SPECIES CONCEPTS:Modes of speciation

6th Sem (C14T)

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The concept of species

A species represents the lowest taxonomic group which is capable of being defined with any degree of precision. It may be defined in a variety of ways and some of these are summarised in table 27.2.

Organisms belonging to a given species rarely exist naturally as a single large population. It is usual for a species to exist as small interbreeding populations, called **demes**, each with its own gene pool. These populations may occupy adjacent or widely dispersed geographical areas. Spatial separation of populations means that the species may encounter a variety of environmental conditions and degree of selection pressure. Mutation and selection within the isolated populations may produce the following degrees of phenotypic variation within the species.

Geographical races

Populations which are distributed over a wide geographical range or have occupied well-separated geographical habitats for a long period of time may show considerable phenotypic differences. These are usually based on adaptations to climatic factors. For example, the gypsy moth (*Hymantria dispar*) is distributed throughout the Japanese islands and eastern Asia. Over this range a variety of climatic conditions is encountered, ranging from subarctic to subtropical. Ten geographical races have been recognised which differ from each other with regard to the timing of hatching of their eggs. The northern races hatch later than the southern races. The phenotypic variations shown by the 10 races are thought to be the result of climatic factors producing changes in gene frequencies within their gene pools. The evidence that these variations are genetically controlled is shown by the fact that under identical environmental conditions the different races still hatch at different times.

Table **Alternative ways of defining a species.**

Biological aspect	*Definition*
Breeding	A group of organisms capable of interbreeding and producing fertile offspring
Ecological	A group of organisms sharing the same ecological niche; no two species can share the same ecological niche
Genetic	A group of organisms showing close similarity in genetic karyotype
Evolutionary	A group of organisms sharing a unique collection of structural and functional characteristics

Ecological races (ecotypes)

Populations adapted to ecologically dissimilar habitats may occupy adjacent geographical areas; for example the plant species *Gilia achilleaefolia* occurs as two races along the coast of California. One race, the 'sun' race, is found on exposed southerly facing grassy slopes, whilst the 'shade' race is found in shaded oak woodlands and redwood groves. These races differ in the size of their petals, a characteristic which is determined genetically.

Clines

A species exhibiting a gradual change in phenotypic characteristics throughout its geographical range is referred to as a **cline**. More than one cline may be exhibited by a species and they may run in opposite directions as shown by fig 27.14.

Species exhibiting marked phenotypic variation within a population according to their degree of geographical isolation are known as **polytypic species**. One classic form of a polytypic species is illustrated by gulls belonging to the genus *Larus* (section 27.8.4).

All cases of phenotypic variation described above represent varying degrees of genetic dissimilarity which may interfere with the breeding potential of members of the populations if brought together.

Speciation

This is the process by which one or more species arise from previously existing species. A single species may give rise to new species (**intraspecific speciation**), or, as is common in many flowering plants, two different species may give rise to a new species (**interspecific hybridisation**). If intraspecific speciation occurs whilst the populations are separated it is termed **allopatric speciation**. If the process occurs whilst the populations are occupying the same geographical area it is called **sympatric speciation**.

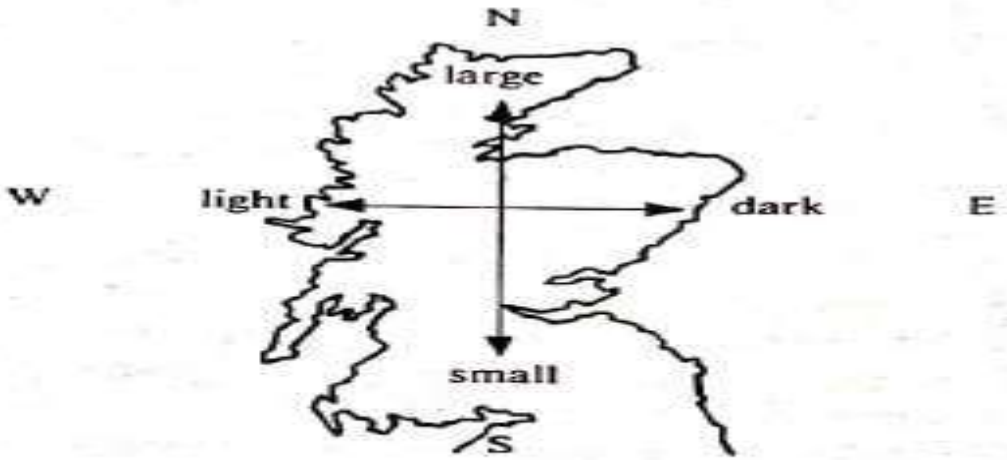


Fig 27.14 *Phenotypic variation in size and fur colour shown by the wood mouse (Apodemus) in Scotland.*

Intraspecific speciation

There are several factors involved in intra-specific speciation, but in all cases gene flow within populations must be interrupted. As a result of this each subpopulation becomes genetically isolated. Changes in allele and genotype frequencies within the populations, as a result of the effects of natural selection on the range of phenotypes produced by mutation and sexual recombination, lead to the formation of races and subspecies. If the genetic isolation persists over a prolonged period of time and the subspecies then come together to occupy the same area they may or may not interbreed. If the breeding is successful they may still be considered to belong to the same species. If the breeding is unsuccessful, then speciation has occurred and the subspecies may now be considered to be a separate species. This is the way in which it is believed evolutionary change can be brought about.

An initial factor in the process of speciation may be the reduction in the intensity of selection pressure within the population. This may lead to increased intraspecific variability. These new phenotypes may enable the population to increase its geographical range if the phenotypes show adaptations to environmental conditions found at the extremes of the range. Providing there is no reduction in gene flow throughout the population, the species, whilst exhibiting the localised phenotypic variation (ecotypes), will share the same gene pool and continue to exist as a single species. This is the situation found in a cline.

Speciation will only occur as a result of the formation of barriers which lead to reproductive isolation between members of the population. Reproductive isolation is brought about by some form of what the geneticist Theodosius Dobzhansky called **isolating mechanisms.**

Isolating mechanisms

An isolating mechanism is a means of producing and maintaining reproductive isolation within a population. This can be brought about by mechanisms acting before or after fertilisation. Dobzhansky suggested a classification of isolating mechanisms which has been modified and is shown in table 27.3.

Allopatric speciation

Allopatric (*allos*, other; *patria*, native land) speciation is characterised by the occurrence, at some stage, of spatial separation. Geographical barriers such as mountain ranges, seas or rivers, or habitat preferences, may produce a barrier to gene flow because of spatial separation. This inability of organisms or their gametes to meet leads to reproductive isolation. Adaptations to new conditions or random genetic drift in small populations lead to changes in

Table 27.3 Isolating mechanisms (after Dobzhansky).

Prezygotic mechanisms (barriers to the formation of hybrids)	
Seasonal isolation	Occurs where two species mate or flower at different times of the year; for example in California *Pinus radiata* flowers in February whereas *Pinus attenuata* flowers in April
Ecological isolation	Occurs where two species inhabit similar regions but have different habitat preferences; for example *Viola arvensis* grows on calcareous soils whereas *Viola tricolor* prefers acid soils
Behavioural isolation	Occurs where animals exhibit courtship patterns, mating only results if the courtship display by one sex results in acceptance by the other sex; for example certain fish, bird and insect species
Mechanical isolation	Occurs in animals where differences in genitalia prevent successful copulation and in plants where related species of flowers are pollinated by different animals
Postzygotic mechanisms (barriers affecting hybrids)	
Hybrid inviability	Hybrids are produced but fail to develop to maturity; for example hybrids formed between northern and southern races of the leopard frog (*Rana pipiens*) in North America
Hybrid sterility	Hybrids fail to produce functional gametes; for example the mule ($2n = 63$) results from the cross between the horse (*Equus equus*, $2n = 60$) and the ass (*Equus hemionus*, $2n = 66$)
Hybrid breakdown	F_1 hybrids are fertile but the F_2 generation and backcrosses between F_1 hybrids and parental stocks fail to develop or are infertile, for example

allele and genotype frequencies. Prolonged separation of populations may result in them becoming genetically isolated even if brought together. In this way new species may arise. For example, the variety and distribution of the finch species belonging to the family Geospizidae on the islands of the Galapagos archipelago are thought to be the result of allopatric speciation.

