelytokous species and races, especially in the Curculionidae (Székessy, 1937; Milliron, 1939; Suomalainen, 1940). Most of these are polyploid. I have found no reference to tychoparthenogenesis in the Coleoptera. Since beetles are of the XY-male type, we might expect haploids to be female.

In males of the aberrant beetle *Micromalthus debilis*, however, Scott (1936) was able to establish somatic haploidy from examination of blastoderm nuclei and tissue of the sternal gland. *Micro malthus*, the only representative of the family-Micromalthidae, is the only example of haploidy reported in beetles and also the only beetle showing paedogenesis. Spermatogonial divisions are regular, showing ten chromosomes. The aberrant spermatocytes have already been mentioned. The life history is complex (Scott, 1938), with hyper-metamorphic larval stages and with paedogenesis suggesting the cecidomyid flies *Miastor* and *Oligarces*. Normally the larval mother of the adult male deposits a single egg, from which there hatches a "metrophagus" larva. This larva, after devouring its mother, pupates and then ecloses as an adult. Scott (1941) was able to show that if the egg is removed before it hatches, the larval mother will then produce female offspring viviparously. Sex is therefore determined in the process of oogenesis. Normally, females are produced viviparously by paedogenetic larvae. Cleavage nuclei in female-producing eggs have twenty chromosomes. Continuous paedogenesis apparently maintains the species, and it is not known whether the adults reproduce.

No sex chromosomes are differentiated cytologically. The diploids, larvae and the adult female, may be heterozygous for sex as in *Habrobracon*, xa/xb. Haploid parthenogenesis would then produce males, xa and xb.

Thysanoptera

Minute insects known as thrips belong to the Thysanoptera, an order of uncertain affinities. Thelytoky occurs as the usual mode of reproduction in several species, which are members of different families in both suborders. Collections show wide deviations in sex ratios of the bisexual species and differences occur in different seasons of the year suggesting arrhenotoky. Of two species of *Anthothrips*, *niger* is thelytokous, *verbasci* is arrhenotokous, as shown by breeding tests (Shull, 1917), and collections indicate that *Chirothrips manicatus* is arrhenotokous. Breeding tests have likewise shown arrhenotoky in *Frankliniella insularis* (Davidson and Bald, 1931). There is some evidence that bisexual generations may alternate with thelytokous in *Physopus pallipes*, but Vandel (1931a) considers that two different races may exist in this species. There seems to be no evidence that males are produced bisexually, and since arrhenotokous types occur in both suborders, parthenogenesis may exist in all species of the order, with some thelytokous, others arrhenotokous, and with still others having racial types differing in this respect.

Trochelminthes

With the exception of a single family, the Seisonidae, which are marine parasites on the crustacean *Nabalia*, the males of rotifers appear at certain periods only and are presumably impater-nate and haploid. The phylum Trochelminthes is characterized by irregular heterogony or alternation of generations (Shull, 1929; Whitney, 1929). Females are of two types, gamic and agamic. All eggs produced by agamic females give rise to females parthenogenetically and cannot be fertilized even though mating may take place. Males appear at certain times and much work has been done in attempts to determine the various causes of male production. In addition to genetic differences in strain or species, factors are temperature, nourishment, and chemical composition of the water. Since agamic females cannot produce males, these factors do not cause the production of males directly, but rather the production of gamic females. If gamic females do not mate, their eggs develop immediately into males by haploid parthenogenesis. Fertilized eggs do not develop for a considerable time. They accumulate reserves of nourishment and a thick shell to tide the species over unfavorable conditions. Eventually they give rise to females, which are always agamic, but the next generation may consist of gamic and agamic females. Eggs of agamic females give off but one polar body and

produce females by diploid parthenogenesis. Eggs of gamic females form two polar bodies whether they are fertilized or not.

Some rotifers have but one sexual period a year, usually in the spring, others have one in the spring and a second in the fall, while still others have many sexual periods, the number of which may vary according to locality. Males are unknown in the Bdelloida and in species of several other groups, so that these forms reproduce by constant thelytoky.

The more primitive rotifers are crawling types, thus showing some resemblance to their possible ancestors, the Turbellarians (Wesenberg-Lund, 1923, 1930). In these rotifers the males are as large in size as the females. Evolution seems to have been in the direction of planktonic habit and of smaller size of males, with correspondingly greater numbers produced in the sexual period. There is no parasitism of the male on the female, but structural degeneration is carried so far that the male may be nothing but a sperm sac, surrounded by protoplasm bearing a tuft of cilia which enables it to reach the female. The sperms in this case are already fully formed before the male emerges from the egg, and the male mates immediately after hatching. Hermaphroditism is lacking in the phylum. In the family Notommatidae, regarded as the primitive type from which most, if not all, of the other families may be derived, very few males are known, but these are in size similar to the females.

The Seisonidae, mentioned above, are said to depart from the rotifer type, in that males are as abundant as females and can be obtained at all seasons. They are supposed to be produced bisexually, and it is stated that there is no parthenogenesis in the group. The single reference to spermatogenesis (Illgen, 1914) does not indicate whether the males are actually diploid and produced bisexually. If this be true, it suggests that a group which has attained haploid arrhenotoky may revert to the usual method of sexual reproduction. However, the family is somewhat isolated taxonomically, is primitive in the sense that the males are equal in size to the females, so that its origin may be separate from that of the other rotifers. A third possibility is that this family has retained haploidy but has given up heterogony. Without breeding tests or cytological study of the spermatocytes, it cannot be stated that Dzierzon's Law does not apply to this group.

