

Evolution

Isolation and Isolating Mechanisms

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ISOLATION AND ISOLATING MECHANISMS

Anyone who has some familiarity with the living world realizes that organisms are not uniformly distributed over the earth's surface, that is, they are isolated. If we look at the literal meaning of isolation then it is "to put or keep things or people entirely apart or having little contact with or nothing in common". Thus, in lay man's language isolation is a mechanism or a barrier to keep populations apart or out of contact with each other. In other words, it is segregation or separation of populations or organisms to form smaller units. For example, if we are sitting in a classroom A which is separated from other such classroom B by a wall, then the wall is the isolating mechanism which keeps the students apart or out of contact with each other. But biologically speaking, the modern definition of isolation is any genetically conditioned impediment or obstacle to gene flow between populations.

Isolation was thought to be important in evolution even at the time of Lamarck and Darwin, who believed that interbreeding of genetically distinct populations results in swamping of differences. Wagner and Romanes, however, stressed the importance of isolation in evolution and stated that organic evolution was not possible without isolating mechanisms because the essential role of isolation in evolution is maintenance of organic variations produced in natural populations through the process of natural selection. But it was Theodore Dobzhansky who coined the term "isolating mechanisms" in his classic work "Genetics and the Origin of Species" in 1937 and divided them into two broad categories:

1. Geographical Isolation operating in geographically isolated populations or allopatric species and
2. Reproductive Isolation where gene exchange between populations is restricted due to genetically controlled mechanisms.

A rigorous test of efficient reproductive isolation is however the ability of populations to co-exist sympatrically with little or no gene flow between them. For example, a crow and a sparrow living on the same tree are sympatric as well as synchronous species but they still do not interbreed and are therefore completely isolated.

There are several important characteristics of isolation which can be underlined. First, there are different types of isolating mechanisms such as geographic, seasonal, habitat etc. Secondly, they co-operate or co-ordinate with each other to bring about complete isolation between the two populations in nature. For example, in *Drosophila pseudobscura* and *Drosophila persimilis* a combination of ethological, temporal, hybrid sterility and hybrid breakdown operate where none by itself is sufficient to block hybridization but in combination bring about complete isolation of the two sympatric species in nature. Moreover, there are various degrees of isolation, that is, it can be complete or incomplete or partial. Extending the same example of the classroom which we had used to illustrate the concept of isolation, the students in the two classrooms are only partially isolated because they can still exchange information by shouting across the wall. But if the classrooms are in different buildings or areas or cities, the isolation is complete as there can be no flow of information or students are out of contact with each other.

There are various types of classifications of isolating mechanisms given by different scientists at different times. Some of them are outlined below:

1. .Savage's Classification:

(i) Spatial Isolation (External Barriers-Barriers between populations)

- a. Ecological
- b. Ethological
- c. Morphological
- d. Physiological

(ii) Genetic Isolation (Internal Barriers-Barriers between hybrid populations)

- a. Hybrid weakness or inviability
- b. Hybrid failure to attain sexual maturity
- c. Hybrid sterility
- d. Hybrid nonviability or sterility in later generations

2. Mayr's Classification:

By geography and level

- (i) Hybridization (maintenance of reproductively isolated hybrids between two species)
- (ii) Instantaneous speciation (through individuals)
 - a. Genetically (single mutation)
 - b. Cytologically
 - i. Chromosome rearrangement
 - ii. Polyploidy
- (iii) Gradual speciation (Through populations)
 - a. Sympatric speciation
 - b. Parapatric speciation
 - c. Allopatric speciation
 - i. Peripatric speciation (by evolution in an isolated colony)
 - ii. Vicariant speciation (division of range by an extrinsic barrier or extinction of intervening populations)

3. Meham's Classification:

(i) Premating/Prezygotic mechanisms (Isolation mechanisms which prevent inter specific crosses)

- a. Potential mates do not meet
 - i. Geographic isolation
 - ii Isolation due to distances
 - iii Climatic isolation
 - iv Seasonal or Temporal isolation
 - v. Habitat or ecological isolation
- b. Potential mates meet but do not mate
 - i. Ethological isolation
- c. Copulation attempted but transfer of sperms does not occur
 - i. Mechanical isolation
 - ii Physiological isolation

(ii) Postmating/Zygotic Mechanisms(Isolating mechanisms which reduce the full success of interspecific crosses)

- a. Sperms are transferred but eggs are not fertilized
 - i. Gametic mortality
- b. Egg fertilized but zygote inviable
 - i. Zygotic mortality
- c. Zygote produces F1 hybrid of reduced viability
 - i. Hybrid inviability/inferiority
- d. Hybrid viable but partially or completely sterile
 - i. Hybrid sterility
- e. Reduce viability or fertility in the progenies of hybrids
 - i. Hybrid breakdown

4. Templeton's Classification:

By population genetic mode

(i) Transilience

- a. Hybrid maintenance (Selection for hybrids)
- b. Hybrid recombination (Selection for recombinants following hybridization)
- c. Chromosomal (Fixation of chromosomal rearrangements by drift and selection)
- d. Genetic (Founder event in a colony)

(ii) Divergence

- a. Habitat (Divergent selection without isolation by distance)
- b. Clinal (Selection on a cline with isolation by distance)
- c. Adaptive (Erection of an extrinsic barrier followed by divergent micro evolution)

We shall follow the Meckam's classification, where the isolating mechanisms are arranged like a series of hurdles, if one breaks down, another must be functioning to accomplish isolation.