David Lack suggested that an original stock of finches reached the Galapagos Islands from the mainland of South America and, in the absence of competition from endemic species (representing relaxed selection pressure), adaptive radiation occurred to produce a variety of species adapted to particular ecological niches. The various species are believed to have evolved in geographical isolation to the point that when dispersal brought them together on certain islands they were able to coexist as separate species.

Sympatric speciation

Genetic differences may accumulate allopatrically in populations which have been geographically isolated for a much shorter period of time. If these populations are brought together, hybrids may form where these overlap. For example, both the carrion crow (*Corvus corone*) and the hooded crow (*Corvus corone cornix*) are found in the British Isles. The carrion crow is completely black and is common in England and southern Scotland. The hooded crow is black with a grey back and belly and is found in the north of Scotland. Hybrids formed from the mating of carrion and hooded crows occupying a narrow region extending across central Scotland (fig 27.15). These hybrids have reduced fertility and serve as an efficient reproductive barrier to gene flow between the populations of the carrion and hooded crows.

In time, selection against cross-breeding may occur, leading to speciation. Since such speciation occurs finally in the same geographical area, this is called **sympatric** (*sym*, together; *patria*, native land) **speciation**.

Sympatric speciation does not involve geographical separation of populations at the time at which genetic isolation occurs. It requires the development of some form of reproductive isolating mechanism which has arisen by selection within a geographically confined area. This may be structural, physiological, behavioural or genetic.

Sympatric speciation is more commonly thought of as providing an explanatory mechanism of how closely related species, which probably arose from a common ancestor by temporary isolation, can coexist as separate species within the same geographical area. For example, in the Galapagos archipelago the finch *Camarhynchus pauper* is found only on Charles Island, where it coexists with a related form *C. psittacula* which is widely distributed throughout the

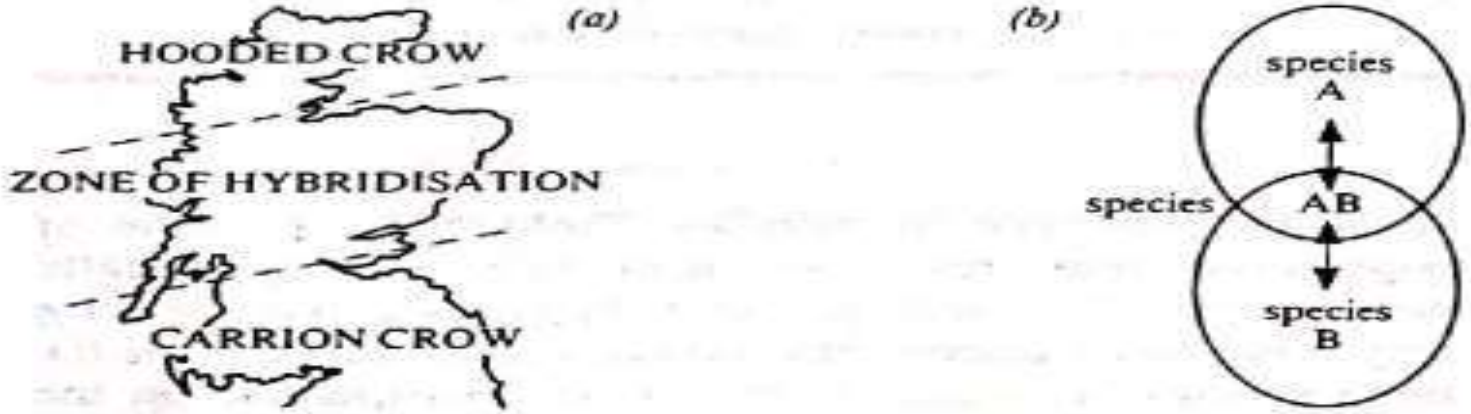


Fig 27.15 *Hybrid barrier as a means of preventing gene flow between two populations. The maintenance of the two crow species is shown to be due to the existence of a zone of hybridisation extending across Scotland as shown in (a). The existence of hybrid barriers between adjacent populations is common and functions as follows. Where the geographical ranges of A and B overlap, mating produces a hybrid with lowered fertility. A will interbreed freely with AB and AB with B but the existence of AB prevents free interbreeding of A and B populations.*

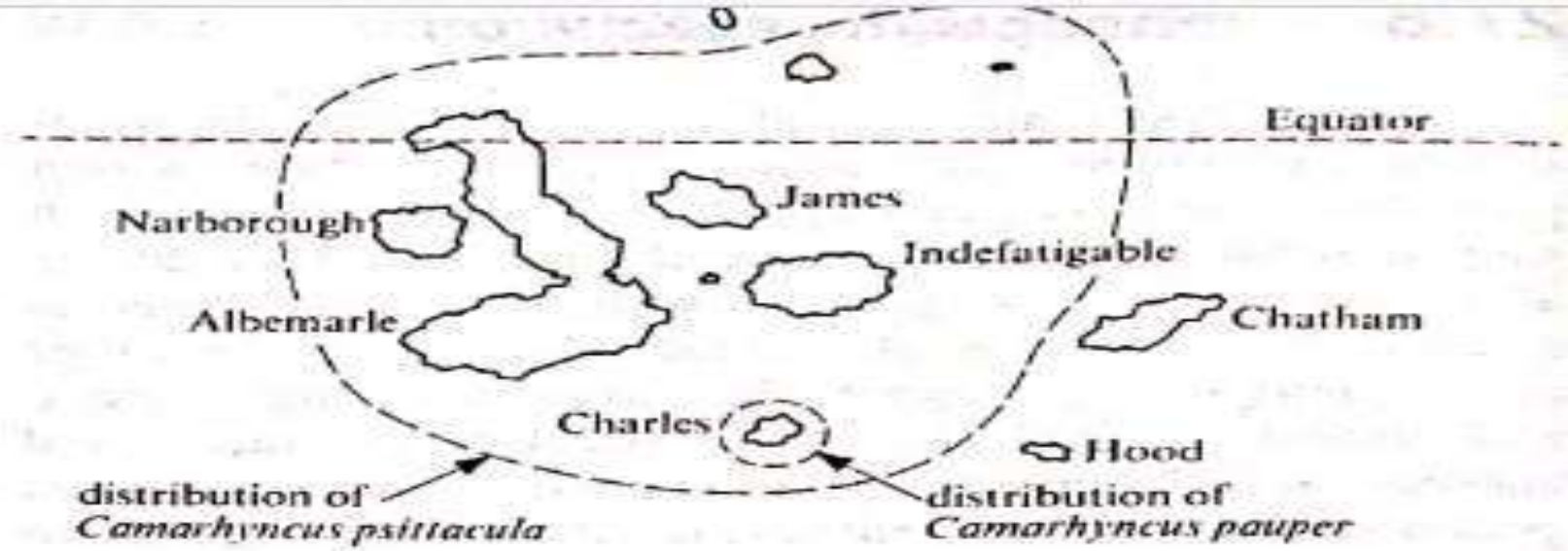


Fig 27.16 *The Galapagos Islands and the distribution of two species of finch illustrating coexistence following allopatric speciation.*

central islands (fig 27.16). The finch species appear to choose their mates on the basis of beak size. The range of beak sizes of *C. pauper* on Charles Island and *C. psittacula* on Albemarle Island are approximately equal, but on Charles Island *C. psittacula* has a longer beak. This difference is significant enough to ensure that the two species, which feed on different foods, appear unattractive to each other during the breeding season. In this way the species remain distinct and are able to coexist.