Acarina

The Acarina, mites and ticks, are the only arachnids in which parthenogenesis has been proved with certainty. Sokoloff (1934) investigated spermatogenesis in six species of the Parasitidae (Gamasidae) showing tetrads with normal division. André (1935) discusses this family and concludes that, despite several supposed cases of parthenogenesis (thelytoky). none has been proved.

André (1935) also discusses the ticks (Ixodoidea) and concludes that thelytoky has been established only in Amblyomma. In Hyalomma aegyptium, Tuzet and Millot (1937) show a large body in the first spermatocyte which they interpret as a heterochromosome. It is probably a sex chromosome but is not illustrated in their drawing of spermatocyte II and should be further investigated. In Argas columbarum, Oppermann (1935) shows a large XY pair, in addition to twenty-four autosomes, in the spermatogonia. The autosomes synapse to form twelve tetrads which divide in the usual manner. Division of spermatocyte I is equational for XY, and division of spermatocyte II is reductional. In addition to twenty-four autosomes, the two X-chromosomes are shown in the oogonia.

André (1935) regards the observations made on Syringobia chelopus of the Sarcoptidae as inexact and as not establishing thelytoky. In the Cheyletidae, there have been several supposed cases, but only one proven. Cheyletus eruditus Schr. is regarded as thelytokous, but Cooper (1937) states that the possibility of its being a self-fertilizing hermaphrodite has not been excluded, and the same applies also to the tick Amblyomma dissimile Koch.

Evidence for arrhenotoky in mites is much more convincing. Putnam (1939) states that unmated females of the plum nursery mite (Phyllocoptes fockeui), of the Eriophyidae, produce males only. Pätau (1934, 1936) has shown that the grain itch mite Pediculoides ventricosus is arrhenotokous, with three chromosomes in the spermatogonia. He has investigated cytological conditions in the egg. The three bivalent chromosomes of the oocyte were followed from pachytene through the growth stage and appear as either rod or ring tetrads in metaphase. There are two meiotic divisions. In early cleavage telophases, the chromosomes form separate karyomers. Pätau

discusses the application of the *Habrobracon* scheme of sex determination, but at the time his paper was written he did not have available the multiple allele principle.

Cooper (1937, 1939) has shown that the grass mite, *Pediculopsis graminum*, is arrhenotokous. His cytological studies revealed conditions very similar to those in *Pediculoides*, with three as the haploid number, six as the diploid, and with karyomeres formed by chromosomes in cleavage. *Pediculoides* and *Pediculopsis* are very closely related genera of the family Tarsonemidae.

Schrader (1923) showed arrhenotoky in the "red spider" *Tetranychus bimaculatus*, with three chromosomes in spermatogenesis, and with three pairs of chromosomes in the female forming tetrads in oocyte I. Cleavage is shown in the unfertilized egg, with three chromosomes, and in the fertilized, with six that form karyomerites in the resting stage. Other species of Tetranychidae mentioned as arrhenotokous are *Tetranychus telarius*, *lintearius*, and *ulicis*.

The Acarina are exceedingly diversified in modes of life, structure, and developmental conditions. There is great disparity in the method of grouping the various families, so that selected species may be far separated or not, according to the system adopted. If the arrangement suggested by Ewing (1934) be followed, placing the Parasitoidea and the Ixodoidea together in the Mesostigmata, which is one of the twelve suborders, then the forms reported as zygogenetic, having normally diploid biparental males, will be grouped together. How many other mites are also zygogenetic, and how widely spread is arrhenotoky, remains to be investigated. Possibly arrhenotoky has arisen and become established but once in the order, which may suggest that the primary phyletic division of the Acarina should be on that basis.

Thelytoky appears to have developed many times and in species of diverse acarine groups. Its incidence probably has no relationship to the more general and basic method of amphimixis, whether that be haploid arrhenotoky or zygogenesis. As for the method of sex determination, the XY shown by Oppermann for *Argas* is the only convincing case. Other investigators seem not to have been interested in this problem, except Sokoloff, who fails to find sex chromosomes in the Parasitidae (Gamasidae).

General comparisons

Male haploidy as a mode of amphimixis appears to have arisen in different groups of Metazoa from the more usual zygogenetic mode, in which males as well as females are normally diploid and biparental. If we except the very aberrant beetle *Micromalthus*, there is no evidence at present available to show that this change has occurred independently more than five or six times. One of these took place in an ancestral rotifer and may now involve the entire phylum Trochelminthes. Possibly it was a single ancestral mite that gave rise to a stem with many arrhenotokous branches, while another conservatively retained zygogenesis. Whether male haploidy has arisen independently more than once in the Acarina is left for future experiments and observations to decide. Evidence is as yet weak, but there appears to be nothing to prove the existence of a zygogenetic thrips, so that we may imagine a single ancestor of the whole order Thysanoptera as having departed from the mode of his now unknown relatives. The same applies to the Hymenoptera, but here we may speak more positively, in view of the wide scatter and considerable amount of breeding data and cytological study devoted to the order.

