Rana sylvatica breeds when temperature is as low as 44°F. *Rana pipiens* starts breeding at 55°F, while *Rana clamitans* breeds at 60°F. Another example is that of American toads — *Bufo americanus* and *Bufo fowleri* (*Fowler's toad*). Both these species remain distinct as the former breeds earlier in season whereas the latter one breeds later. However, under laboratory conditions produce fertile and viable hybrids.

Change in the developmental pattern of a section of a species is one of the means that causes reproductive isolation. For example, in genus of *Cicada* — the common locusts — there are many species which are reproductively isolated. This is due to the change in the lengths of the larval periods. In case of "17-year locusts", the larval period underground is 16 years, so only once in the seventeenth year adult broods appear above the ground and can mate only with their own type in the same territory. Thus, there are 14-year, 11-year, 9-year, 7-year species; and each of them is reproductively isolated in any territory from all others because two species rarely reach maturity in any region during the same season. Similarly, in some of the plants of a species flower earlier or later in the season than others, and they are able to interbreed with only those plants with the same developmental rate.

Seasonal isolation has also been reported in plants. There are ten sub species of cypress trees in California. These species do not interbreed because each fertile race produces pollen at a different time of the year. Similarly in *Cocklebur*s, the flowering time of two species have become so different that in the same area one species flowers only after the other has formed seed capsules.

Mechanical isolation

This type of isolation is provided due to differences in the external-genitalia of the organisms and the structure of flowers in flowering plants, to make the cross difficult between them. Among plants, different species of *Asclepias* of *Asclepiadaceae* differ in the shape of pollinia and that of the stigmatic slits so the pollination is made possible only by a particular insect. Thus, the pollinia of one species cannot bring about pollination on the stigma of another species.

Mechanical isolation has also been reported in the various groups of animals, specially in insects. The external genitalia are developed on the lock and key patterns and only just as one particular key is fitted into a particular lock. Any change in the development of these genitalia prevents the members of unchanged individuals and forces them to breed only with those who have changed, in appropriate fashion. It was asserted by *Dutour* in 1844. For example, in the fish *Anableps*, the male genital orifice is prolonged into a tube. The genital aperture of the female is covered by a special scale, free on one side only. The opening

Chapter 8

ISOLATION

There are three essential factors governing the whole or entire mechanism of evolution. These are *isolation*, *adaptation*, and *variation*. *Mutation*, however, helps in evolution but is not supposed to be the basic factor for evolution. Isolation is a sort of physical or environmental barrier that prohibits promiscuous interbreeding. But environment does not alone control the multiplicity of forms and if it had been true, then one particular environment should always produce the same types of animals and plants. One of the factors that present diversity in animals and plants is *isolation*. Isolation may be defined as the phenomenon that divides a single population into two or more groups by checking interbreeding through some internal or external factors. In the broadest sense, any factor may be said to be isolating means if it interferes with free interbreeding among all members of a species. So preventation of gene-interflow may be called as isolation.

Thus, isolation plays a very important role in evolution. The importance of isolation was first strongly insisted on by *M. Wagner* (1868). Other workers like *Darwin* & *Mendel* also stated the importance of isolation in evolution.

Isolating Mechanisms

The biological characteristics that cause sympatric species to exist i.e. to maintain distinct gene pools — are usually called *isolating mechanisms*. *Mayr* has distinguished three main types of isolating mechanisms :

i) *Restriction of random dispersal* — where the potential mates cannot meet.

(i) *Restriction to random mating* — that does not allow crossing, through the individuals meet.

(iii) *The reduction of fertility* — the hybrid that if produced is sterile.

Dobzhansky described only two types of isolating mechanisms

(i) *Geographical isolation*

(ii) *Permanent isolation*

However, *Goldschmidt* stated only one type of isolating mechanism — the *genetic isolation*. Recently, *Mayr* and *Stebbins* have classified the isolating mechanisms into following types.