Ring species

This is a special form of sympatric speciation which occurs at the point where two populations at the extremes of a cline meet up and inhabit the same area, thus 'closing' the ring. For example, gulls of the genus *Larus* form a continuous population between latitudes 50–80 °N, encircling the North Pole. A ring of ten recognisable races or subspecies exist which principally differ in size and in the colour of their legs, backs and wings. Gene flow occurs freely between all races except at the point where the 'ends of the ring' meet at the British Isles. Here, at the extremes of the geographical range, the gulls behave as distinct species, that is the herring gull (*Larus argentatus*) and the lesser black-backed gull (*L. fuscus*). These have a different appearance, different tone of call, different migratory patterns and rarely interbreed. Selection against cross-breeding is said to occur sympatrically.

Sympatric speciation without geographical isolation in sexually reproducing species is unlikely. However, in asexually reproducing organisms, including vegetatively propagated angiosperms, a single mutant so different from its parent population as to be genetically isolated could give rise to a new species sympatrically. An example is polyploidy in *Spartina*

Interspecific hybridisation

This is a form of sympatric speciation which occurs when a new species is produced by the crossing of individuals from two unrelated species. Fertile hybrids usually appear only in cases of interspecific hybridisation as a result of a form of chromosome mutation known as **allopolyploidy** (section 24.9.2). An example of this was demonstrated by Kapechenko in the case of hybrids formed between the cabbage and the radish. The genetic changes involved in this hybridisation are shown in fig 27.17.