Of the two homopteran families showing male haploidy, the aleurodids have no known zygogenetic species. Among the coccids, on the other hand, of the seven subfamilies only the Monophlebinae include known arrhenotokous species. These make up the tribe Iceryini but are absent from the Llaveiini, which are all diploid, and the males of which have XO chromosomes. According to one theory, the aleurodids have been derived from the coccids. They may have descended along with the iceryines from some common ancestor which adopted male haploidy.

This would total but five known independent phyletic arrhenotokous pedigress, with *Micromalthus* as a lone and inconspicuous sixth. Doubtless, other instances may be found, but the ratio with respect to constant thelytoky is likely to remain very low, for new examples of the latter are frequently appearing in the literature.

The change to haploid arrhenotoky has evidently occurred very rarely and has come to involve large taxonomic groups as a stable mode of reproduction. Whether male haploidy may ever revert to zygogenesis is not known. As a test

for this possibility, search for normally diploid males should be made in arrhenotokous groups.

The change to thelytoky has occurred and is occurring a great many times in nature, and involves only single scattered species or races. Their adoption of this mode is probably relatively recent, as evidenced by their isolation and by the occurrence of spanandric males among them. Constant thelytoky involves the denial of the advantages of amphimixis and no large or successful group has evolved with this handicap. Only by heterogony, the alternation of a bisexual with one or more parthenogenetic generations, can thelytoky be widely incorporated as a permanent mode of life. Thus thelytoky may be alternated with haploid arrhenotoky, as in the rotifers and the gall-wasps; and thus thelytoky, and in this case also diploid arrhenotoky, may be alternated with a zygogenetic bisexual generation, as in aphids, phyloxerans, and cladocerans. In these three groups a generation of impaternate diploid males and females alternates with one or more generations of agamic females.

Race-hybrid Hypothesis

Tychothelytoky in groups of the XY-male type or tychodeuterotoky in groups of the WZ-female type may be regarded as the most primitive form of natural parthenogenesis. It appears merely as a breakdown of the block to post-meiotic mitosis which has been established in animals but which is absent from plants. Being haploid in origin, it encounters the hazards both of low chromatin content and of recessive lethals, and must undergo both quantitative regulation and stringent selection, respectively.

Parthenogenetic (female) races and species have probably originated from tychothelytoky (1) by oogonial tetraploidy, (2) by advancing cleavage into meiosis so that an oocyte nucleus becomes a cleavage nucleus, (3) by parthenogamy from a polar nucleus, (4) by endomitosis following reduction, or (5) by parthenogamy of cleavage nuclei. The first three of these alternatives involve diploid parthenogenesis with zygosis of the impaternate offspring. The last two involve haploid parthenogenesis with production of a diploid azygote. Chromatin rearrangements, genic mutations, and frequently polyploidy may produce such changes that crossing with the bisexual form becomes ineffective. Sterility and other deviations of the spanandric males from their ancestral type are probably due to these cytogenetic shifts, which modify the original genic balance of the sex chromosome in relation to the autosomes.

At first thought, it may seem that tycho-arrhenotoky should logically furnish a first step toward constant arrhenotoky, just as tychothelytoky appears to be the first step toward constant thelytoky. It might be expected that tycho-arrhenotoky should occur in groups with WZ-females, if lack of Z should prove lethal. Possibly such a condition may be found among the primitive Lepidoptera or among the related Trichoptera, if these have not acquired by duplication an "autosomal" Z which could render WW females viable. These insect orders, however, constituting a very large and flourishing WZ-female tree, have given rise to no known arrhenotokous branches. If haploid males have various modifications of the factor Z, male haploidy should arise from WZ-female stock rather than from XY-male stock. As regards the mites, coccids, and *Micromalthus*, the cases in which close zygogenetic relatives of the arrhenotokous branches are known, these relatives are of the XY-male type. The suggestion that male haploidy involves female digamety and is thus related to the WZ-female type also meets with the difficulty that through protection of W by Z there has come about a degeneration of the former, so that "backcrossing" becomes fixed as long as WZ functions as the sex differentiator.

The origin of male haploidy through tycho-parthenogenesis appears improbable, because few offspring are produced, and these must cross with the zygogenetic stock, thus dispersing the parthenogenetic tendency. A theory involving repeated and extensive race hybridization seems more probable, as furnishing abundant material for natural selection.

Probably modifications within the X-chromosome or within some autosome have occurred, to produce a multiple allelic series and the complementary type of sex determination associated with haploid males. The spanandric males of geographic thelytoky presumably have chromosomes that have undergone modification during their period of protection in the parthenogenetic stock. However, the infrequency and predominant sterility of such males would render infinitesimal the chance of success for any of their few progeny surviving the stringent selection leading toward the goal.

What is needed for the evolution of male haploidy is a large population with a strong tendency toward parthenogenesis and with modified chromosomes and normal chromosomes freely recombining and crossing over and thus originating new types. Such a population might be found in the borderlands between the ranges of an ancestral zygogenetic species and of its thelytokous offshoot. To be specific, let us imagine some ancestral hymenopteran species, some protosiricid of the Early Jurassic for example, in which the zygogenetic stock has already given rise by tychothelytoky to a parthenogenetic (female) scion. The latter, breeding in an isolated territory, has multiplied over a period long enough to accumulate several genetic modifications, but still brief enough for retention of crossability with the parental stock. Now, with increasing population, the areas of stock and scion come to overlap and crossing occurs, at first between the males of the zygogenetic stock and the parthenogenetic females, then between the former and the hybrid females, and later between the members of the segregating fraternities. Thus there is furnished abundant opportunity for cytogenetic recombinations. In this population we might expect great numbers of inviable types to be produced and, among the small proportion of viables, there should be many sterile intersexes. Arrays of genetic types would vary from those needing syngamy to initiate cleavage, at one extreme, to parthenogenetic forms at the other, and from femaleness to maleness.

