

presumably as a result of crossing over between the X and Y. The two characters used were Red and Spotted (R and Sp) vs. gold (non-red (r) and non-spotted (sp)). The results obtained from heterozygous ♀, carrying R and Sp on the X and r sp on the Y, backcrossed to gold males, together with their interpretation in terms of X and Y chromosomes are as follows (the Y is represented as being structurally different from the X for purposes of illustration):

$$\begin{array}{c} R \\ Sp \end{array} \left| \int \begin{array}{c} r \\ sp \end{array} \begin{array}{c} r \\ x \\ sp \end{array} \right| \begin{array}{c} r \\ sp \end{array} = \begin{array}{c} r \\ sp \end{array} \left| \int \begin{array}{c} r \\ sp \end{array} \begin{array}{c} R \\ Sp \end{array} \right| \begin{array}{c} r \\ sp \end{array} + \begin{array}{c} r \\ sp \end{array} \left| \int \begin{array}{c} R \\ Sp \end{array} \right| \begin{array}{c} r \\ sp \end{array}$$

$$\text{Red spotted} \times \text{gold } \sigma^{\text{♂}} = 43 \text{ gold } \sigma^{\text{♂}} + 41 \text{ red spotted } \sigma^{\text{♂}} + \frac{1 \text{ red spotted}}{\text{♀ exception}}$$

The exceptional Red Spotted ♀ when crossed with a gold ♂ produced: 15 red spotted ♀ 17 gold ♂ and another exceptional red spotted ♂. . The progeny from the original red spotted exceptional ♀ are expected if R and Sp had crossed over from the X to the Y chromosome. The red spotted ♂ exception that again occurred, presumably represented a crossover of R and Sp from the Y back to the X.

This means that the portions of the X and Y which can be transferred are closely but not completely linked with the portion that carries the factors for sex determination. If a cytological difference between the X and Y is found later, and each is invariably associated with sex, then the sex factors must be closely or completely linked with this cytological difference, otherwise crossing-over would transfer the cytological marker to the other sex (Morgan, 1926a).