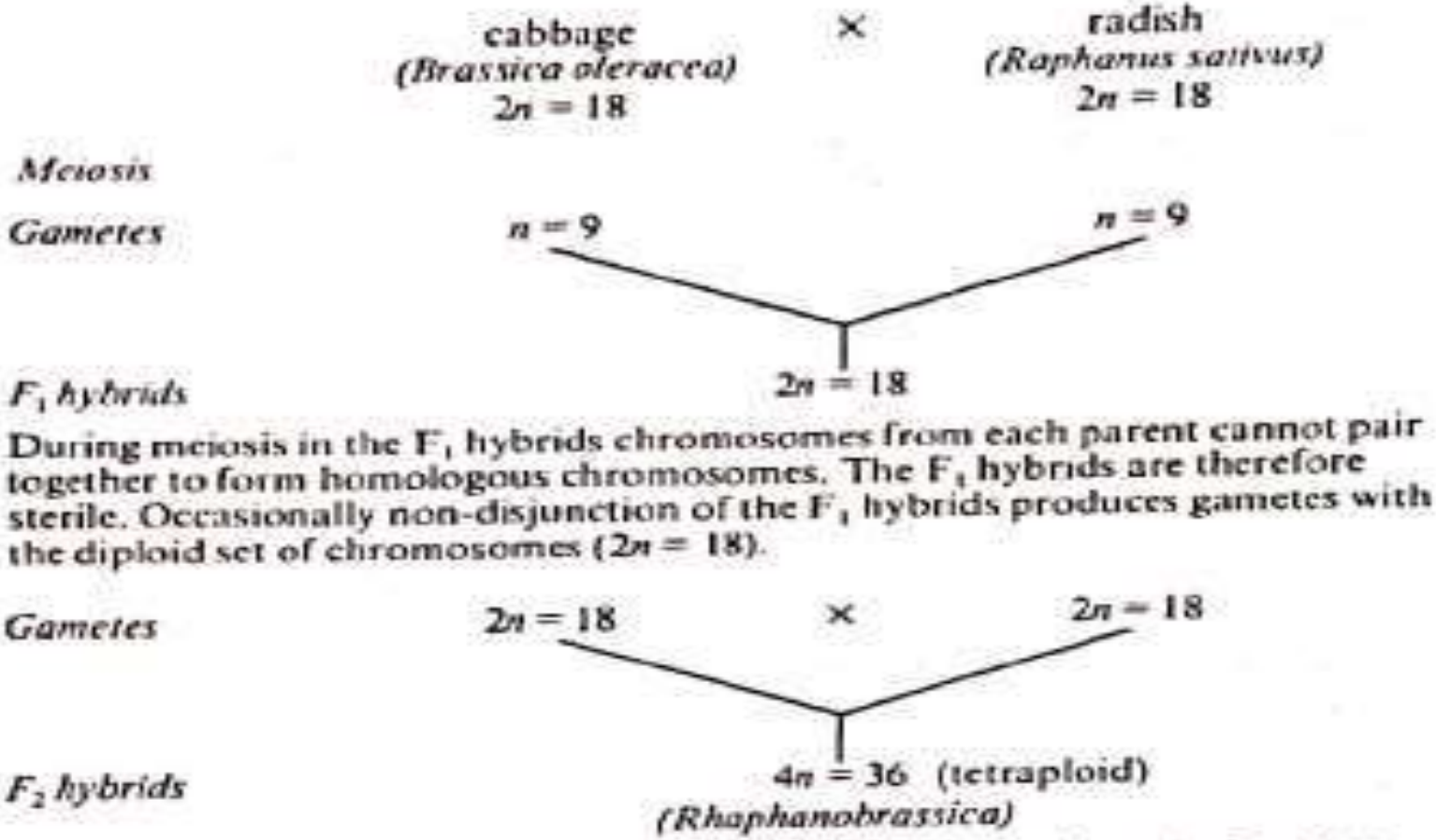


Fig 27.17 *Stages involved in the hybridisation of the cabbage and the radish.*

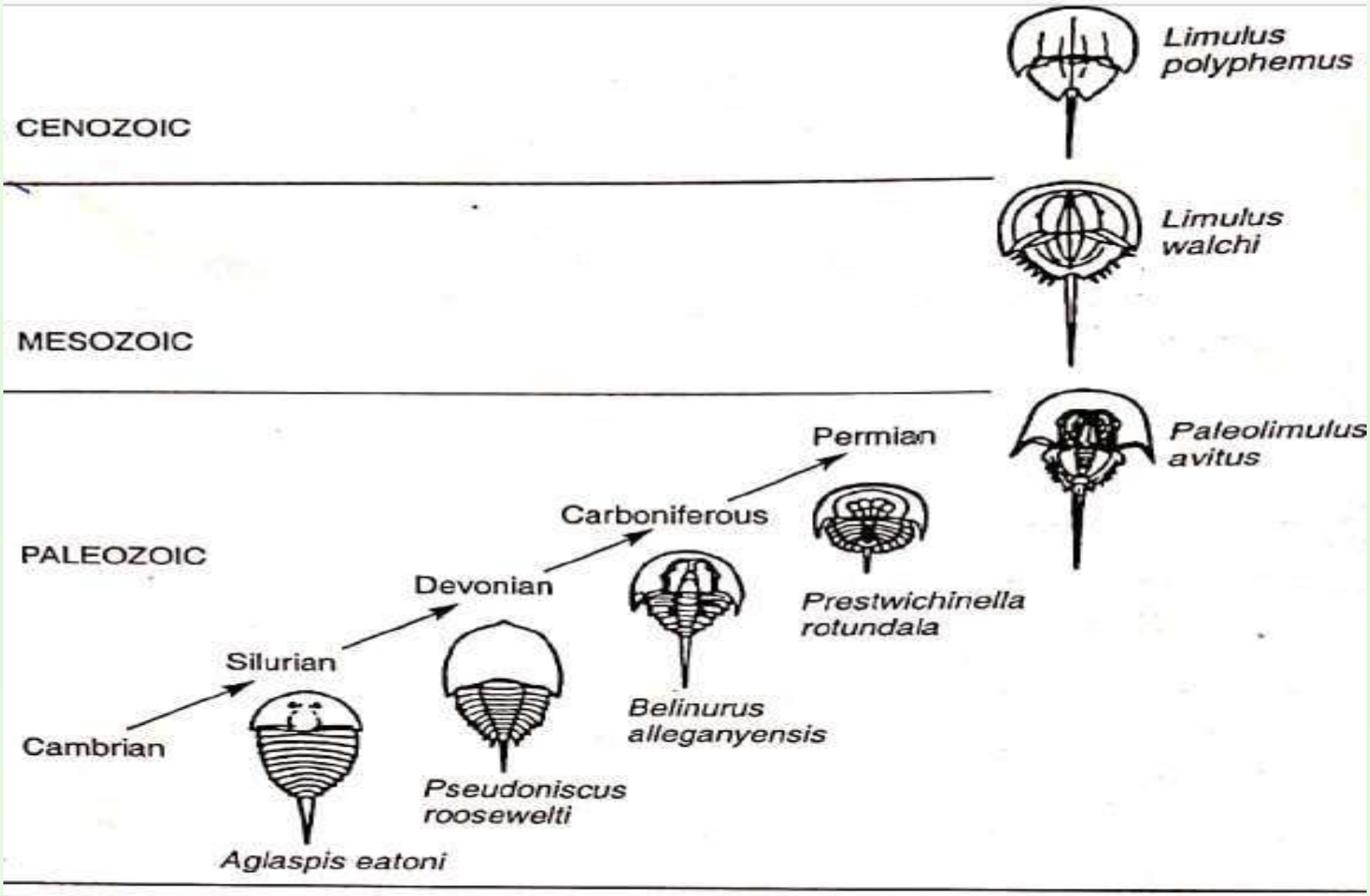


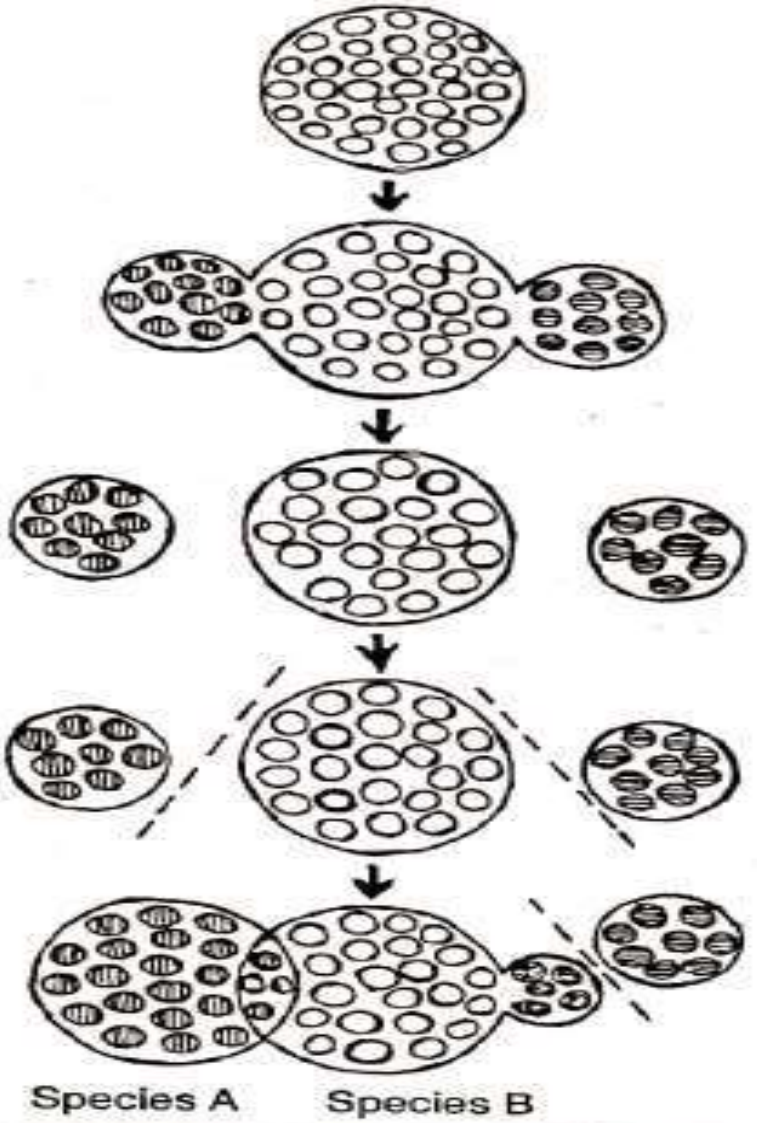
Figure 18.3 : Phyletic evolution in horseshoe crabs. Phenotypic changes were relatively small over long periods of time.

Vries. Simple gene mutations, evidently, cannot produce new species in sexually-reproducing animals, but may lead to speciation in asexually-reproducing animals, like rotifers, nematodes etc. Instantaneous speciation through major chromosomal changes like polyploidy is also very rare in animals although common in plants. However, polyploidy occurs in some sexually reproducing animals like crustaceans, insects, fishes etc. It would be justified to consider these examples as exceptional cases.

Gradual speciation is necessarily a populational phenomenon because it occurs through gradual divergence of populations until they have reached the level of specific distinctness. Majority of authors regard gradual speciation as true speciation and classify it into two modes. One involves geographical separation of diverging species or **allopatric speciation**, another without geographic separation—the **sympatric speciation**.

Allopatric speciation essentially requires geographical isolation

Theory of allopatric (Gr. allos = other; patria = homeland) speciation forwards that in sexually reproducing animals, a new species develops from a population that is geographically isolated from its parental species. That population surely acquires such characters during the period of isolation, which promote or ensure reproductive isolation with its parent species, even when the external barriers break down. Allopatric speciation requires, firstly, spatial isolation of a subpopulation from the remainder of the ancestral species and secondly, divergent selection pressure that establishes new barrier to reproductive isolation based upon a large number of genetic differences (Fig. 18.4).



An interbreeding population in a homogenous environment.

New populations are built up from the parental population due to diversification of environment.

Further differentiation produces geographic isolation of some populations resulting incipient species.

Genetic differences in geographically isolated populations cause reproductive isolation between them and from parent population.

Some reproductively isolated populations evolved as species. Isolating mechanisms prevent their merging even they re-enter the area occupied by parent population.

Figure 18.4 : A Schematic model of allopatric speciation.

Because speciation is a slow and gradual process, it is possible to find natural populations in all stages of "becoming species." These intermediate stages in the process of speciation are called **incipient species** or **geographical isolates**. Many authors have presented numerous species groups which are found to consist of distinct populations throughout their area of distribution. These populations represent the stages of divergence up to completion of speciation. As in genus *Drosophila*, different degree of divergence is demonstrated by Patterson and Stone (1952), which range from partial strain isolation to subspecific divergence, to closely related species, to distantly related species. Similar instances have been described in numerous genera of invertebrates and vertebrates. These observations evidently favor the view that ordinary species differences have come about through the accumulation of steps, through allopatric strains and from subspecies to species.

Study of colonization by avifauna in Australia and North America by Mayr is equally impressive. It is found that earliest immigrants from Asia have evolved into new families and genera, and the later ones into new species or subspecies, but recently arrived ones have not yet started to diverge at all.

It is well known that spatially segregated populations of a species differ in morphology, anatomy, cytology, physiology etc. Occurrence of such variations is called **geographic variation**. When the speciation is allopatric, it is obvious that isolating mechanisms also exhibit geographic variations. Geographic variation in habitat occupation is very common in birds. Every widespread species has been found to contain geographically representative populations that differ from each other to some extent in their ecology. For example, population of island thrush *(Turdus poliocephalus)* in Solomon Island live in high mountain forests above altitudes of 8000 ft. In

nearby Rennell Island, the population inhabits the lowland and feed along sea shore. Rufous fantail *(Rhipidura rufifrons)*, Wilson's warbler *(Wilsonia pusilla)* etc. show similar variations of ecological requirements. Sometimes geographically correlated genetic variation is not gradual. Rather an abrupt shift in genetically determined characters occurs in a geographically variable species; the population involved may reach to subspecies status. Different breeding grounds and different ranges result in two subspecies of Canada goose. *Branta canadensis maxima* breed in central and south-central USA, while *B. c. moffitti* breeds in central and western Canada. Certain species of mammals and mosquitos also show geographic variation in habitat occupation. On the basis of these observations, it is expected that ecological isolation may become well established between geographic isolates (or incipient species) as a step to speciation. Two morphologically distinct populations of squirrels (Fig. 18.5) live in different ranges of the Grand Canyon in Arizona. The Kaibab squirrel live in northern rim of the Canyon, and are darker than Abert squirrel living in southern rim. Whether these two populations will be regarded as separate species is not certain.