The viable fertile types should be stabilized at three modes, (1) zygogenesis of both sexes, (2) parthenogenesis of females with males eliminated, (3) zygogenesis of females, parthenogenesis of males. Theoretically, fertile hermaphroditism might be a fourth mode, but this has not been found as a primitive condition in any of the groups which we are considering. Modes (1) and (2) would be reversionary. Mode (3) would furnish the basic material from which the stable arrhenotokous type might evolve. This third type would be produced from combinations in which factors for maleness were recessive, and genes determining parthenogenesis were present. Thus the zygotes would tend to include the females, while the azygotes would be male.

With multiple factors for sex segregating independently, there would be considerable reproductive wastage because of sterile intersexuality.

This would tend, by selection, toward a concentration of the effective sex genes into a single closely linked group.

Regulative somatic diploidism of the impaternate males might, for a time, permit normal (diploid) meiosis in spermatogenesis, but since the azygotic embryos would originate as haploids, there should be gradual selection for an increase in chromosome size as a regulative process. This should tend to retard numerical regulation so that, eventually, the entire embryo might become haploid. Since tissues of the germ track are relatively undifferentiated, the spermatogonia especially should retain the initial haploidy of the embryo. The spermatocytes, furnished with the haploid set of chromosomes, would then be faced with the necessity of modifying their type of division, and these modifications should be perfected and standardized by selection.

Genes for enlarged cell size should tend to be concentrated along with the genes for maleness and, like them, should be recessive. Thus the haploid males should come to have cells approximating in size the cells of the females, but the diploid males should have much larger cells, for, to the homozygous recessive genes, there should be added the double amount of chromatin. Diploid males should then be reduced in viability. In *Habrobracon*, it is known that the cell size of diploid males is abnormally large, and there is some evidence that among diploid males larger cell size is associated with higher mortality.

As reduction in spermatocyte meiosis initiated by selection in the haploid males becomes characteristic of the species, the diploid males might also be rendered sterile, as they are in *Habrobracon*. Fixation of the meiotic condition adapted to haploid males should effectively eliminate the few surviving diploid males from reproduction.

Evolution of the sex differentiating segment, called the *x* factor in *Habrobracon*, must have come about by reduction in crossing-over within it and by mutation and the selection of minor factors, so that the various alleles, *xa*, *xb*, *xc*, etc., should come to produce a similar phenotype. Genes governing secondary, as well as primary, sex differences must lie in this chromosome segment, the genes for male traits acting as recessives.

Additional alleles in the series might be brought about as follows: a new allele might originate as some repeat of a local duplication, which would at first give a phenotype somewhat different from the

preceding, but this should later be perfected by minor mutations and selection. Whatever disadvantage a new allele might have, because of its production of a divergent phenotype, would tend to be compensated by a selective advantage gained by increasing the number of alleles in the population. Thus in a three-allele population, with the older perfected alleles, xa and xb, relatively more numerous, these alleles are at a disadvantage because half of the fertilized eggs are wasted (inviable or diploid males), but the matings involving the third allele, xc, are much more fecund, even if it be supposed that the females xa/xc and xb/xc and the males xc are somewhat divergent or defective.

In species that are highly differentiated sexually, there may obtain much genetic diversity which does not express itself phenotypically. In this, also, genotypic sex divergence may be greater than genotypic sex convergence without becoming evident. In other words, intersexuality is more obvious than supersexuality, as has been demonstrated in many Lepidoptera, *Lymantria* for example. Seiler's WW females, also, are not only viable but apparently non-separable phenotypically from WZ females. Doubling the genotypic divergence from males, ZZ, produces no visible difference.

It is of interest to note that in all the groups characterized by haploid arrhenotoky, there is a very high degree of sex disparity. The gonadic hermaphroditism of the coccid *Icerya purchasi* appears to be, not a step toward intersexuality, and certainly not in any way primitive, but a secondary modification of a highly differentiated female type, enabling the species to maintain itself and, at the same time, dispense with its highly differentiated males. The sex alleles in haploid arrhenotoky may then differ genically to a considerable extent among themselves without producing perceptible differences. This should aid both in the inception of male haploidy and in the evolution of new alleles in arrhenotokous species.

No phenotypic differences caused by the different sex alleles of *Habrobracon* have yet been demonstrated with certainty. In one inbred stock the males had more antennal segments and the females fewer than in another inbred stock (Whiting, 1943). This indicates the association of genic differences governing antennal segments with the x-factor. The apparent unidirectional feminization in gynandroid mosaic males suggests a difference in autonomy of similar structures determined by different alleles.

It is suggested that the various steps outlined above may have brought about the stable condition of amphimixis known as haploid arrhenotoky, not only in the Hymenoptera, but also, at an earlier or later period, in the evolution of the other five or six groups mentioned.

