CHAPTER

17

Cytoplasmic or Extra-Nuclear Inheritance

The variegated leaves of the shrub, *Acanthopanax.*

In preceding chapters, we have discussed different roles of genes of the nuclear chromosomes in inheritance, cellular metabolism, development and mutation of the organisms in which they occur. Though, the genes of nuclear chromosomes have a significant and key role in the inheritance of almost all traits from generations to generations, but they altogether cannot be considered as the sole vehicles of inheritance, because certain experimental evidences suggest the occurrence of certain extranuclear genes or DNA molecules in the cytoplasm of many prokaryotic and eukaryotic cells. For example, bacterial cells such as *E. coli* possesses a single main chromosome in the nucloid and often extra DNA elements called **plasmids** in the cytoplasm; the eukaryotic cells possess a main complement of chromosomes in the nucleus and extra-DNA molecules or chromosomes in their mitochondria and chloroplasts. Qualifying also as extra hereditary elements are certain viruses, bacteria, and algae (which live as endosymbionts inside the eukaryotic cells). These cytoplasmic extra-nuclear genes or DNA molecules of plasmids, mitochondria, chloroplasts, endosymbionts and cellular surfaces have a char-

acteristic pattern of inheritance which does not resemble with that of genes of nuclear chromosomes and is known by different terms such as **non-Mendelian**, **non-chromosomal**, **uniparental**, **maternal**, **extra-chromosomal**, **cytoplasmic** and **extra-nuclear** inheritance.

EVIDENCES FOR CYTOPLASMIC FACTORS

Traits with extranuclear basis are identified by the accumulated evidence from a number of diagnostic criteria such as follows :

1. Because the female gamete contributes almost all of the cytoplasm to the zygote and male gamete (sperm or pollen) contributes only a nucleus, an inheritance pattern that differs between reciprocal crosses suggests a cytoplasmic involvement. This is clearly the basis for **uniparental** or **maternal inheritance** where the progeny always resemble one parent, most commonly the female parent (*e.g.*, shell coiling in *Limnaea peregra*).

2. Differences in reciprocal crosses which cannot be attributed to six-linkage or some other chromosomal basis tend to implicate extranuclear factors (*e.g.*, chloroplast inheritance in *Mirabilis jalapa*).

3. The uniparental inheritance of a trait which cannot be atributed to unequal cytoplasmic contributions from parental gametes may, however, involve cytoplasmic factors (*e.g.*, streptomycin resistance in *Chlamydomonas*).

The green alga *Chlamydomonas.*

4. Whenever trait fails to demonstrate the classical segregation patterns and deviates from standard ratios, the conclusion is again a cytoplasm based type of inheritance (*e.g.*, mitochondrial inheritance in yeast).

5. When the trait fails to show linkage to any known nuclear linkage groups and assort independently from nuclear genes, a cytoplasmic mode of inheritance is suggested.

6. Many types of mutants that fit the above criteria will show segregation during mitotic division. This is very common in variegated plants that carry more than one type of plastid (chloroplast) per cell.

The cytoplasmic inheritance, therefore, will be understood to be based on cytoplasmically located, independent, self-replicating nucleic acids, which differ from chromosomal genes by their location within the cell, and have their own nucleotide sequences. The smallest heritable extra chromosomal unit is called a **plasmagene**. All of the plasmagenes of a cell constitute the **plasmon**.

A. EXTRA-NUCLEAR INHERITANCE IN EUKARYOTES

Many geneticists have studied various cases of extra-nuclear inheritance in different eukaryotes. Certain most important examples of extra-nuclear inheritance in eukaryotes are the following :

1. Maternal Inheritance

In certain cases, it has been observed that certain characteristic phenotypic traits of F_1, F_2 or F_3 progeny are not the expression of their own genes, but rather those of the maternal parents. Such phenotypic expressions of maternal genes (genotype) may be short-lived or may persist throughout the life-span of the individual. The substances which produce the maternal effects in the progeny are found to be transcriptional products (*i.e.*, mRNA, rRNA and tRNA) of maternal genes which have been manufactured during oogenesis and which exist in the ooplasm of unfertilized eggs in the form of inactive protein coated and late translating mRNA molecules (**informosomes**) or inactivated rRNA and tRNA. These transcriptional products of maternal genes produce their phenotypic effects during

The photograph illustrates mixture of right vs. left handed coiled snails.

early cleavage and blastulation when there occur little or no transcription since, maternal and paternal genes of zygote remain engaged in mitotic replication or duplication of DNA. There may be other reasons of maternal effect which are still little understood. The maternal inheritance has been studied in some of the following cases :

(a) Shell coiling in Limnaea. In the snails (gastropods), the shell is spirally coiled. In most cases the direction of coiling of the shell is clockwise, if viewed from apex of the shell. This type of coiling is called **dextral**. However, in some snails the coiling of shell may be counter clockwise or **sinistral**. Both types of coilings are produced by two different types of genetically controlled cleavages, one being **dextral cleavage**, another being **sinistral cleavage** (Fig. 17.1).

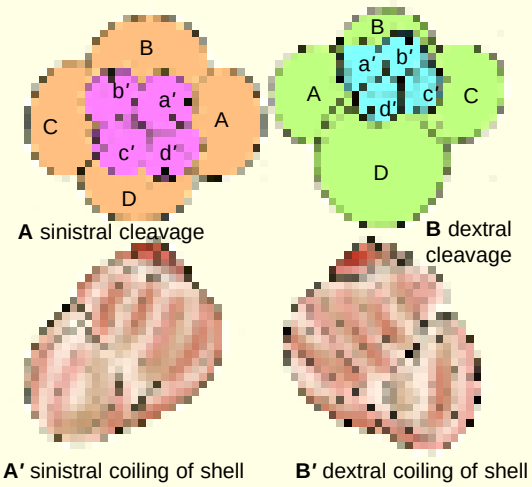


Fig. 17.1. Correlation of sinistral (A) and dextral (B) cleavage with sinistral (A´) and dextral (B´) coiling of the shell in gastropods.