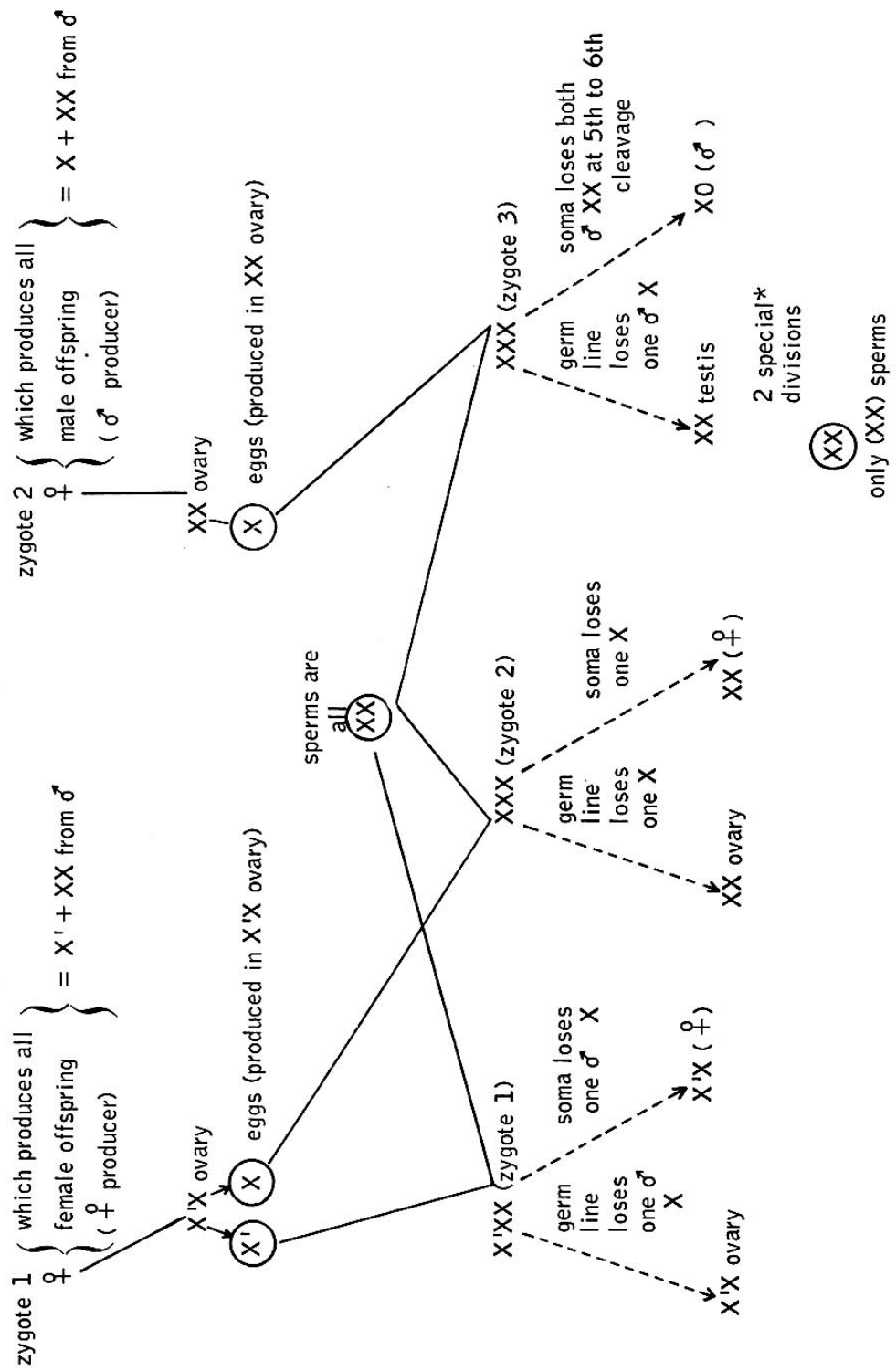
Winge (1934) also found two races in Lebistes in which the XX females showed male-tendencies. A cross between these resulted in a few XX individuals which were phenotypically and functionally males, and showed characters obtained from the mother in one X and from the father in the other X. These, when crossed with normal ♀, produced all females. The original XX♂ mated with these females produced 164♀ and no ♂. The original XX♂ when again mated with these daughters produced one XX♂ which when crossed to XX sisters produced about 1♂ : 1♀. Here a homozygous XX line was established in which sex-determination was taken over by a pair of autosomes in one of which the male-tendency genes had become associated (i.e. brought together in one member of the pair). He was also able to select in XY males until he had XY females, which when mated to XY males produced 28♀:81♂. Among the males 22 were YY.

An attempt to accomplish a similar result in Aplocheilus by accumulation of sex-tendency genes in an autosome was unsuccessful (Aida, 1936).

Sciara

Sex-determination in Sciara coprophila, a dipteran fungus-gnat, involves some interesting departures as to chromosome behavior and inheritance. An outline of certain features in species producing unisexual progenies, based on summaries by Metz (1938) and Bridges (1939) is shown in the diagram in Figure 56.

It will be noted that there are three types of zygotes, all of which are 3X. One of these (type 1) has one chromosome designated X' which differs by carrying a gene or genes which so change the germinal cytoplasm that (X) eggs developed in this X'XX zygote behave differently from the (X) eggs developed in an XXX zygote (type 2).



* during these divisions the other ♂ X is lost and the remaining X by non-disjunction forms XX sperms only.

FIG. 56. Schematic summary of the chromosome mechanism of sex determination in *Sciara coprophila* based on the description by Metz (1938).