SUMMARY

Among invertebrate animals belonging to seven different groups, a mode of reproduction has been established in which males are haploid, developing parthenogenetically from reduced unfertilized eggs. Five problems involved in the attainment of male haploidy are considered.

(1) Induction of parthenogenetic development in eggs is regarded merely as a breakdown of the block to post-meiotic mitosis which is normally established in animals but is absent from plants.

(2) Viability of the azygote resulting from this initial parthenogenesis is attained by a regulative doubling of chromosome number that corrects the nucleoplasmic ratio, and by selection against recessive lethal factors. The few surviving azygotes are diploid with normally diploid meiosis. Because of their infrequent and scattered occurrence their production has been called tychoparthenogenesis.

(3) Meiosis in the haploid male has been modified in different ways in different groups. This has come about by a selective process when the spermatocytes have received a haploid set of chromosomes.

(4) Sex determination in these groups is regarded as complementary, depending upon a single series of multiple alleles having similar effects phenotypically. Each allele is considered a chromosome segment containing many genes, dominant female-producing and recessive male-producing. Females are heterozygous, normal haploid males are recessive. The homozygous recessive combinations (infrequent because of multiple allelism) are inviable or may occasionally develop as diploid males.

(5) Haploidy of the azygous males may be defined as having the haploid type of spermatogenesis, with chromosome reduction lacking. Somatically, these males may be haploid, at least in early developmental stages, or they may have secondary diploidy or polyploidy, as in the drone of

the honey bee, which begins as a diploid because of precocious splitting of the ootid monads.

The hypothesis of the gradual degeneration of one set of chromosomes in the attainment of haploid male viability and in the regulation of meiosis, advanced by Schrader and Hughes-Schrader (1931) on the basis of their studies of coccids, is questioned. It is considered that their postulated stages in chromosome degeneration (asynapsis, heteropycnosis, and male haploidy) are independent phenomena.

Male haploidy is apparently characteristic of the entire insect order Hymenoptera, and probably of thrips and rotifers. A single beetle, *Micromalthus*, has haploid males. It is suggested that the primary phyletic division of the mites, Acarina, may be made on this basis. Among the coccids, the tribe Iceryini are characterized by male haploidy, and it is possible that the related homopteran family Aleurodidae may be derived in common with this tribe.

According to Vandel (1936) parthenogenetic (female) races and species have originated from tychoparthenogenesis by extension of the process of chromosome doubling into meiosis, so that the type of parthenogenesis becomes diploid from the beginning, and a fixed mode of reproduction. Further doubling lies at the basis of the polyploidy characteristic of many parthenogenetic races.

A review and discussion is given of some of the recently published cases of tychoparthenogenesis and of the fixed parthenogenesis of unisexual (female) races and species.

As a possible explanation of the origin of male haploidy, an hypothesis is suggested of hybridization between a normal bisexual race and a parthenogenetic (female) race in which the chromosomes have become modified. Among the segregating types resulting from this hybridization there should be azygous males. Nucleoplasmic regulation in these males should be gradually modified by an increase in the size of chromosomes, so that the haploid number might be retained into progressively later embryonic stages, especially in the germ track. In this way meiosis of the spermatocytes should be changed from the diploid to the haploid type.

LIST OF LITERATURE

ANDRÉ, M. 1935. La parthénogenèse chez les acariens. *Ann. Sci. nat. Zool.*, 18: 103–118.

ASTAUROV, B. L. 1940. Artificial parthenogenesis in the silk-worm (*Bombyx mori* L.). *Izdatel'stvo Akad. Nauk USSR*, Moscow, 240 p.

BADONNEL, A. 1938. Sur la biologie de *Psyllipsocus ramburi* S. L. (Psocoptera). *Bull. Soc. Ent. France*, 43: 153–158.

BEADLE, G. W. 1930. Genetical and cytological studies of mendelian asynapsis in *Zea mays*. Paper #172, Dept. Plant Breeding, Cornell Univ., Ithaca.

BLEIER, H. 1933. Die Meiosis von Haplodiplonten. *Genetica*, 15: 129–176.

BRIDGES, C. B. 1925. Sex in relation to chromosomes and genes. *Amer. Nat.*, 59: 127–137.

——. 1930. Haploid *Drosophila* and the theory of genic balance. *Science*, 72: 405–406.

BRUES, C. T. 1928. A note on the genus *Pelecinus*. *Psyche*, 35: 205–209.

CAPPE DE BAILLON, P. 1939. Sur la parthénogenèse des Tettigonidae (Orthopteres). *C. R. Acad. Sci. Paris*, 208: 463–465.

——, and DE VICHET, G. 1939. La cytologie des males et l'hypothese du rajeunissement periodique de la race par la fécundation chez les Phasmes à parthénogenèse constante. *C. R. Acad. Sci. Paris*, 209: 525–527.

——, and ——. 1940. La parthénogenèse des espèces du genre *Leptynia* Pant (Orthopt. Phasmidae). *Bull. biol. Paris*, 74: 43–87.

COOPER, K. W. 1937. Reproductive behavior and haploid parthenogenesis in the grass mite, *Pediculopsis graminum* (Reut.) (Acarina, Tarsonemidae). *Proc. Nat. Acad. Sci. Wash.*, 23: 41–44.

——. 1939. The nuclear cytology of the grass mite, *Pediculopsis graminum* (Reut.) with special reference to karyomerokinesis. *Chromosoma*, 1: 51–103.