Premating Mechanisms:

1. Geographic Isolation: In this type of isolation the two populations are separated by some physical or geographic barrier, which must be present at the time of breeding. They may be mountain ranges, vast stretches of desert, thick forests, deep oceans or water bodies, land bridges etc. The barriers prevent migration and intermingling of the individuals of the two populations, reducing the exchange of genes between them so that the populations are genetically out of contact with each other and follow an independent evolutionary path. With passage of time each population forms a separate unit. The degree of distinctness between these populations is related to the effectiveness of the barrier, the duration of separation and the degree of migration. For example, the two species of *Drosophila*, *D. persionites* and *D. pseudoobscura* inhabit the same geographical area but are isolated by the altitude, where former occupies high altitude whereas the later is present at low altitudes. Similarly the distribution of land snails in Hawaiian island of Oahu is an example of geographical isolation. Here the volcanic ridges of the island are separated into valleys with abundant vegetation at the bottom and tops being barren. Each valley has a different variety of land snail and the degree of divergence between them is directly related to the distance between the valleys.
2. Isolation due to distance: This type of isolation is seen in sedentary organisms or animals with limited powers of mobility. The members of a widely distributed population without any physical or external barrier, have also been found to be reproductively isolated simply because of their inability to cover large distances. The effectiveness of this type of barrier depends upon the "homing instincts" and "territoriality" behaviour of animals. Animals like to carry on their reproductive activities not far from the region in which they themselves were born and brought up. Thus any possibility of gene exchange between such populations is through occasional migrants or chain of intermediate populations. For

example mammals found in the Holarctic area of north America do not form hybrids because they are unable to cover such long distances.

Isolating mechanisms can be considered as “bridgeless¹ gaps” across which interbreeding doesn’t occur

Climate Isolation:- If there are no physical or external barriers present between the two populations, they can still be isolated into discrete units by the climatic isolation. In this type of isolation differences in climatic factors viz. temperature, moisture, salinity, length of the day, intensity of light etc. act as barriers to exchange of genetic information between the two populations. These factors in turn influence the metabolism and produce physiological differences between organisms e.g. some plant species viz. spiderworts *Tradescantia canaliculata* and *T. subaspera* are sympatric, yet remain isolated because one species grows in sunlight and the other in deep shade.

Seasonal Isolation:- This type of isolation is found between populations in which the members reach sexual maturity either at different times of the season (viz. summer or fall) or even at different times of day (i.e. day or night). Differences in the breeding season are able to check interbreeding between different populations. It is frequently observed in plants, where flowering in different species is strictly under the control of photoperiod, intensity of light as well as temperature e.g. two species of Pines, *Pinus radiata* and *P. muricata* grow together on Monterey Peninsula in California. But no hybrids are seen as the former sheds pollen in early February and latter in the month of April.

In animals, it’s observed in almost all seasonal breeders particularly in insects, amphibians, fishes etc. e.g. Blair found seasonal isolation in two species of toads—the American toad (*Bufo americanus*) which prefers to live in forested areas and fowler’s toad (*Bufo fowleri*) which is found in grasslands. Natural hybrids between these two species are rare because *B. americanus* breeds early in the rainy season whereas *B. fowleri* breeds late. However, during the overlapping season, considerable hybridization occurs and the hybrids resemble another species of toad, *B. woodhousii*. Hybrids can also be produced in laboratories where they reproduce in captivity.

Seasonal isolation is also known as *temporal isolation* and interspecific differences lead to this type of isolation e.g. *Drosophila pseudobscura* and *D. persimilis* are sympatric over a large area in North America. They breed during the same season of the year but at different times of the day. *D. Pseudobscura* is sexually active in the evening while *D. persimilis* in the morning and hence don’t form hybrids. This term was coined by Moore. **Habitat/Ecological Isolation/Environmental Isolation.** It’s caused due to differences in the habits of organisms w.r.t. food and other physiological requirements. According to Mayr and Stebbins, Ecological Isolation by itself is not very effective in preventing interbreeding of populations that move about freely but it’s more effective in plants, or organisms which are sessile. It occurs in species which occupy different habitats (*biotopes*) in the same territory. Since, each population occupies an appropriate habitat or niche by force of inter-specific competition, they develop habitat isolation. Ecological differentiation reduces chances of successful hybridization between sympatric species and hence contributes to their isolation. Here, populations differ genetically in their ecological requirements and preferences e.g. different species of *Drosophila* living in the same area may have different nutritional requirements feeding on different kinds of yeasts. Similarly plants may prefer particular soil type viz. different species of *Ceanothus* in California. – *C. jepsonu* is found exclusively on basic soils, whereas *C. cuneatus* has a broader range of tolerance to soil type. Both the species grow together but natural hybrids are rare, though the two species can be crossed artificially to

produce fertile hybrids. DeBuck, Hackett, Missirolli *et al* did pioneering work on *sibling species* of *Anopheles maculipennis* group. They showed that there are at least five species in Europe and Western Asia that are morphologically similar as adults however distinct in characteristics of their egg “floats”, gene arrangement in chromosomes, in courtship rituals, inability or ability to transmit malaria and in their habitat preferences e.g.

Anopheles labranchiae and *A.atroparvus* live in brackish water while *A. maculipennis* is found in running freshwater and *A. melanoon* and *A. messeae* inhabit stagnant freshwater.