A Classification of Isolating Mechanisms in Animals

1. Mechanisms that prevent interspecific crosses (preventing mechanism)

(a) Potential mates do not meet (seasonal and habitat isolation)

(b) Potential mates meet but do not mate (ethological isolation)

(c) Copulation attempted but no transfer of sperm takes place (mechanical isolation)

2. Mechanisms that reduce full success of interspecific crosses (post-mating mechanisms)

(a) Sperm transfer takes place but egg is not fertilized (gametic mortality)

(b) Egg is fertilized but zygote dies (zygote mortality)

(c) Zygote produces an F_1 hybrid of reduced viability (hybrid inviability)

(d) F_1 hybrid zygote is fully viable but partially or completely sterile, or produces deficient F_2 (hybrid sterility)

Premating or Premature Isolating Mechanisms

The premature or prezygotic isolating mechanisms are those that prevent contact between the species when they are sexually mature or ready to meet. These may also prevent the union of the gametes in animals and plants.

Habitat isolation

In this, the potential and closely related species are confined to different habitats in the same general region, and, therefore, seldom or never come together at least during the reproductive phase, as in species of spade foot toads (*Scaphiopus*) that seldom meet because they occupy different soil types (*Wasserman* 1957), and in parasites that mate on different species of hosts. Another example is taken from the snails of the family Archatinellidae. The members of this family live upon trees and cannot travel any distance over land surface devoid of shade or moisture. Various New Zealand species of *Cicada* are strictly confined to different plant associations.

This mechanism of isolations is not very effective in mobile animals like mouse, river fishes and certain species of water snakes. For example, two sub-species of the American mouse (*Peromyscus manicu-latis*) inhabit regions that share a common boundary. When they are brought to the laboratory and crossed, their hybrids survive, but none have been found in nature. Another similar example is taken from the common water snake of N. America, *Matrix sipedon*. It has two races, fresh water and salt water which are kept separate by their habitat preferences. Apparently members of the two groups rarely encounter each other. *Summer* has made an intensive study, in Florida, of three sub species of mouse, *Peromyscus polionotus*, which is found there. The peculiarity is related to the nature of its habitat.

Ethological or Behavioural isolation

It is also called *sexual isolating mechanism*. It includes differences in the courtship behaviour of males, in the vocalizations, or chemical signals (phenomares) by which one sex attracts the other, or in the colour pattern or other morphological features by which an individual recognizes a potential mate. Female fire flies, for example, respond to the light pattern emitted by males of their own species. It is sometimes possible to induce hybridization by altering such characters, showing that they indeed prevent interbreeding. Smith (1966), for example, induced species of gulle (*Larus*) to interbreed by changing the contrast between the eye and the feathers of the face.

Scent plays a major role in mating responses in *Lepidoptera* while songs play the same role in birds. In spiders, courtship antics and male decoration have a real value as recognition marks. It appears that unless the female recognises the male as belonging to her species she will often eat him, and the peculiar dances of the males assist the females to avoid mistakes. This type of mechanism is also found in higher animals, such as deer, mice, *Peromyscus*, which do not interbreed in a state of nature.

In angiosperms, even if pollen is transferred to the stigma of another species, it may not germinate; or if it dies, the pollen tubes may fail to reach the ovules because they grow slowly: there is physiological incompatibility to a greater or lesser extent between pollen and pistil.

Seasonal isolation

In many cases the photoperiodism, temperature and humidity act as seasonal barriers. In such areas the organisms do not interbreed because they become sexually mature at different times of the year or under different condition. Specific differences in breeding season or seasonal occurrence are extremely common in insects and most of other animals. In the north-eastern United States, three species of *Rana*, all mate in the same ponds at different times at different temperatures.

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may be on either the right or the left side and the males may have the intromittent organ turned in either direction, copulation taking place side ways and the right sided male always pairs with a left sided female and vice versa. Similarly, interspecific crosses in *Drosophila* may cause injury or even death to the participants. The same is true in the case of *Glossina* — the tse-tse fly and in pulmonate snail — the *Polygyrinae*. According to *Mayr*, the intromittent organs in animals are very complicated and are under the control of *pleiotropic genes*. Any change in such genes may change the external genitalia and thus making the inter cross difficult.