CREIGHTON, M. 1938. Parthenogenesis in *Chorthippus curtipennis*. *Genetics*, 23: 145.

DAVIDSON, J., and BALD, J. G. 1931. Sex determination in *Frankliniella insularis* Franklin (Thysanoptera). *Austral. J. exp. Biol. med. Sci.*, 8: 139–142.

DODDS, K. S. 1938. Chromosome numbers and spermatogenesis in some species of the hymenopterous family Cynipidae. *Genetica*, 20: 67–84.

DONCASTER, L. 1916. Gametogenesis and sex determination in the gall-fly, *Neuroterus lenticularis*. Part III. *Proc. Roy. Soc. B.*, 89: 183–200.

DOZORCEVA, R. L. 1936a. Chromosome morphology in *Pteromalus puparum*. *Bull. (Isvestia) Acad. Sci. URSS*, Ser. Biol., 1209–1221.

——. 1936b. On determination of sex in *Pteromalus puparum*. *Bull. (Isvestia) Acad. Sci., URSS*, Ser. Biol., 1223–1233.

——. 1936c. Sex-linked heredity in *Pteromalus puparum*. C. R. (*Doklady*) *Acad. Sci. URSS*, 3: 335–338.

——. 1936d. The morphology of chromosomes in the ichneumon *Pteromalus puparum*. C. R. (*Doklady*) *Acad. Sci., URSS*, 3: 339–342.

DREYFUS, A., and BREUER, M. E. 1944. Chromosomes and sex determination in the parasitic hymenopteron *Telenomus fariai* (Lima). *Genetics*, 29: 75–82.

DZIERZON, J. 1845. *Eichstädte Bienenzeitung*, 1: 113.

EWING, H. E. 1934. The suborders and superfamilies of Acarina. *Proc. Helminth. Soc. Wash.*, 1: 64–65.

FANKHAUSER, G. 1938. Sex differentiation in a haploid salamander, *Triton taeniatus* Laur. *Jour. exp. Zool.*, 79: 35–49.

GOLDSCHMIDT, R. 1917. On a case of facultative parthenogenesis in the gypsy-moth *Lymantria dispar* L. with a discussion of the relation of parthenogenesis to sex. *Biol. Bull.*, 32 : 35–43.

GREENSHIELDS, F. 1936a. Chromosomal relationship between males and females in Hymenoptera Symphyta. *Nature, Lond.*, 137: 662, 746.

——. 1936b. Tetraploidy and Hymenoptera. *Nature, Lond.*, 138: 330.

HUGHES-SCHRADER, S. 1927. Origin and differentiation of the male and female germ cells in the hermaphrodite of *Icerya purchasi* (Coccidae). *Z. Zellforsch.*, 6: 509–540.

——. 1930. The cytology of several species of iceryine coccids with special reference to parthenogenesis and haploidy. *Jour. Morph. Physiol.*, 50: 475–495.

——. 1935. The chromosome cycle of *Phenococcus* (Coccidae). *Biol. Bull.*, 69: 462–468.

ILLGEN, H. 1914. Zur Kenntnis der Spermatogenese und Biologie bei *Seison grubei* Claus. *Zool. Anz.*, 44: 550.

INABA, F. 1939. Diploid males and triploid females of the parasitic wasp *Habrobracon pectinophorae* Watanabe. *Cytologia*, 9: 517–523.

KAWAMURA, T. 1939. Artificial parthenogenesis in the frog. II. The sex of parthenogenetic frogs. *J. Sci. Hirosima Univ.* B (Div. 1), 7: 39–86.

KING, R. L., and SLIFER, E. H. 1933. Genetic analysis of parthenogenesis in Nabours' grouse locusts. *Amer. Nat.*, 67: 80–81.

——, and ——. 1934. Insect development VIII. Maturation and early development of unfertilized grasshopper eggs. *J. Morph.*, 56: 607–619.

LIGHT, S. F. 1944. Parthenogenesis in termites of the genus *Zootermopsis*. *Univ. Calif. Pub. Zool.*, 43: 405–412.

MATTHEY, R. 1941. Etude biologique et cytologique de *Sago pedo* Pallas (Orthoptères-Tettigonidae). *Rev. Suisse Zool.*, 48: 91–141.

METZ, C. W. 1938. Chromosome behavior, inheritance and sex determination in *Sciara*. *Amer. Nat.*, 72: 485–520.

MILLER, H. M. 1931. Alternation of generations in the rotifer *Lecane inermis* Bryce. *Biol. Bull.*, 60: 345–381.

MILLIRON, H. E. 1939. A parthenogenetic new species of the genus *Perimegatoma* Horn (Coleoptera; Dermestidae). *Ann. Ent. Soc. Amer.*, 32: 570–574.

MORRILL, A. W., and BACK, E. A. 1911. White flies injurious to citrus in Florida. *U. S. Dept. Agri., Bur. Ent. Bull.*, 92: 57–94.

MULLER, H. J. 1918. Genetic variability, twin hybrids and constant hybrids, in a case of balanced lethal factors. *Genetics*, 3: 422–499.

NABOURS, R. K. 1929. *The genetics of the Tettigidae*. The Hague: Martinus Nijhoff.

——. 1930. Induced parthenogenesis and homozygosis. *Science*, 72: 502–503.