In all cases the sperms carry XX. In the type 1 zygote, X'XX, the soma and the germ line lose one σ^7 X leaving the somatic line tissue X'X or $\frac{0}{2}$. Two kinds of eggs are produced (X') and (X). (X') eggs fertilized by (XX) sperm again produce X'XX zygotes which become females which in turn produce all female offspring. On the other hand, the (X) eggs fertilized by (XX) sperm produce the XXX zygotes of type 2 which lose one X in the soma tissue, becoming XX females which will produce all male offspring. They also lose one X in the germ line, so that the ovary is XX and produces all (X) eggs. These latter (X) eggs, fertilized by (XX) sperm, produce XXX zygotes of type 3 in which the soma loses the male XX and thus they become XO males. The germ line loses only one X resulting in XX testes in which (XX) sperms are formed. Here sex expression is determined at the fifth or sixth cleavage.

Certain other large autosomes are lost in the early somatic divisions, and are thus "limited" to the germ line. Maturation divisions are normal for all chromosomes in the female. In the male there are several unusual cytological events:

1. The first division spindle is a monaster (one pole).
2. The divisions are such that only the maternal group of chromosomes plus all the "limited" ones are included in the sperm.
3. At the second division, there is always non-disjunction of the X chromosome so that the sperm has two X chromosomes.

By using chromosomal interchanges involving the X and another chromosome Crouse (1943, 1960) was able to demonstrate that only one of the two interchanged chromosomes showed non-disjunction at the second spermatocyte division. This chromosome could be identified in three cases as the one with a proximal segment of the X and the X centromere. Hence this is the portion of the X responsible for the behavior.

Such abnormal chromosomal behavior results in unusual genetic behavior (Metz, 1927, Metz and Schmuck, 1929). Other species of *Sciara* show different breeding behaviors for sex expression.

For a discussion of sex determination in other species of animals and in those with a multiple sex chromosome mechanism consult White (1954), also Darlington (1937).

Trimonoecious species of plants

A genetic analysis of the trimonoecious condition in *Carica papaya* has been reported by Hofmeyr (1938, 1938a, 1939) and by Storey (1938). The following results were obtained from crosses between males, females and hermaphrodites $\frac{0}{2}$:

$$\frac{0}{2} \times \sigma^7 = 1\frac{0}{2} : 1\sigma^7$$

$$\frac{0}{2} \times \frac{0}{2} = 1\frac{0}{2} : 1\frac{0}{2}$$

$$\frac{0}{2} \times \sigma^7 = 1\frac{0}{2} : 1\sigma^7 : 1\frac{0}{2}$$

$$\frac{0}{2} \text{ selfed} = 2\frac{0}{2} : 1\frac{0}{2}$$

To explain the results Hofmeyr assumed three alleles M_1 , M_2 , m , in which $mm = \frac{0}{2}$, $M_1m = \sigma^7$, $M_2m = \frac{0}{2}$, and all homozygous dominant types M_1M_1 , M_2M_2 , or heterozygous M_1M_2 were inviable. As expected there was 25% seed abortion from selfing hermaphro-

dites or in crosses with males, thus accounting for the 1:2 ratios and the missing genotypes (Storey, 1938, 1953). Later different values were assigned to M_1 , M_2 and m and a balance hypothesis proposed to account for differences in stability of the different sex types (Hofmeyr 1939a). In papaya, varieties that segregate $1\frac{1}{2}:1\frac{1}{2}$ have been introduced, since every plant should bear fruit.

In the grape, using European and American cultivated varieties, Breider and Scheu (1938) and Oberle (1938) reported the following results:

$$\text{hermaphrodite selfed} = 3\frac{1}{2}:1\frac{1}{2}, \text{ or all } \frac{1}{2}$$

$$\frac{1}{2} \times \frac{1}{2} = 1\frac{1}{2}:1\frac{1}{2} \text{ or all } \frac{1}{2}$$

$$\frac{1}{2} \times \sigma = 1\frac{1}{2}:1\frac{1}{2}:2\sigma \text{ or } 1\frac{1}{2}:1\sigma$$

$$\frac{1}{2} \times \sigma = 1\frac{1}{2}:1\sigma$$

They explained the results on the basis of two linked factors:

Sp - determines, sp inhibits normal pollen development.