Although habitats of different species may not be far distant from each other, distinct preferences of these species contribute to their reproductive isolation. Similarly pig frog (*Rana grylio*) is aquatic and occurs in deep ponds, lakes and marshes, breeding in deep water, whereas gopher frog, (*Rana areolata*) found in mammals and tortoise borrows during day but active at night around margins of swampy area. It breeds in isolated grassy ponds in shallow water. Therefore differences in ecological preferences eliminates chances of possible mating between species.

Ethological/Psychological/Behavioral/Sexual Isolation. The ethological Isolation derived from the Greek word *ethos* meaning habit or custom is brought about by differences in courtship behaviour displayed by different animals. As we already know that in sexual reproduction, union or fertilization is preceded by a series of acts, the courtship behaviour. Males show specific behaviour towards females of the *same* species and females in turn respond to these displays. This was called as *species recognition* by Patterson. The act of mating is completed only when there is an appropriate exchange of stimuli. Thus, ethological isolation involves barriers to mating, which can be visual, auditory, olfactory chemical ,or tactile. It's a result of weakening or absence of sexual attraction between males and females of different species. Ethological Isolation ensures that mating occurs between members of same species e.g. in peacock, males are more ornamental and they attract the female by its body form and unique plumage and characteristics movements (“dance”). These visual displays are specific and recognized by the female of the same species as the display is highly con-specific. Similarly auditory stimuli or other acoustic signals viz. songs, calls and croaking of frogs etc. play an important role in the courtship of frogs, toads and birds. Marta Martinez Well and Charles Henry (1992) studied three morphologically indistinguishable species of green lacewings (*Chrysoperla*) in which male and female engage in a duet. Closely allied Grey tree frog (*Hyla versicolor*) and pinewood tree frog (*H. femoralis*) frequently breed in same ponds in New Orleans and the principal barrier to interbreeding is behavioral (auditory signals).

Female frogs locate males by the calls given by latter after they reach the breeding ground. It was shown by Little John after recording the sounds and reproducing it by loudspeakers that the call of *H. versicolor* was a short shrill, loud and resonant lasting for 3 seconds whereas that of *H. femoralis* consisted of series of short sonorous dots and dashes. The females could distinguish between these calls and there was no mixed mating. In the same way, chemical mediators also encourage/facilitates mating between same species. Chemical stimuli are detected either on contact or by olfactory organs. Many chemical secretions are produced by certain organisms to attract the females of the same species. e.g. mammals secrete hormones, whereas insects produce “pheromones” or sex attractants which are highly species—specific. Coyne and Coworkers (1994) found that male courtship in *Dorsophila* group depends on their attraction to specific hydrocarbons in the female cuticle.

Mechanical Isolation/Non-Correspondence of physical parts:- This isolation comes about because of different and complex structure of genital organs, in different organisms which, in

turn, doesn't allow copulation to occur between different species. This is particularly true of insects, where according to Dufour, genitalia are supposed to work on "lock and key" principle, like enzymes. The male and female genital organs are exactly fitted to each other and copulation doesn't occur even if there is slight difference in the structure of either organs e.g. Inter-specific crosses between different species of *Drosophila* can cause injury or even death to the female. Copulation between female *Drosophila pseudobscura* and male *D. melanogaster* is simply impossible.

Similarly, males and females of different dog breeds, varying in sizes, may be attracted to each other but are unable to copulate. The Recent view is however that Mechanical Isolation resulting from an imperfect structural fit between genitalia is seldom a barrier to gene exchange among animals not even in insects. Mechanical isolation is very well developed in plants, more so, in insect fertilizing plants. e.g. Grant (1971) observed that floral structure of *Aquilegia formosa* pollinated by humming birds and that of *Aquilegia pubescens* pollinated by hawk moth is very elaborate and quite different in morphology and hence hybrid formation between the two species do not occur. An interesting example is offered by flowers of different species of orchids of North Africa, where different orchid flowers mimic females of different species of wasps. The similarity is so striking that male wasps are attracted to this flower and even engage in "pseudocopulation" with them. But each species has a unique floral structure and there is no inter-specific pollination/breeding. There are many such examples like *Salvia apiana* pollinated by large carpenter/bumble bees and closely allied *Salvia mellifera* by 12 species of small and medium sized honey bees, but in nature no hybrids are found.

Physiological Isolation:- Certain species are isolated on account of physiological differences between them. It's important in some marine animals which discharge their egg cells and spermatozoa into ambient water and let the fertilization take place outside parental bodies. Attraction between eggs and sperms of different species may be reduced or absent due to certain physiological differences between them. Leopard frog (*Rana pipiens*) breeds early in the year and deposits its eggs in globular submerged mass near water's edge. Bronze frog (*R. clamitans*), however breeds early in the month of April and eggs are laid in a thin film at the surface of water. Physiological control of breeding season and egg deposition produces a barrier to mating and fertilization respectively. A classical example is seen in certain species of *Drosophila*, where inter-specific mating is not possible, because vaginal mucous membrane swells up after copulation. This swelling lasts for few hours if mating is conspecific but continues for days if it's inter-specific, known as insemination reaction. It results in the mortality of the fertilized eggs in the parent's body, as they fail to get laid down.

Physiological isolation is also very common in plants e.g. if the pollen grain from one species of plant (say, 'A') fall on the stigma of another species (say, 'B'), the pollen grains either fail to germinate or the pollen tube grows very slowly or the growth is arrested so that it fails to reach the embryo sac.