NACHTSHEIM, H. 1913. Cytologische Studien über die Geschlechtsbestimmung bei der Honigbiene (*Apis mellifica* L.) *Arch. Zellforsch.*, 11 : 169–241.

OEHNINGER, M. 1913. Über Kerngrössen bei Bienen. *Verh. phys.-med. Ges. Würzburg* (n. F.), 42: 135–140.

OHMACHI, F. 1929. Preliminary note on a case of facultative parthenogenesis in *Loxoblemmus frontalis* Shir. (Gryllidae). *Proc. Imp. Acad. Tokyo*, 5: 367–369.

OPPERMANN, E. 1935. Die Entstehung der Riesenspermien von *Argas columbarum* (Shaw) (reflexus F.). *Z. mikr. anat. Forsch.*, 37: 538–560.

PARMENTER, C. L. 1940. Chromosome numbers in *Rana fusca* parthenogenetically developed from eggs with known polar body and cleavage histories. *J. Morph.*, 66: 241–260.

PÄTAU, K. 1934. Ein neuer Fall haploider Parthenogenese. *Naturwiss.*, 22: 648–649.

——. 1936. Cytologische Untersuchungen an der haploid-parthenogenetischen Milbe *Pediculoides ventricosius*. (Newp.). *Berl. Zool. Jb.*, 56: 277–322.

PATTERSON, J. T. 1928a. Sexes in the Cynipidae and male-producing and female-producing lines. *Biol. Bull.*, 54: 201–211.

——. 1928b. Functionless males in two species of *Neuroterus*. *Biol. Bull.*, 54: 196–200.

——, and HAMLETT, G. W. D. 1925. Haploid males in *Paracopidosomopsis*. *Science*, 61: 89.

PEACOCK, A. D., and GRESSON, R. A. R. 1931. Male haploidy and female diploidy in *Sirex cyaneus* F. (Hymen.). *Proc. Roy. Soc. Edinb.*, 51.

PINCUS, G., and SHAPIRO, H. 1940. The comparative behavior of mammalian eggs *in vivo* and *in vitro*. VII. Further studies on the activation of

rabbit eggs. *Proc. Amer. Philos. Soc.*, 83: 631–647.

PUTNAM, W. L. 1939. The plum nursery mite (*Phyllocoptes fockeui* Nal. and Trt.). *Ann. Rept. Ent. Soc. Ontario*, 70: 33–39.

ROBERTSON, W. R. B. 1930. Chromosome studies V. Diploidy and persistent chromosome relations in parthenogenetic Tettigidae. *J. Morph. Physiol.*, 50: 209–258.

ROSS, E. S. 1940. A revision of the Embioptera of North America. *Ann. Ent. Soc. Amer.*, 33: 629–676.

SANDERSON, A. R. 1932. The cytology of parthenogenesis in Tenthredinidae. *Genetica*, 14: 321–493.

SCHMIEDER, R. G. 1938. The sex ratio in *Melittobia chalybii* Ashmead, gametogenesis and cleavage in females and in haploid males (Hymenoptera: Chalcidoidea). *Biol. Bull.*, 74: 256–266.

SCHRADER, F. 1920. Sex determination in the white fly (*Trialeurodes vaporariorum*). *J. Morph.*, 34: 267–305.

——. 1923. Haploidie bei einer Spinnmilbe. *Arch. mikr. Anat.*, 97: 610–622.

——. 1926. Notes on the English and American races of the greenhouse white fly (*Trialeurodes vaporariorum*). *Ann. appl. Biol.*, 13.

——, and HUGHES-SCHRADER, S. 1926. Haploidy in *Icerya purchasi*. *Z. wiss. Zool.*, 128: 182–200.

——, and ——. 1931. Haploidy in Metazoa. *Quart. Rev. Biol.*, 6: 411–438.

SCOTT, A. 1936. Haploidy and aberrant spermatogenesis in a coleopteran, *Micromalthus debilis* LeConte. *J. Morph.* 59: 485–515.

——. 1938. Paedogenesis in the Coleoptera. *Z. Morph. Ökol. Tiere*, 33: 633–653.

——. 1941. Reversal of sex production in *Micromalthus*. *Biol. Bull.*, 81: 420–431.

SEILER, J. 1923. Geschlechtschromosomen-Untersuchungen an Psychiden. *Z. ind. Abst.- Vererb.*, 31: 1–99.

——, and SCHAEFFER, K. 1941. Der Chromosomenzyklus einer diploidparthenogenetischen *Solenobia triquetrella*. Die automiktischen Vorgänge zu Beginn der Furchung. *Rev. Suisse Zool.*, 48: 537–540.

SHULL, A. F. 1917. Sex determination in *Anthothrips verbasci*. *Genetics*, 2: 480–488.

——. 1929. Determination of types of individuals in aphids, rotifers and *Cladocera*. *Biol. Rev.*, 4: 218–248.

SLIFER, E. H., and KING, R. L. 1932. Parthenogenesis and haploidy in grasshoppers (Acrididae). *Proc. 6th Intern. Cong. Genetics*, 2: 187.

SMITH, S. G. 1941. A new form of spruce sawfly identified by means of its cytology and parthenogenesis. *Sci. Agric.* (Ottawa), 21: 245–305.

SMITH, T. L. 1938. Genetical studies in the wax moth *Galleria mellonella* Linn. *Genetics*, 23: 115–137.