So - inhibits, so determines normal ovule development.

$$\text{then } \frac{\text{so sp}}{\text{so sp}} = \frac{1}{2} \quad \frac{\text{So Sp}}{\text{so sp}} = \sigma \quad \frac{\text{So Sp}}{\text{so Sp}} = \frac{1}{2} \quad \text{or} \quad \frac{\text{so Sp}}{\text{so sp}} = \frac{1}{2}$$

On this basis, $\frac{1}{2} \times \frac{\text{So Sp}}{\text{so Sp}} \sigma$ should give $1\sigma:1\frac{1}{2}$ and the other ratios also are explainable.

A ratio of $9\frac{1}{2}:3\frac{1}{2}:4\sigma$ was reported by Loomis et al. (1954) from $\frac{1}{2}$ selfed or sibbed. Apparently an independent factor for sex expression was segregating also.

In Spinacia oleracea the proportion of pistillate to staminate flowers per plant shows a continuous range. One line, selected for monoecism, when selfed segregated monoecious and pistillate offspring. The progeny of another were completely monoecious (Janick and Stevenson, 1955). The breeding behavior of sex expression in this and in various crosses was explained by assuming monoecism, X and Y are three alleles of a single gene. Monoecious plants are either $X^m X^m$ or $X^m X$, but $X^m Y$ are staminate. In addition there are many modifying genes which made it possible to select true-breeding monoecious lines with high or low proportions of $\frac{1}{2}:\sigma$ flowers per plant.

In cultivated species that are not monoecious, the original mode of sex determination may have been modified by selection. For example, in hemp there has been selection for uniform ripening of σ and $\frac{1}{2}$ plants for improvement in fiber production. In grapes there has been selection for hermaphroditism.

Bisexual species

(either monoecious or with hermaphroditic flowers).

In those species in which the two "sexes" are in different organs of the same plant, the chromosomes and genes are supposedly the same in all tissues; hence the mechanism that determines the formation of a female or a male sex organ in a particular region may be similar to that which determines the differentiation of different tissues or organs in other parts of the plant. In many of these species the σ and the $\frac{1}{2}$ flowers also contain the rudiments of the other sex organs. Mutants may occur in which the development of these rudimentary organs is modified. For example, in maize, anther-ear and several other dwarf mutants develop anthers on the ear. There are several tassel seed characters in

which ovules and silks develop in the tassel and produce grains.

A dioecious strain of maize was produced by Jones (1934, 1939) by combining two recessive characters, silkless (sk) which has no silks and produces no seed and tassel seed (ts₂) which has in place of the tassel a branched, ramosa-like ear structure with silks. The cross sk sk ts₂ ts₂ ♀ x sk sk Ts₂ ts₂ ♂ produced a ratio of 1♀ : 1♂ plants. The sk sk ts₂ ts₂ combination is tassel seed but has normal ears. In this cross the ♂ was heterogametic.

Both types of sex-determination were established experimentally by Emerson (1932) in maize by combining certain genetic markers. For the one in which the male was heterogametic, two recessive characters were used, barren stalk (ba) which has no ear and tassel seed (ts₂). The cross of ba ba ts₂ ts₂ ♀ x ba ba Ts₂ ts₂ ♂ segregated 1 ♀ : 1 ♂.

For the one in which the female was heterogametic, a dominant tassel seed character, Ts₃, was used with ba. The cross of ba ba Ts₃ ts₃ (tassel seed) x ba ba ts₃ ts₃ (normal tassel) also segregated 1♀ : 1 ♂.

In either type a subsequent chromosomal change might produce a heteromorphic chromosome pair carrying the pair of heterozygous genes. To behave in a manner simulating a pair of sex chromosomes, the structural change would have to be closely linked with the locus of the differential gene pair, or crossing over would have to be suppressed.