Post Mating Isolating Mechanisms

The post mating isolating mechanisms do not interfere in pollination or copulation but prevent the growth of hybrid individuals. Thus, this category includes the mechanisms that reduce full success of interspecific crosses as given under the following sub-heads:

(i) Gametic mortality

The gametes remain viable for a considerable period that varies from organism to organism. The male gametes or sperms can tolerate only narrow range of fluctuation like pH, temperature, etc., while outside the body, but inside the female reproductive tract of the same species they meet favourable environment, that is why their viability may be prolonged. If the sperms are introduced in the female tract of other species, deviation from the physiological compatibility would prove lethal to sperms. *Patterson* reported such "insemination reactions" to occur in many *Drosophila* which leads to an enormous swelling of the walls of the vagina and the subsequent killing of the spermatozoa.

(ii) Zygomatic mortality

In this, the pollination or copulation takes place in a usual way. The process of fertilization is also normal but the zygote dies off due to the irregular development. The causes for the development arrest or mortality may be cytological, genetical, developmental, biochemical or physiological. For example, under laboratory conditions the hybrids of *Rana pipiens* and *R. sylvatica* do not develop beyond the early gastrula stage (*Moore* 1961). Similarly, the hybrids of *Ambystoma* lack nucleolus that is why the zygotic mortality is brought about. This type of zygotic mortality has also been studied in some plants. The inter-specific hybrids of two species of *Datura* result in the death of the embryo at the eight celled stage.

(iii) Hybrid inviability

In this category, the mechanism upto the formation of zygote remains normal but the zygote produces an F_1 hybrid of reduced viability. The hybrids between the frog *Rana pipiens* and *R. sylvatica* do not develop beyond the early gastrula stage, but if they develop, may fail to survive in nature. Similarly, the hybrids between the butter chips *Ranunculus millanii* and *R. dissoctifolius*, which occupy wet and dry habitats respectively, cannot compete successfully with either parent in the parent's habitat and so in nature occur only in intermediate, disturbed habitats. Hybrids that do survive often fail to reproduce, either because they are sterile or because they have inappropriate mating behaviour. *Rao* and *De Bach* (1969) found that male hybrids between species of parasitic wasps (*Aphytis*) were accepted by hybrid females but not by females of either parent form.

Hybrid sterility

In this category the F_1 hybrid zygote is fully viable but partially or completely sterile, or produces deficient F_2. The hybrid sterility can have a chromosomal or a genic basis, although the distinction sometimes breaks down. Gross differences in chromosome structure such as multiple translocations, commonly cause sterility because many or most of the gametes are deficient for whole chromosomes (Aneuploid) or for portions of chromosomes (*Grant* 1981).

The diploid hybrid between the primoses *Primula verticillata* and *P. floribunda* is sterile, but tetraploid hybrids called *P. kewensis* have been produced by artificial means, and these are fully fertile. It is only because of the occurrence of unpaired chromosomes in diploid hybrid and paired chromosomes in tetraploid hybrid. This example shows that the sterility of the diploid hybrid is caused by incompatibility in chromosome structure rather than in genes. In contrast, the chromosomes of the hybrid between *Drosophila pseudoobscura* and *D. persimilis* pair normally, yet the males have atrophied testes and are sterile. This is called the *genic sterility*. Likewise the functional offspring, mules of horse and donkey are sterile. The horse and donkey each contributes 33 chromosomes to the offspring. These chromosomes fail to pair in mule that is why it becomes sterile.

Hybrid breakdown

Sometimes, the hybrids can be more or less fertile, but give rise to weak, abnormal, or sterile offspring in second generation or F_2. The phenomenon is called *hybrid breakdown*. *Merrell* (1962) described that even vigorous fertile F_1 hybrids produce hybrid breakdown in F_2. F_2 generation may be responsible for reproductive isolation.