Post-mating Mechanisms

We have already seen that isolating mechanisms are arranged like a series of barriers. If one breaks down, the others come up to prevent hybrid formation. Thus, if premating isolating mechanisms fail which are most economical, nature takes the help of a second line of defence i.e. the post-mating mechanisms to bring about isolation amongst populations. These mechanisms are of following types:-

Gametic mortality:- It is seen in both types of organisms with external or internal fertilization. Here, the sperms fail to fertilize the eggs leading to gamete mortality e.g. *Volpe* observed in toad species of *Bufo fowleri* and *B. valliceps* that a male with non-functional gonads but with normal sex behaviour induces the female to lay eggs in water but the eggs perish, when they're not fertilized. The same phenomenon is also encountered in sea urchins (*Lillie*). In abalones (large gastropods), the sperm carries a lysin protein that dissolves a hole in the egg's vitelline envelope but only if egg and sperm are of same species.

Gametic mortality is more developed in forms showing internal fertilization e.g. *Patterson* observed that sperms from different species, while passing through the vaginal canal of female faces an antigenic reaction. It may in turn; get immobilized or killed. Therefore, hybrids between related species of *Drosophila* viz. *D. americana*, *D. virilis*, *D. montana* etc. are not found.

Zygote mortality:- In nature, it's observed that if an organism is able to elude all the earlier isolating mechanisms and somehow able to form a hybrid, the zygote so formed shows irregular embryogeny which can cease at any stage of development. Since there is no perfect matching of two chromosomes, zygote fails to be formed or the sperm nucleus is totally eliminated from the spindle. e.g. eggs of fishes can be artificially inseminated by sperms of many different species, but development is abnormal. However hybrids between goat and sheep proceed normally in early stages of development but die before birth.

Similarly, the hybrids between bullfrog and gopher frog pass successfully through early stages of development but die before reaching tadpole stage.

Hybrid invariability/inferiority:- Some hybrids not only survive but exhibit luxuriance e.g. mule (a cross between horse and ass), but they are like the proverbial needle in a haystack. Normally the hybrids in nature don't survive or form unisexual progenies (hybrids of one sex specially male die). e.g. embryos produced by crosses between female fowler's toad and male Gulf coast toad develop normally into adult, but adults are all males and sterile. Natural hybrids are also found to be weak and the weakness is probably due to physiological disturbance or ecological differences. *Leibach* described hybrid inferiority in a cross between *Linum perenne* (male) and *L. austriacum* (female). The hybrid embryo [the seeds] are so weak that they're not able to break open the testa and hence die within the seed and fail to germinate. But, when they are artificially freed from the seed coat, they show luxuriant growth, growing into healthy seedlings and maturing as fertile plants. *Moore* found various degrees of inviability among hybrids between closely related species of *Rana* e.g. Even artificial crosses using sperm and egg preparations obtained in the laboratory between *Rana pipiens* and *R. catesbeiana* show wide range of inviability. In some crosses, no egg cleavage occurred, in others cleavage and blastula stages were normal but gastrulation failed and in still others early development was normal but later stages failed to develop. *Sonneborn* and his students observed conjugation between sibling species of *Paramecium aurelia* group. If exchange of nuclei between conjugating pairs takes place, hybrids may die (hybrid inviability); if they survive their progenies may show various degrees of inviability (hybrid breakdown). In hybrid viability, only one survives and it's usually homozygous e.g. human females (XX) have better chances of survival.

Hybrid Sterility:- The hybrids arising from certain inter-specific crosses are either partially or completely sterile. This might be because of failure of pairing of chromosomes at meiosis, or abnormalities like formation of fused spindle or failure of cell division in the spermatocytes or disharmonious interaction of genes. Mule is the classical example of vigorous but completely sterile hybrid. The sterility is due to disturbances in sex cell formation and failure

of gene complements of distinct species to function harmoniously. Another example is of embryos produced by crosses between female Fowler's toad and male Gulf Coast toad, which form the so called "normal" adults. Adults are all male and sterile. Very frequently only one sex is sterile in the hybrid and that is *heterogametic sex* (*Haldane's Rule*), supported by Coyne and Orr (1989).

Hybrid breakdown:- Some interspecific hybrids are partially or completely fertile in one or both sexes. If so, it still doesn't necessarily follow that gene exchange between populations of such species can take place without any problem. Hybrid breakdown may occur in second or backcross generations. Its cause is formation of genotypes of low fitness, owing to recombination of gene complements of parental species. F₁ hybrid females from *Drosophila pseudobscura* and *D. persimilis* crosses are vigorous and deposit as many eggs as non-hybrid females. Yet, when these females are backcrossed to males of either parental species, individuals of both sexes in offspring's are weak and many of them are sterile. The degree of hybrid breakdown varies depending on strains of parental species used to produce hybrids. Many examples of hybrid breakdown have also been observed in plants e.g. hybrids between cotton species *Gossypium barbadense*, *G. hirsutum* and *G. tomentosum* have been thoroughly studied by Stephens. With some exceptions, these cotton species give rise to vigorous and fertile F₁ hybrids but F₂ hybrids die in the seed or seedling stages or produce "unthrifty" plants.