Geographical variations of other isolating factors are also evidently observed in many animal species. Variations of plumages (visual stimuli) in birds of paradise, of songs (auditory stimuli) in warblers, are examples of variations of ethological barriers. Even genital armature of insects shows much geographic variability. In genus *Drosophila*, sterility barrier is found to have geographic variation. *D. virilis*, *D. peninsularis* etc. have sterility barrier between their geographical races. All these differences in ecology, behavior, fertility etc. between geographical races of a species are ultimately a reflection of their difference in genetic constitution. More barriers of gene flow between populations and their stronger local adaptedness will result in greater genetic rebuilding of them. At the same time, there will be greater probability of changes in the components of isolating mechanisms.

In the process of allopatric speciation, the key units are the geographic isolates. In a widespread species, most distinct isolates are generally situated along the periphery of the species range—called **peripheral isolates**. Many well-studied polytypic species have such peripheral isolates, various authors consider them as subspecies, some even

species. There are dozen of peripheral isolates of spangled drongo *(Dicrurus hottentottus)* throughout its distributional range. Some of these isolates are considered as species, such as *D. balieassius* of Philippines, *D. montanus* of Celebs. One isolate of New Ireland *(D. megarhynchus)* is so aberrant that recently it is considered as seperate genus. Observations of many animal genera exhibit similarly that geographic isolates are at various stages of species formation, such as, junco *(Junco)*, vole *(Clethrionomys)*, rattlesnake *(Crotalus)* etc. It is obvious that majority of these isolates have some but not all attributes of new species, and isolating mechanisms between them have developed incompletely; they are referred as **borderline cases.** Unless detailed study is done, it would be difficult to realize how many evolutionary intermediates are concealed in the isolates of a polytypic species.

Species originate due to spatial isolation and then rejoin, often compete with each other. The result of such competition is more intense selection that creates greater character differences. Two species may diverge faster from each other after they resume their contact than they did when they were separated. This process in which there is selection for accentuated differences in species characters under conditions of interspecific competition is called **character displacement.** The process is observed in finches (Fig. 13.14) of Galapagos Islands. In larger Islands where two species of seed eating finches share the same habitat, beak size differs widely. Where only one of the two species exists, beak size is intermediate between the two extreme sizes.

If species originate allopatrically and only a fraction of all incipient species actually reach the rank of full species, an abundant supply of incipient species is required. Habitats are mostly saturated with species at any given time and new species are needed when new niches are opened. As a result, most isolates are ephemerals; they become extinct before reaching the qualification of full species. In nature, isolates are produced far greater number of times than new species. So we may conclude that most geographic isolates do not evolve into new species, but when a new species evolves, it is most likely from a geographical isolate.

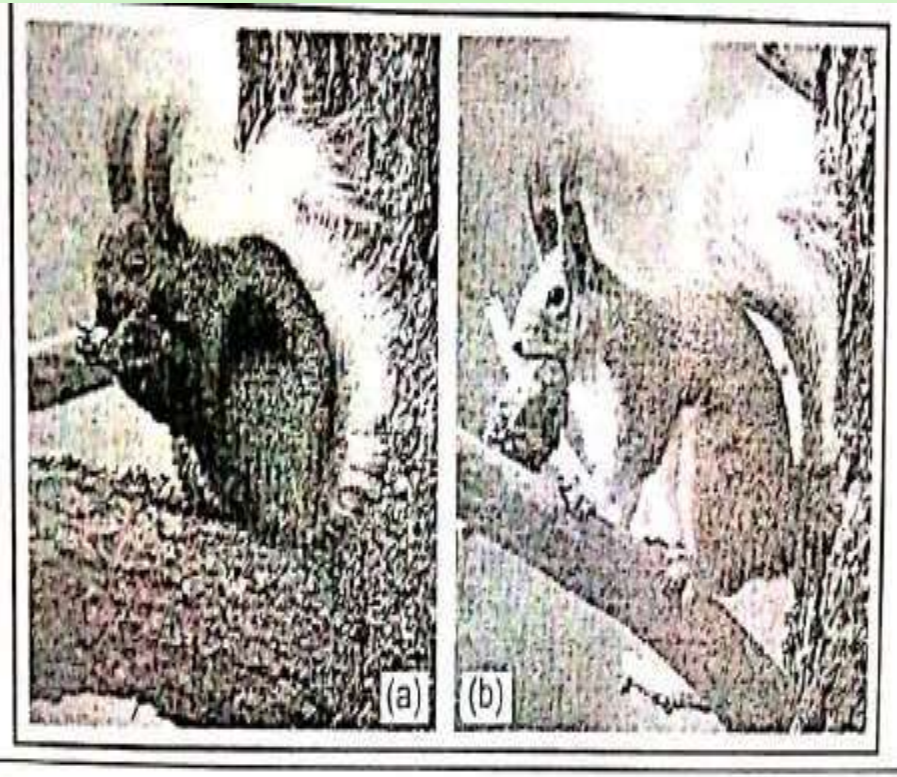


Figure 18.5 : Kaibab squirrel (a) and Abert squirrel (b) are two populations living in different ranges of Grand Canyon. They are morphologically distinct but whether speciation is completed, is not certain.

so numerous in nature, that universal occurrence of allopatric speciation is no more questioned. Now before we shift our discussion to the other probable processes of speciation among sexually reproducing animals, we shall discuss different models of allopatric speciation.

Different models of allopatric speciation :

Two major models of allopatric speciation are forwarded—

(a) When large and widespread population is fragmented into subpopulations, each of which becomes a new species, such allopatric speciation is called **vicariant speciation**. Fragmentation of population may occur in three ways.

(i) A physical barrier may emerge to divide a widespread species. This is the most popular idea and almost accepted as synonymous to allopatric speciation. As for example, when the Isthmus of Panama emerged in Pliocene, many marine organisms were divided into Caribbean and Pacific populations. Many of these populations have diverged into distinct species.

(ii) Extinction of intervening populations may result in division of a widespread population. Tulip poplar (*Liriodendron*) was once widely distributed across North America, Siberia and eastern Asia. But climatic change has made much of northern North America and Siberia unsuitable for these trees. Now the

(iii) Migration into separate regions may result in an isolated population from the parental one. During colder periods of Pliocene and Pleistocene, many species migrated into habitable areas. In their new refuges, they differentiated into subspecies or even species.

(b) When a small colony is derived from a large and widespread parent population, which becomes diverged genetically and acquires reproductive isolation, it is called **peripatric speciation**. This model of allopatric speciation is also called Founder's effect speciation. Several species of *Drosophila* in Hawaiian Islands have evolved rapidly following colonization of one island and is considered as a common example of peripatric speciation. Despite some examples, peripatric speciation is regarded as a hypothetical form of allopatric speciation.