Other Types of Isolation

(i) Geographic Isolation

Most important and familiar isolating agency is that of geography of the particular region. In regions broken by few barriers, migration

and interbreeding being allowed, we find widely distributed species, homogeneous in their character, the members showing individual fluctuations and climatic effects, but remaining uniform in most regards, all representatives slowly changing together in the process of adaptation by natural selection. In regions, broken by barriers which isolate groups of individuals, we find a great number of related species, though in most cases the same region contains a smaller number of genera or families. In other words, the new species will be arising depending on the isolating conditions, though these same barriers may shunt out altogether forms of life which would invade the open district.

Just as islands of land in seas, water plays the role of isolating factor, similarly islands of water in seas, land plays the role of isolating measures. Thus, isolated ponds or lakes separate the aquatic types from others found in other parts of world. Similarly, on the other hand, there are many types of plants characteristic of high mountains which are commonly isolated from others of their kind by means of valley or by mountain chains.

In Britain, a famous example of geographic isolation among birds has been given by *Salomonsen*. *Gulick* also explained the distribution of Himalayan landsnails by geographic isolation. *Mayr* also noted that if birds, which while travelling, are separated by storm, they establish a new place of residence isolated from others.

(ii) Isolation due to distance

Sometimes what happens is, if a species occupy a wide territory is broken by some barrier, there will be isolation because of great distance between the types. Thus, isolated types will show diversity. A body of land known as "Holarctica" embodying Northern Asia, Northern Europe and N. America, is believed to have been the principal theatre of mammalian evolution. In this area, there are many chances for animals to get spatially isolated even without positive barriers. It is also believed that all original divergences occurred in this area and it gave origin to the principal sub-divisions of mammals.

Wrens of South America which are present almost all over the continent, show great diversities in colour, size, proportions and habits from place to place. In certain regions, even transitional forms are missing. Thus, sheer distance apart also tends to produce local races.

(iii) Biotic Isolation

Living organisms have abiotic and biotic environment and we have seen that abiotic factors influence the life of animals and plants. Similarly any species of animal or plant is always surrounded by other types. Each species affects all the other species with which it is spatially associated, every species is a part of biotic environment of all the others.

If, then, the biotic environment varies within the range of the species, the pressure of selection will vary and certain characters will appear favourable for one biotic condition.

(iv) Psychic Isolation

Among lower animals, there is tendency known as "Assortative mating" which means to mate with like types. In human beings, this conventional mating is highly developed. In many insects, copulation occurs without elaborate courtship behaviour. Females readily accept only males which observe the courtship behaviour characteristic of their species. Birds are also of great interest in the study of behavioural factors.

Origin of Isolation

The mechanism of isolation has been described in two most convincing theories by *Muller* and *Dobzhansky*. According to *Muller*, reproductive isolation is an incidental by product of genetic divergence, which takes place during the origin of sub-species and species in *allopatric populations*.

On the other hand, according to *Dobzhansky*, reproductive isolation takes place because of natural selection. Nature, itself selects the suitable species and reduce the wastage of gametes.

Isolation and Inbreeding

One of the consequences of the isolation of a small group from the main body of the species is inbreeding. More or less close, the offsprings of such a pair, if they breed at all, must breed together, and for successive generations there will be much close inbreeding. It is also confined genetically that continuous inbreeding decreases heterozygous and increases homozygous individuals.

Isolation and Selections

Selection promotes divergence in the species. Whenever any group of species becomes isolated from the parent stock, selection tends to preserve individuals with either the dominant or the recessive of any unit character or any combination of these which prove to be advantageous to the individuals. So during this process, it is possible that some genes may be entirely eliminated from a stock. In this way, a small section of a species becomes isolated in a particular region and new characters and combinations were adopted and thus same species get them isolated into different groups.

Genetic basis of isolating mechanisms

Each type of isolating mechanism is based upon differences in respect to many different genes or chromosomal segments. The sterility of hybrids may be due to the following reasons:

(1) Failure of chromosomes to pair
(2) Chromosomal aberration like translocation, duplication, deletion and inversion.
(3) Homologous genes fail to arrange in pairs
(4) Combined effect of some genes.