Origin of Reproductive Isolation:- There are two views regarding the origin of Reproductive Isolation, which are not mutually exclusive. One is *Muller's view*, which believes that Reproductive Isolation is accidental by product of *genetic divergence* in *allopatric populations*. Here, first the geographic isolation brings about splitting of original population into two sub-populations which occupy two different environments and are subjected to independent evolutionary pressures i.e. mutation, selection and genetic drift occur independently in these sub-populations in accordance with its immediate environment. Therefore, the gene pool of each population changes in response to its own particular environment. When this continues for several generations, leads to complete reshuffling and remodelling of the genetic constitution. In other words, the genotype of the two sub-populations becomes disharmonious or "out of contact" with each other. Now, if these populations happen to become sympatric or get an opportunity to interbreed, will not form hybrids because of their disharmonious genotype. The other viewpoint was originally put forward by A.R. Wallace in 1889 and later developed by some modern authors, particularly Theodore Dobzhansky. They observed that hybrids of certain species are often weak, sterile, inviable or less adapted to the environment than the wild type, and hence eliminated by Natural Selection. Natural Selection doesn't favour hybridization and establishes reproductive isolation between closely related populations.

Therefore, it can be concluded that post-mating isolation mechanisms arise mainly as by products of genetic divergence and premating ones are induced/enhanced by Natural Selection e.g. Evolution of several endemic (populations confined on Island) species of plants and animals in Hawaiian archipelago. Ancestors of such species arrived long ago and became adapted to local conditions. Although Natural Selection didn't directly promote reproductive isolation but later on, it became complete: the process of speciation involves both the processes postulated by the two theories. *Reproductive Isolation starts as incidental byproduct of genetic divergence but it's completed when it becomes directly promoted by Natural Selection. Multiple Gene Hypothesis or Multiple Allele Substitutions* has also been proposed to explain origin of Reproductive Isolation. This was called as *gradual speciation*

by Mayr. It's probable that formation of isolating mechanisms involves mutations in more than one gene and may involve building up of system of complementary genes. Assume that population has a genetic constitution (aabb) where a and b are single genes or groups of genes. If the population is broken up into 2 allopathic sub-populations. In one gene, a mutates to A local race AAbb is formed and if 'b' mutates to B, another local race aaBB arises. Since individuals of constitution aabb and AABB interbreed freely, there is no difficulty in establishing in the population the gene A.. Similarly for 'B'. But crosses between AAbb and BBaa is difficult or impossible, because interaction between genes 'A' and 'B' produces reproductive isolating mechanism. If these populations become sympatric, they're reproductively isolated because interbreeding is not possible. Thus, development of reproductive isolating mechanisms between Mendelian populations occur when these populations are geographically separated and also due to genetic changes in these populations involving mutations in several genes.

Role of isolation

Isolation has been recognized as one of the most important factors in the process of speciation. There are several modes of this speciation.

- (1) ***Allopatric speciation:*** - is the evolution of genetic reproductive barriers between populations that are geographically separated by an extrinsic, physical barrier viz. topography, water (or land) or unfavourable habitat. The physical barrier reduces gene flow sufficiently for genetic differences between the populations to evolve, by Natural Selection or genetic drift. Thus, the two populations or sub-populations separated from each other by geographical-environmental barrier acquire genetic diversity. This diversity or difference is further accentuated by the duration of separation and after several generations the two populations become so genetically "disharmonious" or "out of contact" with each other that now even if they happen to become sympatric, at some point of time, there is no gene flow or exchange of genetic information between them. In other words, they get *reproductively isolated*.

Although there is debate about how frequently the other types of speciation (i.e. parapatric and sympatric speciation occur), all evolutionary biologists agree that allopatric speciation does occur and many hold that it is the prevalent mode of speciation in animals (Mayr, 1963, Futuyama and Mayer, 1980, Coyne, 1992).

Two major models of allopatric speciation differing in population structure and genetic dynamics have been postulated.

(i) **Vicariant speciation:-** Occurs when two rather widespread populations are divided by the emergence of an extrinsic barrier, the extinction of intervening populations or migration into a separate region.

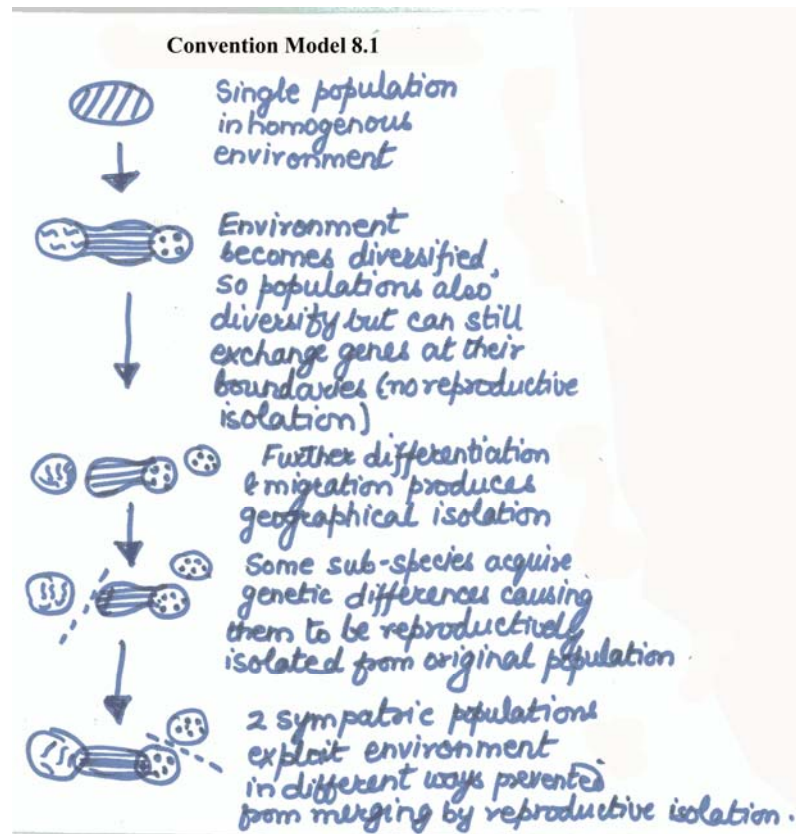


Table 8.2 : Two Classifications of potential modes of speciation in sexual organisms^a