Sympatric speciation occurs by splitting of population within a common area

This is the mode of speciation without geographic isolation. Sympatric (Gr. sym = together; Patria = homeland) speciation is based on two successive events—(i) establishment of new

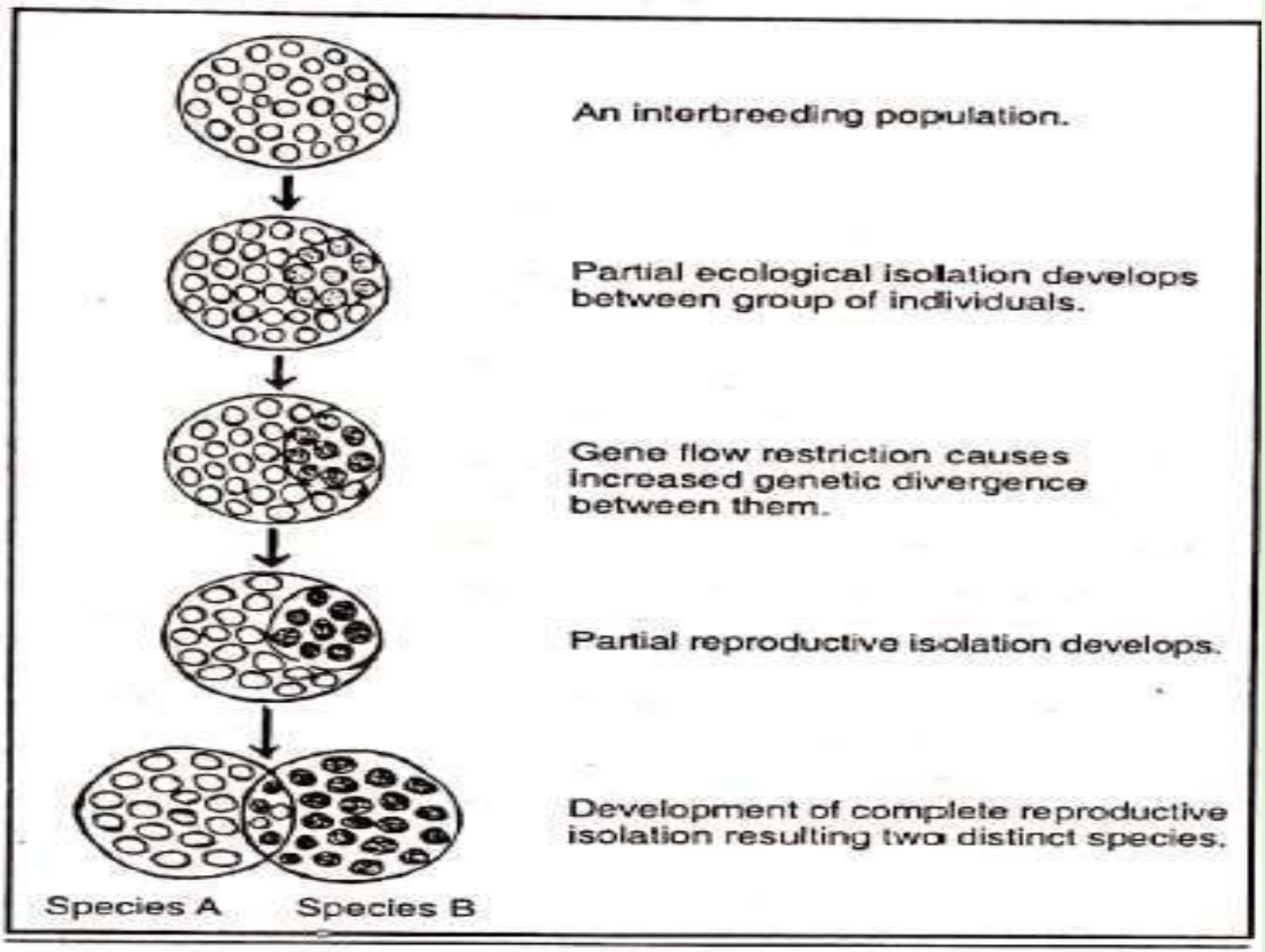


Figure 18.6 : A schematic model of sympatric speciation.

populations of a species in different ecological niches but within the normal reaching range of parental population, and (ii) establishment of reproductive isolation between the individuals of new population from those of parental population (Fig. 18.6).

The concept of sympatric speciation is much older than allopatric speciation. The concept is apparently supported by many phenomena. Firstly, a number of related sympatric species led us to assume that these have originated where they are now found. Secondly, sympatric speciation is based on the view that all species are perfectly adapted to their particular environment. It is forwarded that such fittings of species into ecological niches have not evolved by accidental genetic changes accumulated during geographic isolation. Finally, emphasis on ecological differences rather than morphological differences among species is another cause of popularity of sympatric speciation.

Evolutionary geneticists believe that geographical separation between populations is necessary to accumulate the initial genetic differences leading to speciation. But supporters of sympatric speciation have forwarded various models in favor of their views that populations inhabiting same geographical area may develop reproductive isolation leading to speciation. In a model, it is proposed that a population selected for adaptation to different habitats within a single locality can produce genetic variability leading to polymorphism. Such phenomenon is known as disruptive selection and an important example is the mimetic polymorphism in the butterfly *Papilio dardanus* (see section 16.4). Disruptive selection can result in isolation between different groups in the same locality, if they can exist independently. In laboratory condition, selection for high and low bristle number was carried on in a population of *Drosophila melanogaster*. After a few generation of selective breeding, when random mating was allowed, it was found that males with high bristle number prefer to mate with females with high bristle number and low bristle number males with similar females. Another model proposed that speciation may occur within a single geographical range by adapting of different kinds of host species as found in various insect groups to different host food plants.

It is well known that allopatric speciation does not involve gross chromosomal changes. But there are increasing evidence that sympatric speciation can occur without major chromosomal rearrangements or polyploidy. Of course, reproductive isolation is essential for successful sympatric speciation, but that can result by other means. One such mean is host specificity that works like geographic isolation. Treehoppers *Euchenopa* have several species, each of which is restricted to different genus of host plants. These species are reproductively isolated for various reasons. Firstly, each species mate only on its respective host plant upon which they feed. Secondly, eggs on different host plants hatch at different times, which results in different maturation times for adult, hence results in partially segregated breeding seasons. Thus gene flow among these species is reduced by differential host preferences

Another mechanism that may contribute to sympatric speciation without involving major chromosomal changes is sexual imprinting, particularly found in birds. Young members of many species memorize features displayed by their parents or siblings, which may be auditory, visual or olfactory. This memory or imprinting (please see section 34.4) enables these individuals to identify suitable mates in later life. If an offspring imprint on a mutant feature displayed by its parents, like a bright colored spot on head or some noble change in courtship song, it will interbreed with an individual of opposite sex showing similar display. This breeding pair may start a new population that will not interbreed with the rest of the species. Therefore, imprinting may play an important role in reproductive isolation, and hence, in separating populations.

A classical example of sympatric speciation due to habitat preference is found in picture-wing fruit fly, *Rhagoletis pomenella*. These flies court and lay eggs on hawthorn berries. Larvae emerge from eggs and feed on fruit, then pupate and emerge as adult. At some early life, these flies imprint an odor of hawthorn that help them to locate a suitable host plant. But there are species of parasitic wasp,

which kill about 90% of growing fruit fly larvae. In northern USA, hawthorns are less common and some fruit flies began to lay eggs on apple, probably by mistake. But subsequent generations are imprinted to apples and reproductive isolation is nearly complete between the two populations — the original having host plant hawthorn and the new having apple tree as host plant. Fruit fly larvae grow much better in hawthorns than in apples but larvae within apples suffer far less parasitism. Fruit flies lay more eggs in apples than in hawthorns. It is not known whether full speciation has occurred between those populations of fruit flies, but potential for sympatric speciation is, no doubt, clear.