There are some species of gastropods in which all the individuals are sinistral but the main interest attaches to a species in which sinistral individuals occur as a mutation among a population of normal dextral animals. Such a mutant was discovered in the freshwater snail *Limnaea peregra* (**A. Sturtevant**, 1923). Breeding and cross breeding of dextral and sinistral snails showed that the difference between the two forms is dependent on a pair of allelomorphic genes, the gene for sinistrality being recessive (S), and the gene for the normal dextral coiling being dominant (S^+). The two genes are inherited according to Mendelian laws, but the action of any genic combination is visible only in the next generation after the one in which a given genotype is found.

The eggs of a homozygous sinistral individual (SS) are fertilized by the sperm of a dextral individual (S^+S^+), the eggs cleave sinistrally and all the snails of this F_1 generation show a sinistral coiling of the shell. Thus, the gene of sperm (S^+) do not manifest themselve, although the genotype of the F_1 generation is S^+S. If a second generation (F_2) is bred from such F_1 sinistral individuals, it is all dextral, instead of showing segregation as would be expected in normal Mendelian inheritance. In fact, segregation does take place in the F_2 generation so far as the genes are concerned, but the new genic combinations fails to manifest themselves, since the coiling is determined by the genotype of the mother. The genotype of F_1 mother being S^+S, the gene for dextrality dominates and is responsible for the exclusively dextral coiling of the second generation. Only in the F_3 generation does segregation in the ratio of 3 : 1 becomes apparent, since the individuals of the F_2 generation had the genotypes —$1S^+S^+$; $2\ S^+S$, 1SS, 1/4 of them, on the average, produce eggs developing into sinistral individuals (Fig. 17.2).

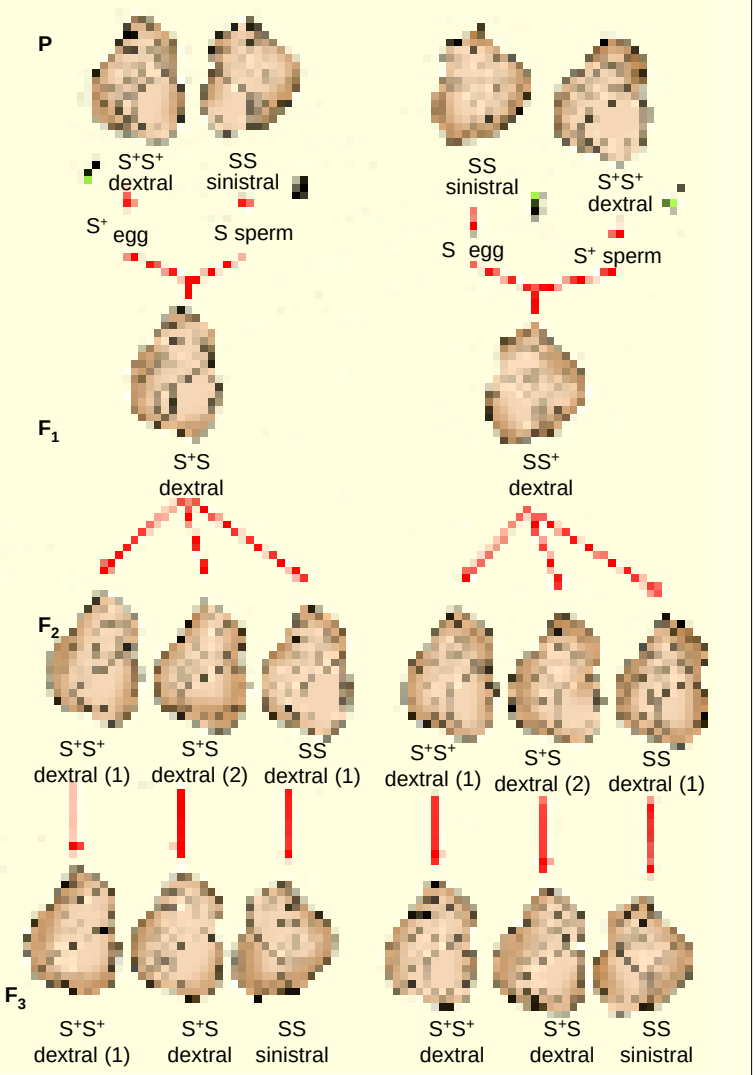


Fig. 17.2. Maternal effect in direction of coiling of the shell in *Limnaea.*

It is easy to understand that the results of a reciprocal cross that is, of the fertilization of the eggs of a homozygous dextral individual (S^+S^+) by the sperm of a sinistral individual (SS)—will lead to a somewhat different type of pedigree : the F_1 generation will be dextral (with genotype S^+S) and the F_2 generation again all dextral (with genotypic ratio of $1S^+S^+:2S^+S$: ISS). The F_3 generation will show segregation among broods, just as in the cross examined first.

The whole case becomes clear if it is realized that the type of cleavage (sinistral or dextral) depends on the organization of the egg which is established before the maturation division of the oocyte nucleus. The type of cleavage is, therefore, under the influence of the genotype of the maternal parent. The sperm enters the egg after this organization is already established. Lastly, the direction of coiling of shell depends upon the orientation of the mitotic spindle of first cleavage of the zygote. If the spindle is tipped toward the left of the median line of the egg cell, the sinistral pattern will develop; conversely if the mitotic spindle is tipped toward the right of the median line of the cell, the dextral pattern will develop. The spindle orientation is, thus, controlled by the organization of ooplasm which becomes established during oogenesis and before fertilization.