By geography and level (after Mayr 1963)

1. Hybridization (maintenance of reproductively isolated hybrids between two species)
2. Instantaneous speciation (through individuals)
 - A. Genetically (single mutation)
 - B. Cytologically
 - a. Chromosome rearrangement
 - b. Polyploidy
3. Gradual speciation (through populations)
 - A. Sympatric speciation
 - B. Parapatric speciation
 - C. Allopatric (geographic) speciation
 - a. Peripatric speciation (by evolution in an isolated colony)
 - b. Vicariant speciation (division of range by an extrinsic barrier or extinction of intervening populations)

By population genetic mode (after Templeton 1982a)

1. Transilience
 - A. Hybrid maintenance (selection for hybrids)
 - B. Hybrid recombination (selection for recombinants following hybridization)
 - C. Chromosomal (fixation of chromosome rearrangements by drift and selection)
 - D. Genetic (founder event in a colony)
 2. Divergence
 - A. Habitat (divergent selection without isolation by distance)
 - B. Clinal (selection on a cline with isolation by distance)
 - C. Adaptive (erection of an extrinsic barrier followed by divergent microevolution)
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Figure 8.3 : Diagrams of successive stages in each of four models of speciation, differing in geographic setting. (A) Allopatric speciation by vicariance. A physical barrier divides a widespread species into two populations, which diverge in features that cause reproductive incompatibility. They become sympatric if the barrier breaks down or if they disperse over it. (B) The peripatric, or founder effect, model of allopatric speciation. A localized colony diverges from a widespread "parent" species, which remains little changed. Range expansion may establish sympatry. (C) Parapatric speciation, in which populations of a widespread species diverge by adaptation to different environments. Divergent selection even at a narrow environmental discontinuity may oppose gene flow and result in reproductive isolation. (D) Sympatric speciation, in which genetic differences (white versus dark symbols) develop gradually among members of an initially randomly mating population, resulting in reproductive isolation.

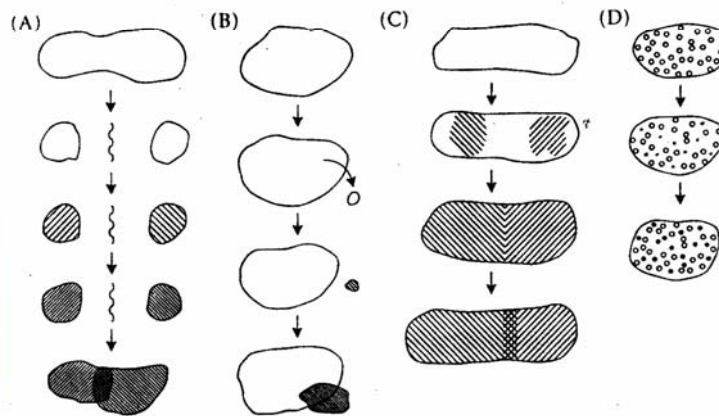
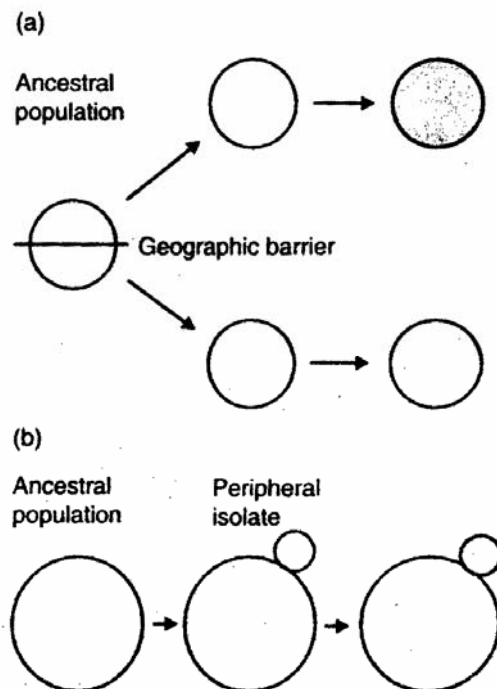


Figure 8.4 : Two models of allopatric speciation.