Parapa r' . speciation is considered as a variant of sympatric mode

This model is a variation of sympatric speciation and does not require geographic isolation (Fig. 18.8). It is a rapid process and requires only a few individuals of adjacent populations whose distribution do not overlap but come in contact with each other at one or more points. When structural rearrangements of chromosomes or other genetic changes occur in a relatively small number of individuals often on the periphery of a population's range, reproductive isolation may develop. Individuals

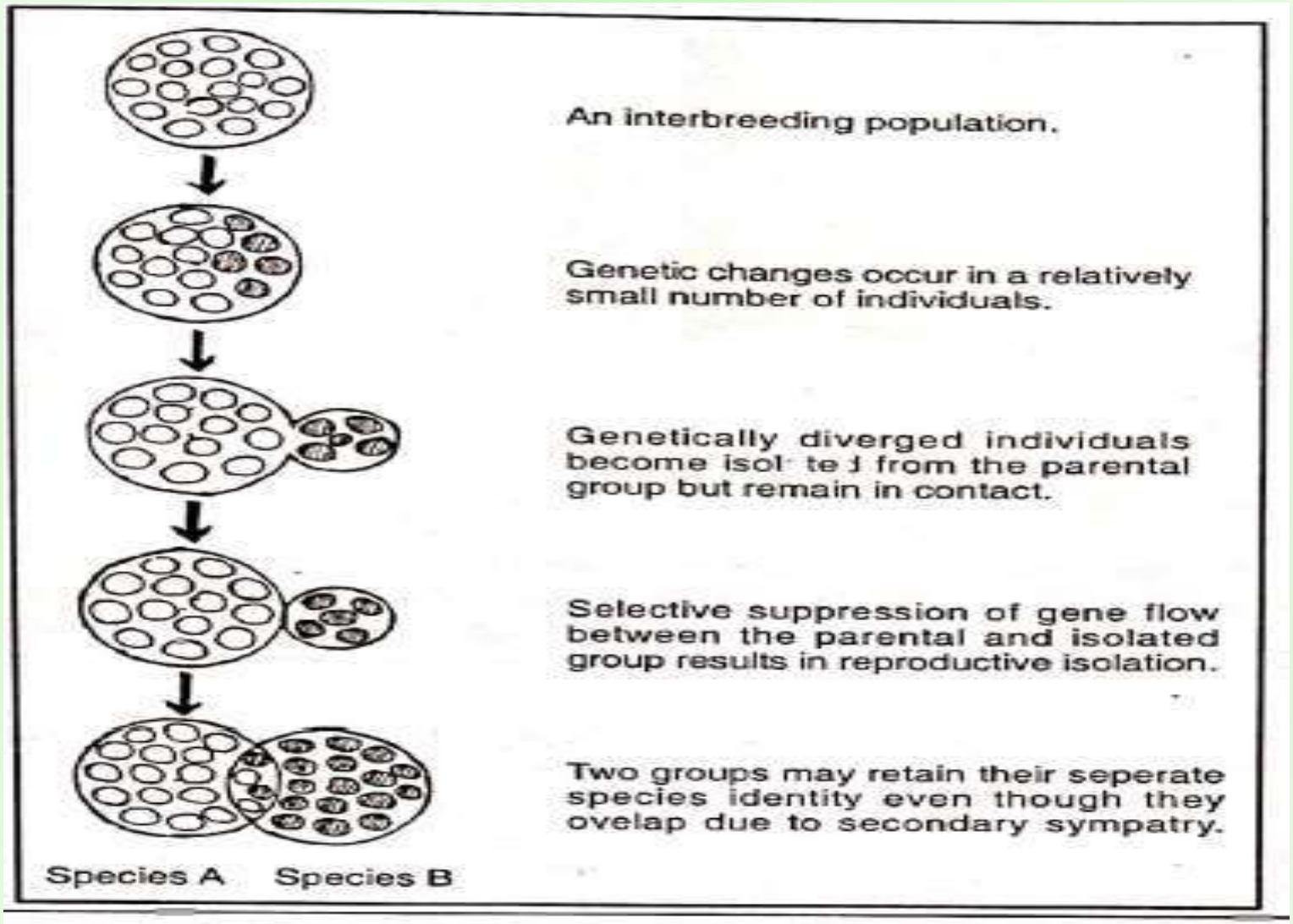


Figure 18.8 : A schematic model of parapatric speciation.

carrying new rearrangements become isolated from other members of the population and become new species.

Parapatric (Gr. para = beside; Patria = homeland) speciation is exemplified by the old world mole rat, *Spalox ehrenbergi*. There are four chromosomal subspecies of this burrowing mammal in and around Israel. Two northern subspecies have 52 and 54 chromosomes; central Israeli subspecies has 58 and southern subspecies has 60. Hybrids of these subspecies rarely occur and when occurred, fertility is reduced. It is entirely reasonable to consider these four subspecies as distinct species. Fossil evidences indicate that all four subspecies (or species) are descended from an ancestral species *S. mimtus* that lived in the said area about 500,000 yrs ago.

Some populations of grass (*Anthoxanthum*) growing near mines have evolved tolerance to heavy metals. But their neighbouring populations

growing on uncontaminated soil are non-tolerant. The former populations have diverged from the non-tolerant populations not only in heavy metal tolerance but also in flowering time. Again, self-pollination allows the tolerant population considerable reproductive isolation from adjacent non-tolerant grasses. The divergence is evidently emerging within the last few centuries and cited as an example of parapatric speciation.

The parapatric model of speciation is most plausible for organisms with limited mobility. Examples available in support of this model show that the time involved in the development of partial reproductive isolation may be only hundreds of years. However, it is neither known how frequently speciation occurs by this mean. nor it is sure that there was not at some time an episode of discrete allopatry.

Controversy on sympatric speciation

Because sympatric speciation is also a gradual process, there should be some intermediate populations in nature, which can be regarded as incipient species. Detailed survey of animals living in same area, who are clearly separable by biological characters but have no or slight morphological differences (known as biological races) provide no evidence for the occurrence of incipient sympatric species. But there are certain situations in nature, which are claimed to be explained only by sympatric speciation. These situations have provided strong arguments in favor of sympatric speciation. But today, they are criticized logically.

1. It is claimed that sympatric sibling species can only originate through sympatric speciation. But reproductive isolation may develop more quickly between geographic isolates than morphological differences, thus sympatric speciation is not the only cause of origin of morphologically similar species.
2. Speciation in parasites appears to be incompatible with geographic isolation. There occurs coexistence of several related species on different host species in same geographical area. For example, four species of lice from different species of South American monkeys are derived from human louse *(Pediculus)*. It is now known that populations of lice in each host monkey are introduced through infection from man, and are actually spatial isolates because they harbor different hosts.
3. Many cases have been described by paleontologists where a single lineage splits into two separate species suddenly. But recent interpretation of those cases proves that appearance of a second species in same horizon is not due to speciation but to immigration.

There are a few more arguments in favor of sympatric speciation, but reanalysis prove that such cases may also occur due to allopatric speciation. Many authors believe that models of sympatric speciation are proposed to eliminate the difficulties met in the theory of allopatric speciation.

It is now well-established that genetic repatterning of populations is the essential components of speciation. Such repatterning can only occur if the populations are protected, at

least temporarily, from inflow of alien genes. Only spatial isolation can provide this protection through geographic barriers. Thus all considerations make it clear that geographic isolation is a pre-requisite for successful speciation. Nevertheless, possibility of genetic divergence in individuals with highly specialized ecological requirements is not entirely ruled out, although there may not be any geographical isolation.

Speciation in plants differs considerably from that in animals

Several phenomena radically affect the divergence and speciation patterns in plants and animals. They include—

(a) **Plants are less complex organisms than animals**. Number of different kinds of differentiated cells found in adult body is much less in plants. As for example, kinds of differentiated cells in a flowering plant is between 47 to 52; the number is about 66 in earthworms, 100-150 in insects and 200-250 in higher mammals. Consequently, required integration and balance between tissue and organs is far greater in animals than in plants. Moreover, plants have an open system of growth based on potentially immortal meristem. Animal growth is rather closed as is demanded by their finite body size and compactness. These differences affect speciation because when developmental patterns are relatively simple, the possibility of a functional intermediate is greater than when the developmental pattern is complex.

(b) **Animals possess highly developed sense organs.** Because animals have highly complex sense organs, barriers of reproductive isolation can easily evolve between them. Particularly, barriers based upon divergent behavioral patterns or ethological isolation is a common occurrence in animals, which reinforces prezygotic isolations based on other kinds of barriers. All these barriers more readily result in speciation. Plants have no or less developed sense organs, hence possibility of developing prezygotic barriers of reproductive isolation is less.