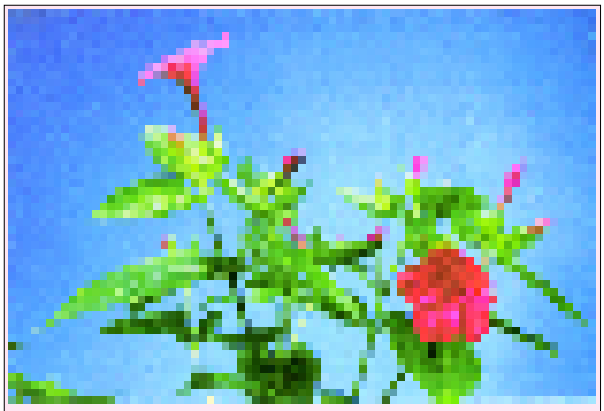
(b) Eye pigmentation in water fleas and flour moths. Like the *Limnaea* and *Ambystoma mexicanum,* the maternal effect has also been observed in at least two very different invertebrates, the water flea (*Gammarus*) and the flour moth (*Ephestia kuhniella*). The normal colour of the eye in both invertebrates is dark due to the dominant gene (AA or KK) in which the dominant gene K directs the production of a hormone-like substance called **kynurenine** which is involved in the pigment synthesis. The recessive mutants do not possess pigment in the eye (*viz.*, kynurenineless) and have the genotype aa or kk. When aa or kk female is crossed with heterozygous male with Aa or Kk genes, only half of

the larvae show dark pigment in the eye. But, a cross between Aa or Kk female and aa or kk male produces all larvae with dark eyes. On reaching the adult stage, half of the offsprings (those of the genotype aa) become light eyed. This indicates that some kynurenine diffuses from the Aa mother into all young (larvae), enabling them to manufacture pigment regardless of their genotype. The aa progeny, however, has no means of continuing the supply of kynurenine, with the result that their eyes eventually become light. This example suggests an ephemeral type of maternal effect.

2. Extra-nuclear Inheritance by Cellular Organelles

Chloroplasts and mitochondria are organelles that contain their own DNA and protein-synthesizing apparatus. A widely held theory concerning their origin proposes that they were once infectious endosymbiotic prokaryotes that evolved such a dependence on the gene products of the host that they are no longer able to function autonomously.

This theory has been supported by the fact that the genetic components of these organelle are often similar to those found in prokaryotes. For example, the chloroplasts of certain algae and *Euglena* contain 70S type small ribosomes and "naked" chromosomes or DNA which is circular. Their protein synthesis begins with the amino acid N-formyl methionine, as does prokaryotic protein synthesis, and their DNA-dependent RNA polymerase is sensitive to the inhibitor **rifampicin**. The genetic materials of chloroplasts and mitochondria will be transmitted to offspring almost exclusively via the egg. Maternal inheritance due to chloroplast and mitochondria is well illustrated by the following examples:



The four o'clock plant with a green branch.

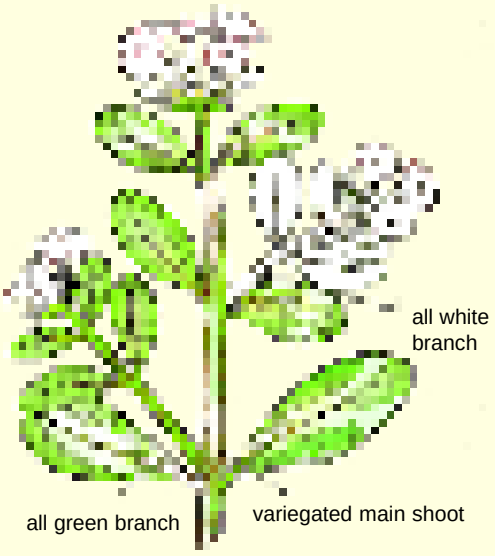


Fig. 17.3. Leaf variegation in *Mirabilis jalapa*, the four-o'clock plant. Flowers may form on any branch (variegated, green, or white), and these flowers may be used in crosses.

(a) Chloroplast inheritance in variegated four o' clock plant. The cytoplasmic or extra-nuclear inheritance of colour in plant by plastids was first of all discribed by **C. Correns** in 1908 in the four o'clock plant, *Mirabilis jalapa*. In contrast to other higher plants, *Mirabilis* contains three types of leaves and parts : (1) Full green leaves or branches having chloroplast, (2) White (pale) leaves and branches having no chloroplast, (3) Variegated branches having leukoplast in white (pale) areas and chloroplast in green patches (Fig. 17.3). Because, the chlorophyll pigment of chloroplast is related with photosynthesis of food and leukoplasts are incapable to perform photosynthesis, so the white or pale parts of plant survive by receiving nourishment from green parts. **Correns** reported that flowers on green branches produced only green offsprings, regardless of

the genotype and phenotype of pollen parent and likewise, flowers from the white or pale branches produced only white or pale seedings regardless of genotype and phenotype of pollen parent. The plants developing from the white or pale seedings die because they lack chlorophyll and cannot carry on photosynthesis. **Correns** further reported that flowers from the variegated branches yielded mixed progeny of green, white (pale) and variegated plants in widely varying ratios (Fig. 17.4). These results are summarized in Table 17-1.

The irregularity of transmission from variegated branches could be understood by considering cytoplasmic genes (plasmagenes) of plastids. A study of the egg during oogenesis in *Mirabilis* reveals that the ooplasm contains plastids like cytoplasm of other plant cells. If the egg cell is derived from green plant tissues, its ooplasm will contain coloured plastids; if derived from white plant tissues, its ooplasm will contain white plastids; if derived from variegated tissues, its cytoplasm may contain coloured plastids only, white plastids only or a mixture of coloured and white plastids. A study of the pollenogenesis, however, reveals that pollen contains very little cytoplasm which in most cases is devoid of plastids. Without the plastids, the pollen cannot affect this aspect of the offspring's phenotype.

Mitotic segregation. Variegated branches of *Mirabilis jalapa* produce three kinds of eggs : some contain only white chloroplasts, some contain only green chloroplasts and some contain both types of chloroplasts. In the subsequent mitotic divisions, some form of cytoplasmic segregation occurs that segregate the chloroplast types into pure cell lines, thus, producing the variegated phenotype in the progeny individual. This process of sorting might be described as "**mitotic segregation**"of this is a pure extra- nuclear phenomenon. In mitotic segregation since both segregation and recombination of organelle genotype takes place, so it is called **cytoplasmic segregation and recombination** (its acronym is **CSAR**).