Male sterility

A male sterile condition in which the anthers are usually shriveled and little or no viable pollen is produced is determined by a single recessive gene in barley, tomatoes, maize, and many other species of plants. Female fertility is usually normal. In maize 20 such genetically different male-sterile characters, 13 of them reported by Beadle (1932), have been identified (Emerson et al. 1935). One of these, ms₁ is closely linked with the yellow (Y) vs. white (y) locus and its use to produce hybrid corn by open pollination without detasseling was suggested by Jones and Everett (1949). Ears from

$\frac{y\ ms}{y\ ms} \times \frac{Y\ Ms}{y\ ms}$ segregated for yellow and white seeds. Since the white seeds produce mostly male sterile plants, they could be used as the ♀ parent of the hybrid. Hybrid seed could be produced in the field by growing a number of rows of male sterile plants from white seeds alternated with a single row of the pollinator (any desired strain). The seed on the male sterile rows would be the hybrid seed. It would produce a crop that segregated yellow and white seeds on the ears if the pollinator had been yellow.

In barley, male sterile plants in drier climates such as California and Arizona often set seed from natural crossing, but the frequency is so variable that hybrid barley thus far is not feasible (Suneson, 1951).

In maize, a number of the genes produce irregular meiosis, e.g. polymitotic (po), asynaptic (as), and sticky (st) (see Emerson et al. 1935). These are characterized by poor seed set as well as male sterility.

Cytoplasmic male sterility

In flax, Bateson and Gairdner (1921) first reported that a procumbent strain crossed with normal tall produced in F₂ 3 normals:1 male sterile while the reciprocal cross pro-

duced in F_2 all normals. They ascribed the behavior to unequal splitting in pollen and eggs and proposed the term "anisogony".

Later Chittenden (1927) and Chittenden and Pellew (1927) suggested an interaction of cytoplasm and a gene as the explanation. The tall varieties were assumed to carry a factor ms for male sterility which produced only normals when present in cytoplasm of the tall varieties, but which produced male sterility when present in cytoplasm of the procumbent strain. The hypothesis may be illustrated by the diagrams in Fig. 57 in which the cytoplasm of the two parents are represented as ● and ○.



FIG. 57. Diagrams showing the genotypes for Ms vs ms (normal vs male sterile) and the cytoplasmic constituent in reciprocal crosses: on the left, procumbent ♀ x tall ♂; on the right, tall ♀ x procumbent ♂. ● = cytoplasm of procumbent, ○ = cytoplasm of tall. Male steriles appear only in procumbent cytoplasm, and hence, the cross of procumbent ♀ x tall ♂ segregates 3 normal : 1 male sterile; whereas the reciprocal cross produces all normals in F_2 . (Based on the description and diagrams by Chittenden, 1927)

The ms ms genotype is male sterile only in the presence of the cytoplasm of the procumbent strain, represented as ●.

Crosses between the male sterile F_2 plants and plants of the tall variety (ms ms) produce only male sterile offspring. The cross between male sterile plants and procumbent (MsMs) as the ♂ produces only plants with normal fertility. Hence procumbent may be referred to as a fertility restoring strain, a terminology now applied to similar stocks in maize. They carry the fertility restoring gene designated Ms in the above diagrams. Preferably they should have normal cytoplasm rather than the type found in procumbent flax.

A large-seeded strain of flax from Crete behaves in a manner similar to procumbent (Burnham, unpub.). All but one other variety tested had the ms ms genotype. This one exception was MsMs but in a normal cytoplasm, since crosses using it as the female parent produced only normals in F_2 . This would be satisfactory as a fertility restorer.

Cytoplasmic male sterility and factors for fertility restoration have been reported in Geranium endressii x G. striatum (Sansome, 1936), and in sugar beets (Owen, 1945). In sugar beets, several factors are involved in the restoration of fertility.

Studies of male sterility that originated in a South American variety of corn collected by R. A. Emerson and F. D. Richey were reported by Rhoades (1933b). Crosses of male sterile with pollen from normal plants produced only male sterile offspring. Occasionally they shed a little pollen but crosses using this pollen produced only male fertile progeny. Hence transmission was cytoplasmic and only through the ♀. Substitution of normal chromosomes with gene markers for all the linkage groups then known showed no linkage with the sterility nor any change in the inheritance. This type proved too variable for use as an effective substitute for detasseling, since it produced pollen under some conditions (Richey in a personal communication).