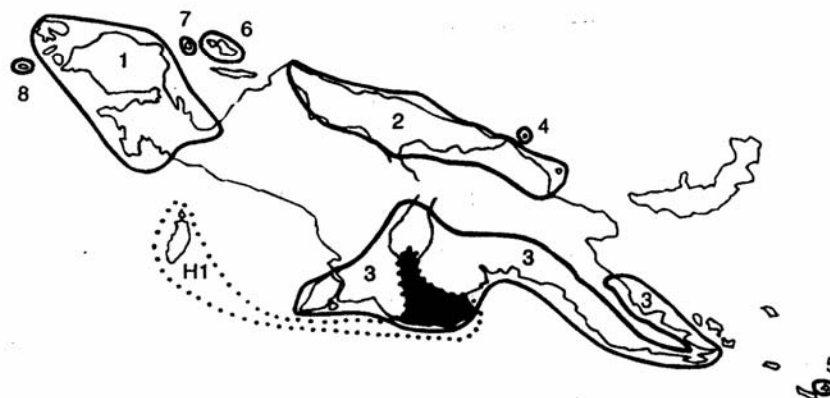
Stippling indicates evolution of new species. (a) The "dumb-bell" model in which the ancestral species is divided into two roughly equal halves, each of which forms a new species. (b) The peripheral isolate model, in which the new species forms from a population isolated at the edge of the ancestral species range.



e.g. the emergence of Isthmus of Panama in Pliocene, divided many marine organisms into Pacific and Caribbean populations, some of which have diverged into distinct species (Knowlton *et al.*, 1993). “Vicariant species” of tulip poplar (*Liriodendron*) in Eastern Asia and Eastern North America are remnants of once wider distribution across northern North America and Siberia. Climatic change (colder periods of late Pliocene and Pleistocene) forced many species to disjunct refuges where they differentiated into species and semispecies (Hewitt, 1996).

- (ii) **Peripatric speciation:-** The other major mode of allopatric speciation occurs when a colony derived from a more widespread parent population diverges and acquires reproductive isolation..Mayr (1982) called this as *peripatric* speciation.

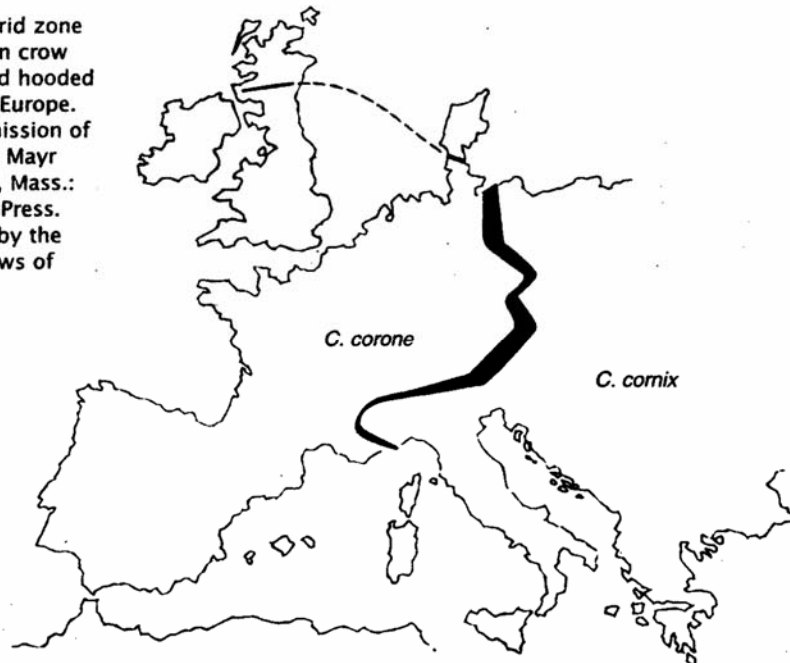
Figure 8.5 : Kingfishers of the *Tanysiptera hydrocharis-galatea* group in the New Guinea region. The three forms on mainland New Guinea (1, 2, 3) are almost indistinguishable. The five island forms (4–8) are strikingly distinct and most were originally described as separate species. The Aru Islands (H1) and southern New Guinea once formed an island, on which the form *hydrocharis* evolved. When southern New Guinea (H2) joined the main island (dotted line), the southeast New Guinea subspecies (3) invaded the area, but did not interbreed with *hydrocharis*. *Tanysiptera hydrocharis* had, therefore, evolved into a full species while isolated. From Mayr (1942). Copyright © 1942 by Columbia University Press. Reprinted with permission of the publisher.



Some geneticists believe that genetic changes underlying this speciation are same as those in vicariant speciation whereas some like Mayr (1954, 1963), Hampton Carson (1975) and Alan Templeton (1980) have explained it on the basis of “*peak shift*” (Wright’s shifting Balance Theory), which Templeton (1980) calls as *Transilience*. This model is sometimes also called “*Founder Effect Speciation*”. Here the colony during its founding or at other times when its effective population size is low undergoes allelic frequency changes at some loci by genetic drift, which changes genetic constitution. e.g. Kingfisher *Tanysiptera galeata* shows only slight geographic variation in plumage throughout climatically very different regions of New Guinea, but it has given rise to several markedly different forms on small Islands nearby. Hence, it’s considered being a good example of peripatric speciation.

- (2) **Parapatric speciation:** - Here, the new species evolve from continuous populations, rather than completely separate ones (as in allopatric speciation). The crucial evidence for this kind of geographic variation is known as *hybrid zone*. It's a zone or an area of contact between two noticeably different forms or races of a species, at which hybridization takes place. The forms on either side of the zone may be different enough to merit classification as separate species e.g. the carrion crow (*Corvus corone*) and hooded crow (*Corvus cornix*) in Europe. The hooded crow is distributed east and is gray with black head and tail whereas carrion crow to the west, is black all over. The two species meet along a line in Central Europe. At that line – the *hybrid zone*, they interbreed and produce hybrids i.e. speciation between them is incomplete.

Figure 8.6 : Hybrid zone between the carrion crow (*Corvus corone*) and hooded crow (*C. cornix*) in Europe. Reprinted, by permission of the publisher, from Mayr (1963), Cambridge, Mass.: Harvard University Press. Copyright © 1963 by the President and Fellows of Harvard College.