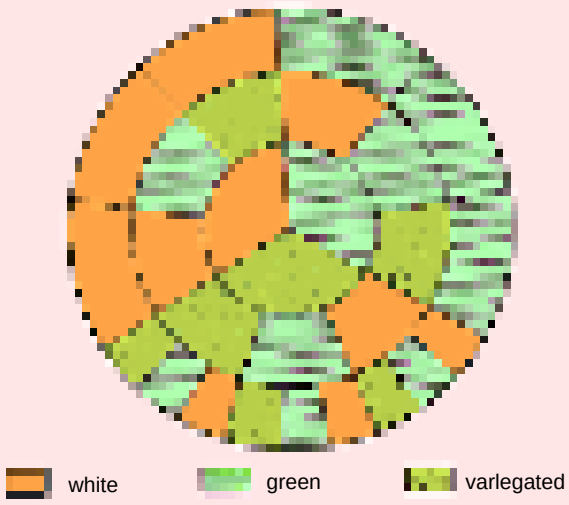


Fig. 17.4. Plastid inheritance of *Mirabilis jalapa.* The central circle represents the type of branch that produces flowers which are pollinated. Intermediate circle represents branch from which pollen is used and outer circle shows the progeny.

(b) Maternal inheritance by iojap gene of corn. Another example from higher plants also suggests the existence of plastid genes controlling plastid integrity. A gene in corn plant called **iojap** (**ij**) has been mapped by **M. Rhoades** (1946) to nuclear chromosomes 7. Plants homozygous for ij are either inviable white seedings or variegated with a characteristic white striping, the phenotype being known as **striped**. When the variegated plants serve as females in a cross, they give rise to green, white, and striped progeny, regardless of the nuclear genotype of the paternal parent. Thus, if the pollen derives from a normal green Ij/Ij plant as in Figure 17.5 b, the resulting progeny will be Ij/ij heterozygotes, but many will exhibit abnormal plastid pigmentation : the presence of the "normal" Ij gene has no curative effect. In the reciprocal Ij/Ij female X ij/ij male cross (Fig. 17.5). On the other hand, the Ij/ij progeny are all normally pigmented.

Table 17-1. **Chloroplast inheritance in variegated four o'clock plants.**

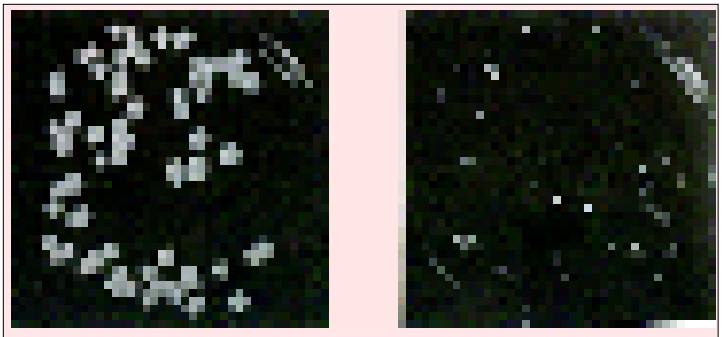
Branch of origin of the male parent	Branch of origin of the female parent	Progeny
Green	Green	Green
	Pale or white	Pale or white
	Variegated	Green, pale or white, variegated
Pale or white	Green	Green
	Pale or white	Pale or white
	Variegated	Green, pale or white, variegated
Variegated	Green	Green
	Pale or white	Pale or white
	Variegated	Green, pale or white, variegated

The iojap trait, thus, exhibits classical maternal inheritance once it has become established in an ij/ij plant. Moreover, once established, it becomes independent of the ij gene, as can be demonstrated by crossing F_1 Ij/ij variegated females to Ij/Ij normal males. As shown in Figure (17.5c), a mixture of green, striped and white progeny again results, even though some of the striped and white plants now have an Ij/Ij genotype. Thus, the iojap trait, once established, is permanent.

The iojap phenomenon has been explained by two hypotheses. One hypothesis holds that the ij/ij genetic constitution could bring about or permit, frequent mutations in the chloroplast genome that result in the production of lines of abnormal plastids. Another hypothesis suggests that certain cytoplasmic elements other then chloroplast mutations come into being or residence in ij/ij cells, are later inherited in the absence of this "susceptible" or "permissive" genotype, and bring about the bleaching of chloroplasts.

This type of maternal inheritance by plasmagenes of chloroplasts has been also studied in many other higher plants such as barley, *Oenothera* sp., rice, etc.

(c) Extra-nuclear inheritance by mitochondria. The most important work on the genetics of mitochondria done in yeast which was initiated by the discovery of petite mutants by **B. Ephrussi** (1953). Subsequently mt DNA was studied in several organisms including plants and animals.



A comparison of normal vs. petite colonies in the yeast *Saccharomyces cerevisaiae.*

(i) Petite in yeast. Yeast, *Saccharomyces cerevisiae,* are single-celled ascomycetes fungi. In the life cycle, diploid and haploid adult alternates, the former reproducing by asexual meiospores called **ascospores**, the latter by **isogametes**. The **petite** mutants in yeast fail to grow on carbon source such as glucose and produce smaller colonies (the "littles") when grown on sugars such as glucose. Since this difference can be observed only when such yeast cultures are kept in a oxygen-containing environment; so it is concluded that petite mutants have a defective aerobic respiratory mechanism. In

other words, slow growth of petite can be attributed to yeast cells utilization of less efficient fermentation process. These petites differ from wild type, called **grande** and are characterized by (i) their insensitivity to inhibitors of aerobic pathways (such as cyanide), (ii) absence of cytochromes a, a_3, b and a number of other changes in mitochondrial respiratory enzymes; (iii) incomplete development of mitochondria; and (iv) lack of stainability of petite mitochondria.