Cytoplasmic male sterile lines in maize have been established also from the iojap (ij) stock (Rhoades, 1943, 1950a). Lines homozygous for iojap showed male sterility in occasional plants, and in crosses of $\underline{ij} \underline{ij}^{\circ}$ with normal σ° , an occasional $\underline{Ij} \underline{Ij}$ F_1 plant was male sterile. By crossing again with normal, a male sterile plant that was $\underline{Ij} \underline{Ij}$, normal green and not carrying \underline{ij} , was produced. This is similar to the procedure by which a chlorophyll defective character showing cytoplasmic inheritance was established from ij (Rhoades, 1943). Ten different sources of cytoplasmic male sterility were listed by Jones (1955). The Texas source of cytoplasmic male sterility (T), reported by Rogers and Edwardson (1952), requires two major genes plus modifiers to restore complete fertility. These major genes have been designated \underline{Rf}_1 and \underline{Rf}_2 (Duvick 1956). Their action is similar to that of the \underline{Ms} gene and \underline{rf} to that of \underline{ms} described above for flax. One restorer gene was linked with two 1-3 interchanges (Linden 1956). Subsequent tests have shown that \underline{Rf}_1 is located in chromosome 3 between \underline{d}_1 and \underline{ts}_4 (Blickenstaff et al. 1958, Duvick et al. 1961). Most inbreds in the United States are $\underline{rf}_1 \underline{rf}_1 \underline{Rf}_2 \underline{Rf}_2$. There are different degrees of restoration. Varieties and inbreds vary widely in their ability to restore fertility. (Jones 1950, 1955, Newlin, 1955, Edwardson, 1955, Briggles 1957, Gabelman, 1949, 1952).

Jones and Everett (1949), Jones and Mangelsdorf (1951) and Rogers and Edwardson (1952) have outlined methods by which male sterility might be used to replace the usual detasseling needed to produce double cross hybrid seed. According to one plan, applied as an example to the double cross (AxB)x(CxD), only the inbred D or both C and D would carry fertility restoring factors. The AxB single cross used as the female parent is produced by crossing male-sterile A with B. Since B is free of restoring genes, this avoids detasseling of the single cross (AxB), as well as male-sterile A. A pollen fertile inbred A must be maintained as a pollen source to produce male-sterile inbred A (the male-sterile equivalent of A produced by successive backcrosses to pollen fertile A as the male parent). The method has been used successfully in the production of hybrid seed corn; and a larger and larger proportion of the hybrid corn sold is being produced in this manner.

The method has been successful for hybrid sorghum (Stephens and Holland, 1954, Quinby and Martin, 1954); and also for onions (cf. Jones and Clarke, 1947).

Sex ratios

In general, in dioecious plants, females are more numerous than males. In the hop, Humulus lupulus L., Holubinsky (1939) reported the percentages of males from 3 different females, each pollinated by several different males or a mixture of pollen as: 1%, 7.4%, and 23.9%. Correns reported from 9.8% to 22.8% of males. In Humulus japonicus, Kihara and Hirayoshi (1932) reported an excess of females following heavy application of pollen. Counts reported by Winge (1923) showed an excess of females in both species.

In Lychnis dioica, L. alba and Rumex acetosa, Correns (1928) found a larger proportion of males following scanty pollination, even approaching 50%. Aging the pollen or treatment of the dry pollen with alcohol vapor also increased the proportion of males. Differences in age of ovules had no effect. Tischler (1925) found an increased proportion of males from Lychnis pollen subjected to alcohol vapor at the time of germination. In all these cases, the pollen was of two kinds. The various treatments may have acted to change their competitive ability. Sex ratios (sex expression) may be modified also by the growing conditions (see latter part of this discussion).