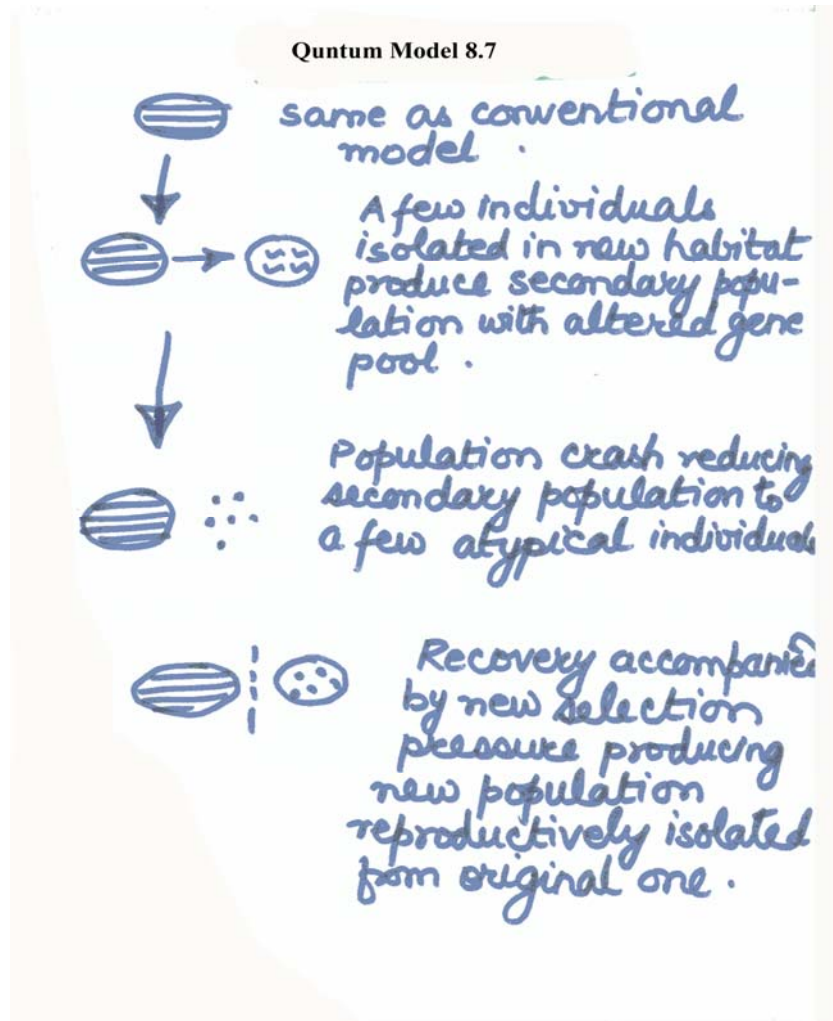


- (3) **Sympatric speciation:-** It develops by instantaneous development of reproductive isolation between units of population due to sudden change in their genotype. According to Savage, it may occur in five principal ways (i) *polyploidy*: polyploid individuals are usually isolated from the parental species. (ii) *hybridization* between distinct species, frequently the hybrids have faulty meiosis and produce hybrid polyploid offsprings reproductively isolated from all other species (iii) by self-fertilization unless cross fertilization becomes reestablished later and (iv) by apomixis:(asexual mode of reproduction) when apomixis arises suddenly in an originally sexual population, the asexually reproducing individuals immediately form isolated gene pools. (v) by ecological differentiation resulting in disruptive selection.

A fourth type of speciation was outlined by Simpson, called as

- (4) **Quantum speciation** (Simpson, 1944):- Here, the pathway runs directly from local race to a new species. It refers to those modes of speciation that involve *acceleration*

of process particularly of first stage of geographical speciation. Here, appearance of post zygotic reproductive isolating mechanisms require short periods of time. To



compare with geographic speciation, which requires thousands or sometimes millions of years. It is slow and gradual whereas quantum speciation requires only few generations. It's also known as *Rapid speciation* or *Saltation speciation* (Carson, 1973). The original population is small to begin with and the precursor here being a local race in contrast to geographic speciation where it's a geographical race. Moreover, quantum speciation includes one or more stochastic or chance events. Furthermore, conventional speciation is promoted by drastic reduction in population size which is not necessary for quantum speciation (Grant – 1941).

The differences between individuals and population may be due to single gene or a single chromosome. Such differences can't be swamped by the process of interbreeding because in the offsprings of a hybrid, segregation takes place and ancestral traits appear unmodified. No isolation is needed to preserve variations due to changes in single genes however for *maintenance of species and races as distinct populations, isolation is a necessary factor*. They differ from each other in several genes and chromosomal aberrations. Interbreeding of races and species results in breakdown of these systems, although gene differences as such are preserved. Therefore, race and species formation without isolation is impossible.

Process of mutation produces great variety of genes and chromosomal structure and through the processes of sexual reproduction several types of gene combinations are generated. Some of them are harmonious, well adapted to different ecological niches and environment and are: preserved in population through natural selection. Once a well-adapted distinct genetic population is thus established, further interbreeding of this population with other population is to be checked in order to preserve its identity. Continued interbreeding may also produce gene combinations unsuitable for particular environment, which may produce inviable individuals. Thus, process of isolation is necessary not only to preserve identity of species and races but for survival of several distinct populations.

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