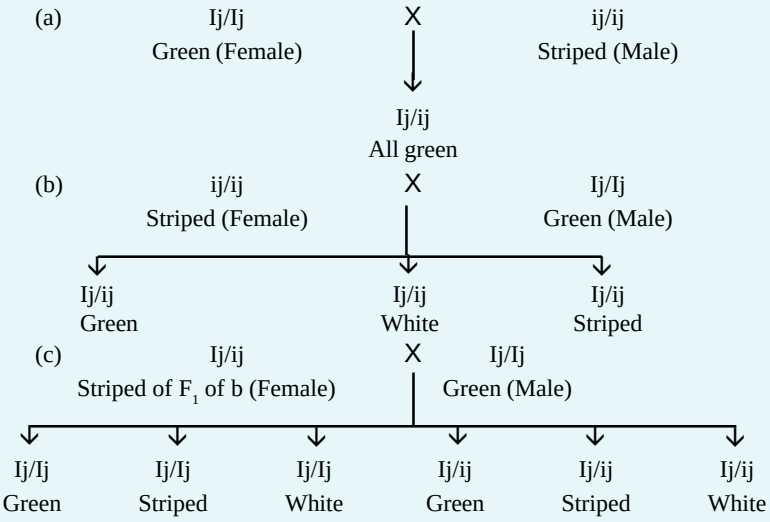
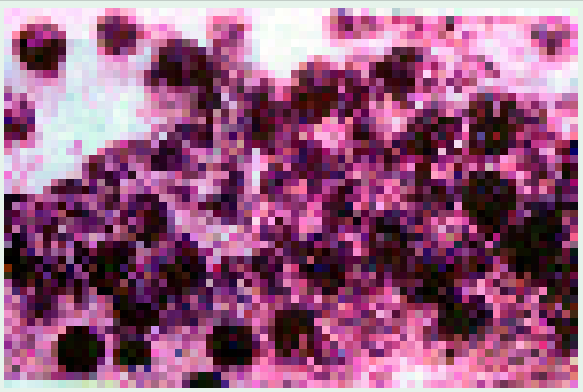


Fig. 17.5. (a) Cross between green (normal) and striped (iojap) plants. (b) Reciprocal of cross (a) (c). Cross of F_1 striped females (of cross b) to normal (green) males.

The petite mutants can be **segregational**, *i.e.*, they follow mendelian segregation and, therefore, presumably controlled by chromosomal genes. They may also be **vegetative**, *i.e.*, non-segregational or extra-chromosomal. The genetic basis of petite character is a cytoplasmic factor ρ+ (rho) which may be absent or defective in petites. Thus, a vegetative petite can be **neutral** (ρ^0) which completely lack ρ^+ or it may be **suppressive** (ρ^-) having a defective ρ^+. The neutral petites are not transmitted while suppressive petites are transmitted to a fraction of vegetative diploid progeny. In various strains of yeast, the suppressiveness varies from 1–99 per cent petites. The following two lines of evidences have suggested the association of ρ^+ with mitochondrial DNA (mt DNA); (1) **Ethidium bromide**, which induces petite mutations with 100 per cent efficiency, causes degradation of mt DNA after prolonged exposure of cells. In fact, neutral petites have been found lacking in mt DNA. (2) Supressive petites contain mt DNA which is greatly altered in base composition with respect to wild mt DNA.

(ii) Poky strain of Neurospora. In fungi, *Neurospora crassa* a number of mutations of mitochondria are inherited via the female parent. The best studied of these is the **poky strain** of *N. crassa*, first isolated by **Mitchell** and **Mitchell** (1952). A poky mutant differs from wild type strain of *Neurospora* in the following aspects : (1) it is slow growing; (2) it shows maternal inheritance, and (3) it has abnormal cytochromes. Of the three cytochromes—cyt a, b and c



Micrograph illustrating the growth of the pink bread mold *Neurospora crassa.*

found in wild type, cyt a and cyt b are absent, and cyt c is in excess in poky mutant. In reciprocal crosses, poky character shows maternal inheritance:

poky (female) × wild type (male) → all poky

wild type (female) × poky (male) → all wild type

However, there are other marker nuclear genes (ad^+/ad^-) which show 1 : 1 mendelian segregation. The following evidences suggested that poky trait may be located in mitochondrial DNA: (i) slow growth may be due to lack of ATP energy and source of this energy is mitochondria; (ii) cytochromes in poky strain differ from those in wild type in quality and quantity and these cytochromes are found in mitochondria.

(iii) Male sterility in plants. In plants, the phenotype of male sterility is found to be controlled either by nuclear genes or plasmagenes (cytoplasm) or by both. Therefore, the trait of male sterility of plants is controlled by the following three methods :

(a) Genetic male sterility. In this type of male sterility, the sterility is controlled by a single nuclear gene which is recessive to fertility, so that the F_1 progeny would be fertile and in F_2 generation, the fertile and sterile individuals will be segregated in the typical 3 : 1 ratio (Fig. 17.6).

(b) Cytoplasmic male sterility (CMS). In maize and many other plants, cytoplasmic control of male sterility is known. In such cases, if the female parent is male sterile (having plasmagene for male sterility), the F_1 progeny would always be male sterile, because the cytoplasm is mainly derived from the egg which is obtained from the male sterile female parent (Fig. 17.7).