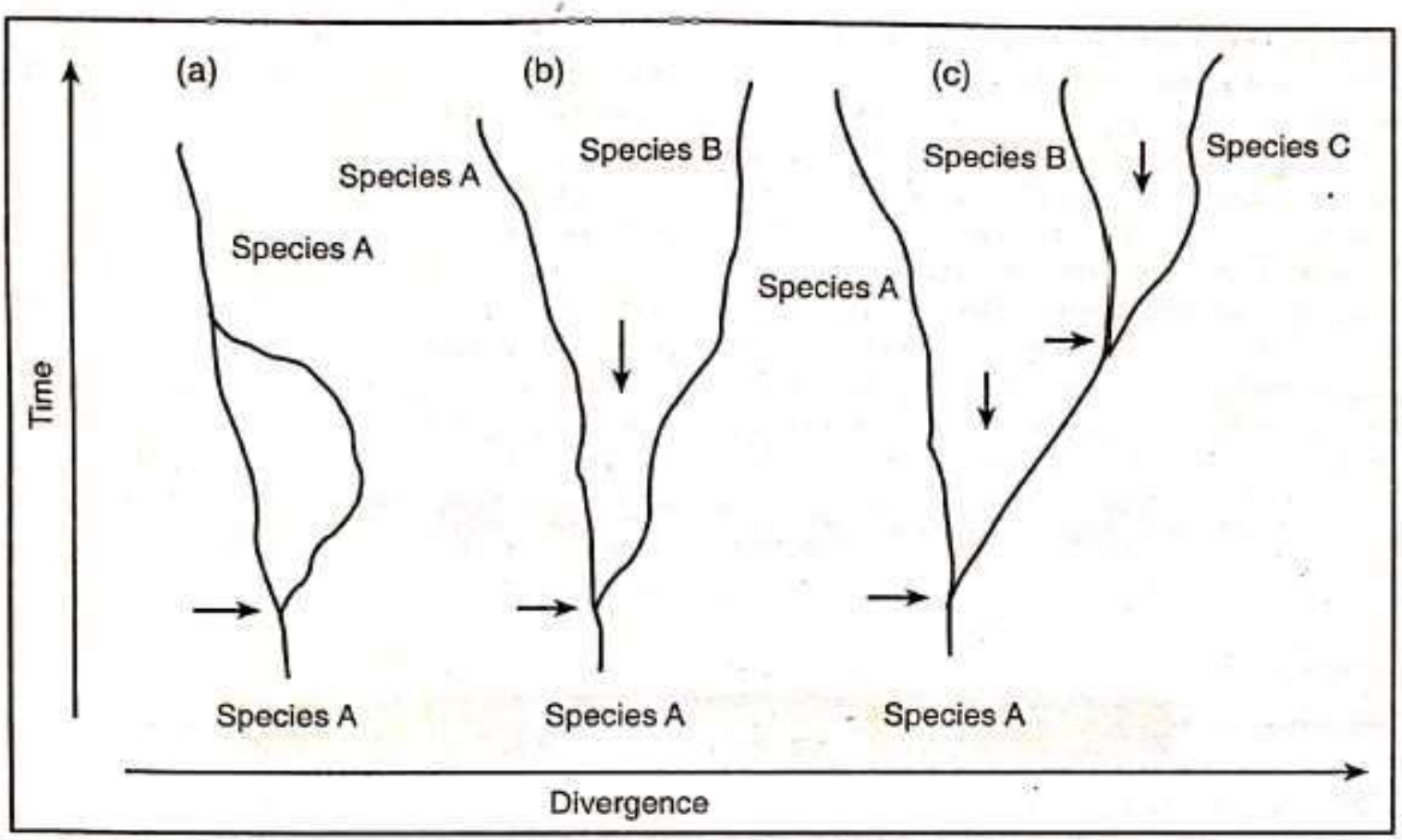


Figure 18.12 : A model showing speciation results in long-term evolution. Horizontal arrow (→) denotes geographic isolation and vertical arrow (↓) denotes reproductive isolation. Diverged population may lose divergence due to interbreeding (a), but may become new species if reproductive isolation evolves as in [(b) and (c)].

Speciation is essential for adaptation and diversity of organisms

It has been said in the previous chapter that reproductive isolation is a by-product of adaptive changes in each diverging population. Consequently, speciation is also a by-product of genetic differentiation of populations, which are brought by selection and/or genetic drift. But speciation itself is important for adaptation. In the phylogenetic tree of sexually reproducing organisms, each branch represents a speciation event. In this event, population became reproductively isolated, underwent independent and divergent evolution acquiring some adaptive features, which mark that taxa. In fact, **microevolution** (genetic change within population) **becomes macroevolution** (origin of higher taxa) **through speciation**.

Paleontologists argue that many fossil lineages change morphologically very little over the course of million years. This long-term morphological stasis is punctuated by a rapid morphological change, resulting in a burst of species. The proposed hypothesis is known as **punctuated equilibrium** (please see section 19.5). But population geneticists suggest that natural selection can readily modify the characters of populations, which does not conform with the pattern forwarded by punctuationists. Actually, recombination in sexually reproducing organisms breaks down the combination of genes, which can provide different adaptation. As for example, if disruptive selection favors both large and small beaks of birds in an environment with different food sizes, both types of birds are equally adapted. If the beak size is a polygenic trait, a random mating will produce most individuals with intermediate beak size. Only if there is a barrier to free interbreeding, the phenotypes ideally adapted to different resources will persist.

Local populations may respond to selection and diverge adaptively to different resources.

environmental conditions may change so that diverged populations interbreed; as a result divergence is lost. These events occur more frequently to be evident in fossil records and will appear as stasis. Contrarily, if the diverged populations become reproductively isolated, their distinctive characters are retained indefinitely, even if they become sympatric. The morphological differences in populations become almost permanent and can be evident in fossil records. Reproductive isolation is the first step to permanent divergence between populations and provides the

opportunity for further divergence leading to speciation. Therefore, speciation can facilitate long-term evolutionary changes in morphology and other phenotypic characters (Fig. 18.12).

Finally, history of evolution in organisms tells us that evolution is not a story of single lineage changing progressively. Rather, it is a story of radiation – diverse species (Fig. 18.1) originate from common ancestors. According to Mayr (1963) "speciation — is the method by which evolution advances. Without speciation, there would be no diversification of the organic world, no adaptive radiation and very little evolutionary progress."

CHAPTER SUMMARY

1. Origin of species includes two concepts – transformation of species over time or **phyletic evolution** and multiplication of species in space or **speciation**. Geologists preferred the terms anagenesis for phyletic evolution and cladogenesis for speciation.
2. **Speciation** is splitting of a single species into several ones, and grouped into two broad classes. Instantaneous speciation is an individual phenomenon and occurs through major chromosomal changes. Gradual speciation is a population phenomenonal and is regarded as true speciation.
3. Allopatric speciation occurs when a new species evolves from a parental species through geographical isolation. Geographically segregated populations acquire genetic divergence leading to reproductive isolation. Because it is a gradual process, many intermediate stages or incipient species are found. There are several models of allopatric speciation of which vicariant and peripatric speciations are important.
4. Sympatric speciation does not need geographical isolation, rather reproductive isolation occurs between two populations occupying same area. A variation of sympatric speciation is parapatric speciation, where genetically diverged individuals become isolated from the parental group but remain in contact.
5. Though sympatric speciation is favored by many examples, evolutionary geneticists believe that initial genetic divergence between populations require geographical separation.
6. Speciation in plants differs considerably from that in animals in several respects. Relative simplicity of plant structure, their capacity for vegetative reproduction and self-fertilization, common occurrence of polyploidy and hybridization are the factors which contribute to the difference.
7. Polyploidy plays significant role in speciation, particularly in plants. Polyploid series exists in about 1/3 genera of flowering plants. Polyploidy has a minor role in animal speciation.
8. Hybridization results in a variety of recombination. When hybrids are fertile, speciation may occur and is known as recombinational speciation. Again, speciation due to hybridization is much more common in plants than in animals.
9. Methods of pollination increase the sharpness of species boundaries in plants. In general, plants adapted to different methods of pollination show high proportions of distinct characters, particularly in flowers.