SOKOLOFF, I. 1934. Untersuchungen über die Spermatogenese bei den Arachniden. V. Über die Spermatogenese der Parasitidae (= Gamasidae, Acari). *Z. Zellforsch.*, 21: 42–109.

SPEICHER, B. R. 1935. Cell size and chromosomal types in *Habrobracon*. *Amer. Nat.*, 69: 79–80.

——. 1936. Are Hymenoptera tetraploid? *Nature, Lond.*, 138: 78.

——. 1937. Oogenesis in a thelytokous wasp, *Nemeritis canescens* (Grav.). *J. Morph.*, 61: 453–471.

SPEICHER, B. R., and SPEICHER, K. G. 1940. The occurrence of diploid males in *Habrobracon brevicornis*. *Amer. Nat.*, 74: 379–382.

SPEICHER, K. G. 1934. Impaternate females in *Habrobracon*. *Biol. Bull.*, 67: 277–293.

SPEICHER, K. G., and SPEICHER, B. R. 1938. Diploids from unfertilized eggs in *Habrobracon*. *Biol. Bull.*, 74: 247–252.

STOLL, N. R., and SHULL, A. F. 1919. Sex determination in the white fly. *Genetics*, 4: 251–260.

STURTEVANT, A. H. 1923. The probable occurrence of parthenogenesis in *Ochthiphila polystigma* (Diptera). *Psyche*, 30: 22–27.

SUOMALAINEN, E. 1940. Polyploidy in parthenogenetic Curculionidae. *Hereditas*, 26: 51–64.

SZÉKESSY, W. 1937. Über Parthenogenese bei Koleopteren. *Biolog. Gen.*, 12: 577–590.

TAUSON, A. 1927. Die Spermatogenese bei *Asplanchna intermedia* Huds. *Z. Zellforsch.*, 4: 652–681.

THIENEMANN, A., and STRENZKE, K. 1940a. Terrestrische Chironomiden. III–IV. Zwei parthenogenetische Formen. *Zool. Anz.*, 132: 24–40.

——, and ——. 1940b. Terrestrische Chironomiden. VI. *Pseudosmittia holsata*, eine neue Art mit fakultativen Parthenogenese. *Zool. Anz.*, 132: 238–244.

THOMSEN, M. 1927. Studien über die Parthenogenese bei einigen Cocciden und Aleurodiden. *Z. Zellforsch.*, 5: 1–116.

——. 1929. Sex determination in *Lecanium*. Trans. IV. *Intern. Cong. Entomol. Ithaca* (1928), 1: 18–24.

TORVIK-GREB, M. 1935. The chromosomes of *Habrobracon*. *Biol. Bull.*, 68: 25–34.

TUZET, O., and MILLOT, J. 1937. Récherches sur la spermiogenèse des Ixodes. *Bull. Biol. France Belg.*, 71: 190–205.

VANDEL, A. 1931a. *La Parthénogenèse*. Paris: Encyclopédie Scientifique.

——. 1936. L'evolution de la parthénogenèse naturelle. *C. R. XII Cong. Intern. Zool. Lisbonne (1935)*, 1: 51–64.

——. 1937. Chromosome number, polyploidy and sex in the animal kingdom. *Proc. Zool. Soc. Lond., Ser. A.,* 107: 519–541.

——. 1938. Recherches sur la sexualité des Isopodes. III. Le déterminisme du sexe et de la monogénie chez *Trichoniscus (Spiloniscus) provisorius* Racovitza. *Bull. Biol. France Belg.,* 72: 148–186.

——. 1940. La parthénogenèse géographique. IV. Polyploïdie et distribution geographique. *Bull. Biol. France Belg.,* 74: 94–100.

WARMKE, H. E., and BLAKESLEE, A, F. 1940. Further differences in the determination of sex in *Melandrium* and *Drosophila. Collecting Net,* 15: 174.

WESENBERG-LUND, C. 1923. Contributions to the biology of the Rotifera. *Mem. Acad. Roy. Sci. Lettres Danemark, Copenhague, Sect. Sci.* (8) 4: 189.

——. 1930. II. The periodicity and sexual periods. *Mem. Acad. Roy. Sci. Lettres Danemark, Copenhague, Sect. Sci.,* (9) 2: 3.

WHITING, P. W. 1935. Sex determination in bees and wasps. *J. Hered.,* 26: 263–278.

——. 1940a. Multiple alleles in sex determination of *Habrobracon. J. Morph.,* 66: 323–355.

——. 1940b. Sex-linkage in *Pteromalus. Amer. Nat.,* 74: 377–379.

——. 1943. Multiple alleles in complementary sex determination of *Habrobracon. Genetics* 28: 365–382.

——, GREB, R. J., and SPEICHER, B. R. 1934. A new type of sex-intergrade. *Biol. Bull.,* 66: 152–165.

——, and SPEICHER, K. G. 1935. Impaternate daughters of females heterozygous for a sex-linked gene in *Habrobracon. Amer. Nat.,* 69: 82–83.

——, and WHITING, A. R. 1927. Gynandromorphs and other irregular types in *Habrobracon. Biol. Bull.,* 52: 89–121.

WHITNEY, D. D. 1929. The chromosome cycle in the rotifer *Asplanchna amphora. J. Morph. and Physiol.,* 47: 417.