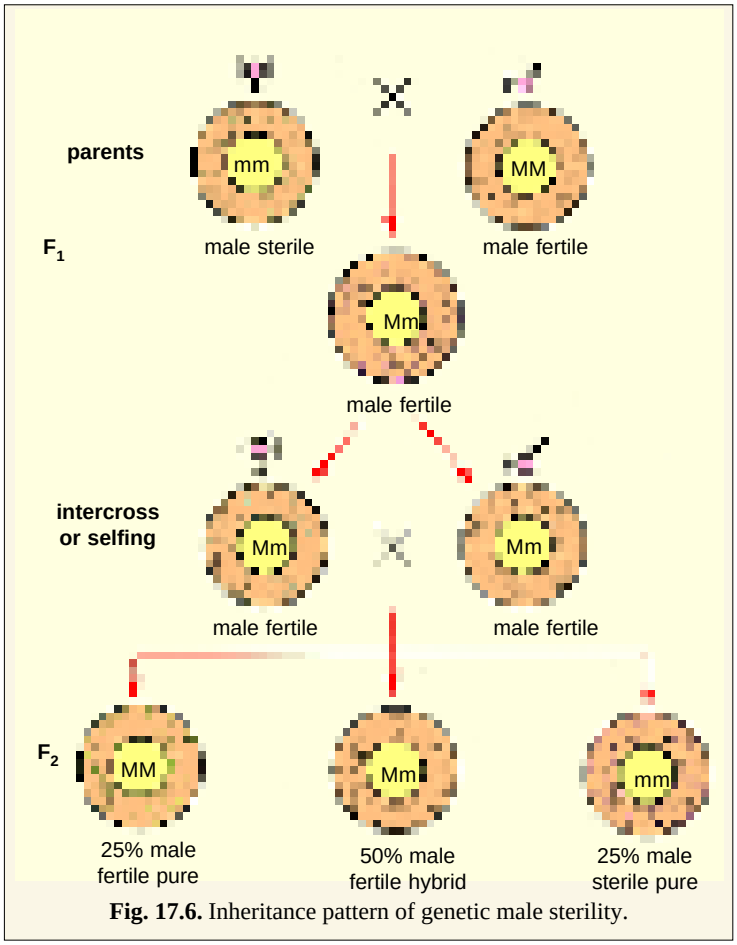


Fig. 17.6. Inheritance pattern of genetic male sterility.

(c) Cytoplasmic genetic male sterility. In certain plants, though the male sterility is fully controlled by the cytoplasm, but a **restorer gene** if present in the nucleus, will restore fertility. For example, if the female parent is male sterile (due to plasmagene of male sterility) then the nuclear genotype of the male parent will determine the phenotype of F_1 progeny. Thus, if male sterile female parent contains recessive nuclear genotype rr of restorer gene and male parent is RR, having homozygous dominant restorer genes. Their F_1 progeny would be male fertile Rr. However, if the male parent is male fertile rr, the F_1 progeny would be male sterile rr. If the F_1 male fertile heterozygote (Rr) is test crossed with male fertile rr male, a progeny with 50 per cent male fertile and 50 per cent male sterile will be obtained (Fig. 17.8).

Since, in maize expression of male sterility depends on an interaction between nuclear and extra-chromosomal genes. Male sterile lines can bear seeds only after cross-pollination. For this reason they are useful in raising hybrid seeds, especially on large scale.

Later on, in maize the following four types of cytoplasms have been recognized : the normal (N) cytoplasm and three types of male sterile cytoplasms (T, C and S). The recent studies of mitochondria in these cytoplasm revealed that the factors responsible for cytoplasmic male sterility are located in mitochondrial DNA (mt DNA) and mt DNA of N, T, C and S cytoplasms are found to be different. The cytoplasmic male sterility (CMS) of C and S type can be reversed by nuclear storer genes, however, the CMS-T cannot.

3. Extra-Nuclear Inheritance by Endosymbionts

Certain intra-cellular parasites such as bacteria and virus particles maintain symbiotic relationship with host cells. They are self-reproducing and look like the cytoplasmic inclusions. Sometimes they exhibit an infection like transmission with a hereditary continuity of their own. Generally such symbionts are coined by letters of the Greek alphabets (sigma, kappa, mμ, etc.). The various types of infective symbionts are as follows :

(i) Sigma virus in Drosophila. L. Heritier and **Teissier** found that a certain strain of *Drosophila melanogaster* shows a high degree of sensitivity to carbon dioxide, where as the wild type strain can be exposed for long periods to pure CO_2 without permanent damage, the sensitive strain quickly becomes unco-ordinated in even brief exposure to low concentrations. This trait (extra-sensitivity) is transmitted primarily, but not exclusively, through the maternal parent. Tests have disclosed that CO_2 sensitivity is dependent upon an infectious DNA virus called **sigma**, found in the cytoplasm of **CO_2 sensitives** Drosophila. These infective particles are transmitted normally via the egg's larger amount of cytoplasm but occasionally through the sperms as well. Carbon dioxide sensitivity may even be induced in normal flies by injections of cell free extracts of sigma particles from CO_2 sensitive flies.

(ii) Spirochaetes and maternal sex ratio in Drosophila. Females of many *Drosophila* species can harbour a population of **spirochaete bacteria** known generally as **SR**. When SR spirochaetes infect the eggs of the host and when these eggs are fertilized, virtually all XY zygotes are killed early in embroyonic development and XX zygotes survive. Thus, the spirochaete can be considered as an endosymbiont of female but not of male *Drosophila*, and its presence in the female gives rise to the condition called **maternal sex ratio**, in which the progeny are exclusively or almost entirely female.

The SR spirochaete is infectious, for when isolated from the haemolymph of female carriers and introduced into normal females the latter become carriers. Why the fe-

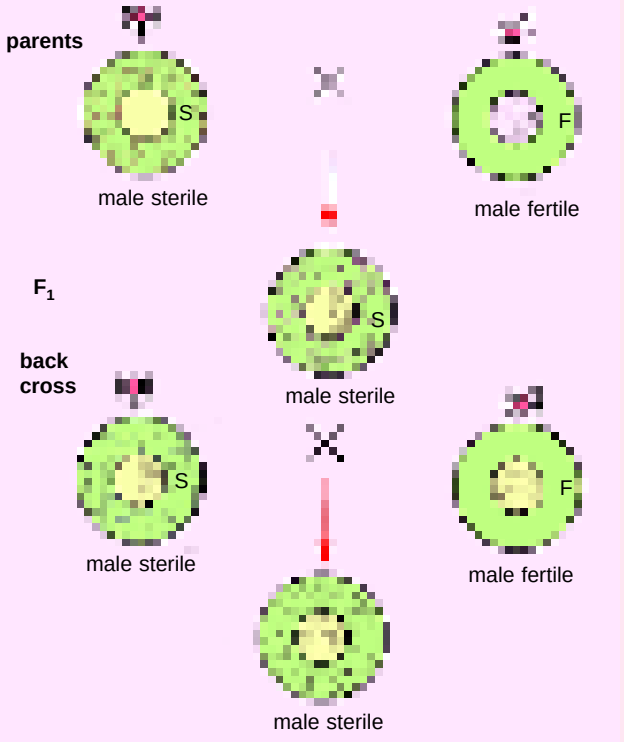


Fig. 17.7. Maternal inheritance of cytoplasmic male sterility.

male genotype permits their retention, and conversely, why XY cells are sensitive to their presence is not yet known. **K. Oishi** and **D. Poulson** (1970) have reported DNA-containing viruses in these endosymbiont spirochaetes of female *Drosophila.*

(iii) Kappa particles. In 1938, **T.M. Sonneborn** reported that some races (known as "**killers**" or **killer strain**) of the common ciliate protozoan, *Paramecium aurelia* produce a poisonous substance, called **paramecin** which is lethal to other individuals called "**sensitives**". The paramecin is water soluble, diffusible and depends for its production upon cytoplasmically located particles called **kappa**. Electron microscopic observations have shown that kappa particles are about 0.4µ long symbiotic bacteria, *Caedobacter taeniospiralis* ; 20 per cent of kappa bacteria of the killer strain contain a refractile protein containing "**R body**" and are called "**brights**". They are infected with a virus that controls the synthesis of toxic viral protein, the paramecin (see **Gardner** *et al.*, 1991). A killer *Paramecium* may contain hundreds (*e.g.*, 400) of kappa particles. The presence of kappa particles in the killer *Paramecium* is dependent for their maintenance and replication on the chromosomal dominant gene K. Paramecia with nuclear genotype kk are unable to harbour kappa particles.

T.M. Sonneborn (1905-1981).

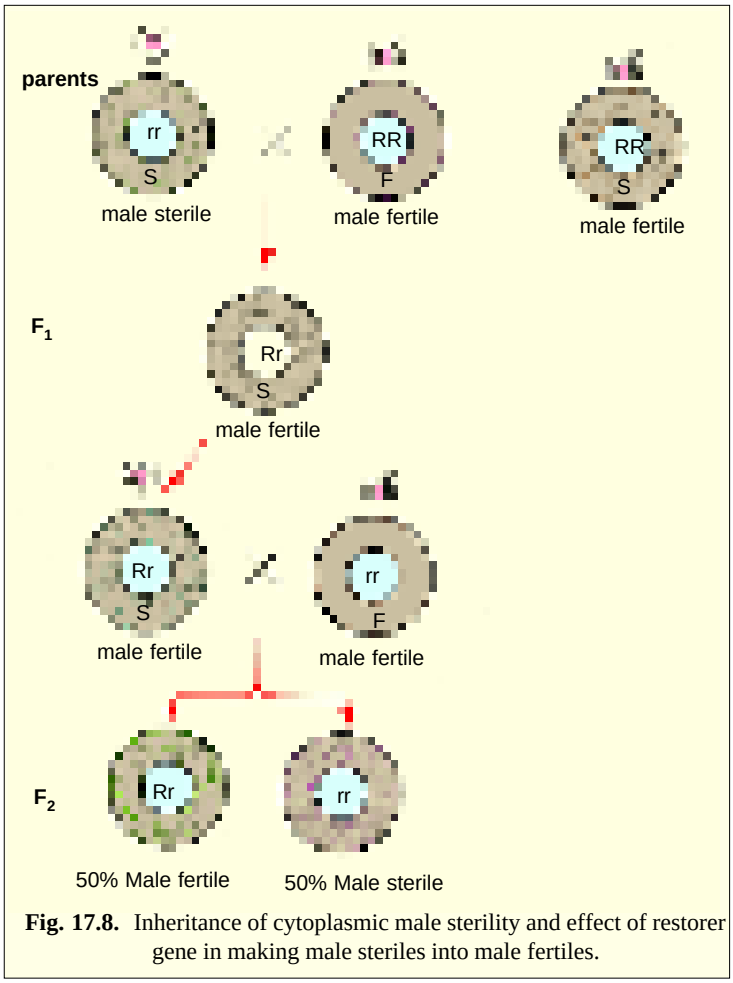


Fig. 17.8. Inheritance of cytoplasmic male sterility and effect of restorer gene in making male steriles into male fertiles.

When a *Paramecium* of killer strain having the genotype KK or (K^+) conjugates with the *Paramecium* of non-killer strain having the genotype kk, the exconjugants are all heterozygous for Kk genes (Fig. 17.9). The Kk genotype suggests that both exconjugant should be killers. But this is not the case. If conjugation is normal, *i.e.*, lasts only for a short time, and no exchange of cytoplasm takes place between the two, both killers and non-killers (sensitive) are produced. However, rare or prolonged conjugation (*i.e.*, lasting for long time) permits mixing of cytoplasm of both conjugants and results killers only. The killer trait is stable only in killer strain with KK genotype and is suitable in sensitive strain with kk genotype.

(iv) mµ particle. Another type of killer trait known as **mate killer** has been reported in *Paramecium* by **R.W. Siegel** in 1952. The mate killer trait is imparted by a

cytoplasmic mμ particle and a *Paramecium* with a mμ particle is called **mate killer** because when it conjugates with a *Paramecium* without any mμ particle is called **mate sensitive**, then it kills the latter. The mμ particles exist only in those cells whose micronucleus contains at least one dominant gene of either of two pairs of unlinked chromosomal genes (M_1 and M_2). The mμ particles are composed of DNA, RNA and other substances and are symbionts.

(v) Milk factor in mice. Bittner found that females of certain lines of mice are highly susceptible to mammary cancer and this trait was found to be maternally transmitted trait. Results of reciprocal crosses between these and animals of low-cancer-incidence strain depend on the characteristic of the female parent. When the young mice of a low-incidence strain are allowed to be nursed by susceptible foster mothers produces a high rate of cancer in them. Apparently this is a case of infective agent transmitted in the milk. This so called milk factor resembles in many respects with a virus and has been discovered to be transmissible also by saliva and semen. The presence of milk factor also depends on nuclear genes.

4. Uniparental Inheritance in *Chlamydomonas reinhardi*

Like fungi, algae rarely have different sexes, but they do have mating types. In many algal and fungal species, there are two mating types that are determined by alleles at one locus. A cross can occur only if the parents are of different mating types. The mating types are physically identical but physiologically different. Such species are called **heterothallic** (literally "different bodied"). In *Chlamydomonas*, the mating type alleles are called mt^+ and mt^- (in *Nerospora* they are A and a; in yeast a and α).

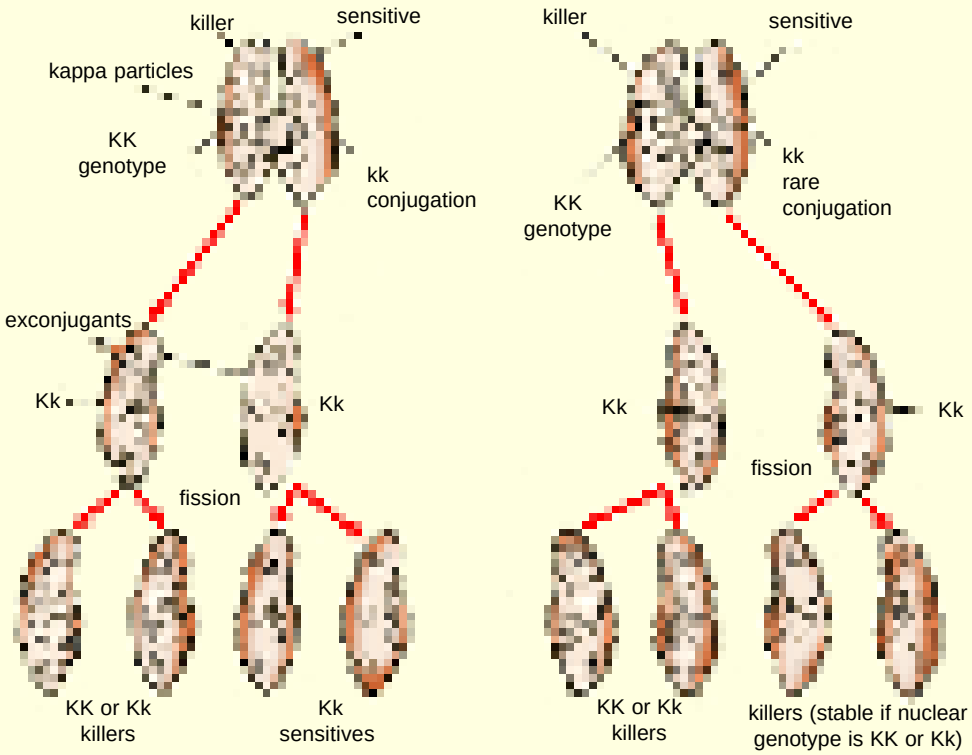


Fig. 17.9. Conjugation in *Paramecium* and the killer trait. Progeny of sensitives are killers only in rare situations where conjugation persists for a longer period so that kappa-containing cytoplasm is introduced into the conjugating sensitive. Kappa particles, however, are maintained only in the presence of K-nuclear genotype (after Burns, 1969 and Gardner, 1968).

In 1954, **Ms. Ruth Sager** isolated a **streptomycin - sensitive** (**sm-s**) mutant of *Chlamydomonas* with a peculiar inheritance pattern. In the following crosses, sm-r and sm-s indicate streptomycin resistance and streptomycin sensitivity, respectively, and mt is the mating-type gene :

mt^+ sm-r × mt^- sm-s → progeny all sm-r

mt^+ sm-s × mt^- sm-r → progeny all sm-s

Here, occurs a difference in reciprocal crosses; all progeny cell show the streptomycin phenotype of the mt^+ parent. Like the maternal inheritance this is a case of **uniparental inheritance**. In fact, **Sager** now refers to the mt^+ mating type as the female, using this analogy.

Ruth Sager.

REVISION QUESTIONS AND PROBLEMS

1. (a) What is the basic test by which cytoplasmic inheritance is distinguished from nuclear inheritance in almost all organisms ?
   (b) What specific properties do chromosomal genes possess?
2. Answer each of the following as briefly and completely as possible :
   (a) Which do you think would be easier to identify, the effects of plasmagenes or the effects of chromosomal genes? Explain
   (b) Why is it often difficult to distinguish between cytoplasmic gene (plasma genes) and viruses?
   (c) What conditions must be satisfied to prove that cytoplasmic genes are present in the chloroplast? Discuss.
3. Discuss the role of chloroplasts and mitochondria in the cytoplasmic inheritance.
4. Write short notes on the following :
   (i) Plasmagenes; (ii) Maternal inheritance; (iii) Male sterility; (iv) Kappa particle; (v) 'Petite' in yeast.
5. Suppose that a snail had a dextral coiling. Upon self-fertilization, it produces progeny all of which showed sinistral coiling. How do you explain results.
6. A male and female *Ephestia* moth, both coloured as larvae, were crossed. About half of the adult progeny were coloured, half were white. What colour did the male and female parents possess as adults?
7. Most strains of *Chlamydomonas* are sensitive to streptomycin(s). A strain is found which requires streptomycin in the culture medium for its survival (sd). How could it be determined whether streptomycin-dependence is due to a chromosomal gene or to a cytoplasmic element ?
8. Exposing a culture of white yeast to the mutagenic action of mustard gas produced some red individuals. When the red mutants were propagated vegetatively, some white cells frequently reappeared. How can these results be explained ?
9. Given seed from a male sterile line of corn, how would you determine if the sterility was genic or cytoplasmic ?
10. A four-o'clock plant with three kinds of branches (green, variegated and "white") is used in a breeding experiment. What kinds of progeny are to be expected from each of these crosses :
    (a) Green female X White male, (b) White female X Green male ;
    (c) Variegated female X Green male ?
11. Determine which of the three paramecial phenotypes (killer, unstable, or sensitive) is produced by the following combinations of genotype and cytoplasmic state.

	Genotype	Cytoplasm
(a)	KK	Kappa
(b)	Kk	No Kappa
(c)	kk	Kappa
(d)	KK	No Kappa
(e)	Kk	Kappa
(f)	kk	No Kappa