of natural selection and random drift. The conventional dividing line between macro- and microevolution is at speciation, so that events below that level are microevolution and those above it are macroevolution.

The distinction between micro- and macroevolution has traditionally been not only between the timescales of the events but also between the methods used, microevolution has been studied with genetic techniques, and has used observation and experiment on the timescale of human lifetimes. Macroevolution has been studied with fossil evidence, comparative morphology, and phylogenetic inference.

As we know how microevolution proceeds. So it is noteworthy to explain how macroevolution proceeds. Many examples suggest that macroevolution is actually microevolutionary processes that persist for a long time, or in other words macroevolution is due to "extrapolated" microevolution.

SPECIATION

Species is a latin word meaning "kind" or "appearance." Indeed, we learn to distinguish between different kinds of organism from differences in their appearance. Linnaeus, the founder of modern taxonomy, described individual species in terms of their physical form; the study of form or structure, called morphology or phonetic characters, is still the method most often used to characterize species. If one group of organisms consistently differs from other organisms, it will be defined as a separate species. The formal definition of the species will be in terms of characters that can be used to recognize members of that species. The taxonomist who describes the species will have examined specimens of it and of related species, looking for characters that are present in specimens of the species to be described, and absent from other closely related species. These are the characters used to define the species. Modern taxonomists also consider differences in body function, biochemistry, behaviour, and genetic makeup. Here we will discuss some commonly used species concept to describe species.

The biological species concept

The biological species concept is widely accepted species definition was first described by evolutionary biologist Ernst Mayr in 1942. Mayr's definition is answer to the question, what factors divide biological diversity into separate forms that we identify as species?

According to this concept "species are group of population which can freely interbreed in nature and produces viable, fertile offsprings and are reproductively isolated from members of other species." The expression reproductively isolated means that members of the species do not interbreed with members of other species, because they have some attributes that prevent interbreeding. The biological species concept is important because it places the taxonomy of natural species within the conceptual scheme of population genetics. In terms of population genetics a group of interbreeding organisms make up, a gene pool. In theory, the gene pool is the unit within which gene frequencies can change. In the biological species concept, gene pools become more or less identifiable as species. The identity is imperfect, because species and populations are often subdivided. The species, in this concept, is the unit of evolution. Organisms do not evolve but species do, and higher taxonomic groups such as phyla only evolve in so far as their constituent species are evolving.

The biological species concept explains why the members of a species resemble one another, and differ from other species. When two organisms breed within a species, their genes pass into their combined offspring, as this process is repeated in every generation, the genes of different organisms are constantly shuffled around the species gene pool. Different family lineages (parents, offspring, grandchildren, and so on) soon become blurred by the transfer of genes between them. The shared gene pool gives the species its identity. By contrast, genes are not transferred to other species, and different species therefore evolve a different appearance. The movement of genes through a species by migration and interbreeding is called gene flow. According to the biological species concept, gene flow explains why each species forms a phonetic cluster.

In summary, the biological species concept is based on reproductive isolation, with each species isolated by factors (barriers) that prevent interbreeding, thereby blocking genetic mixing with other species.

Limitation of biological species concept

The biological species concept does not work in all situations. For instance, it is inadequate for grouping extinct forms of life, the fossils of which must be classified according to morphology. The criterion of interbreeding is meaningless for organisms that are completely asexual in their reproduction, as are all prokaryotes, some protests, some fungi, and even some plants (such as commercial banana). Many bacteria do transfer genes on a limited scale by conjugation and other processes, but there is nothing similar to the equal contribution of genetic material from two parents that occurs in sexual reproduction. Different lineages of descent give rise to clones, which genetically speaking, represent single individuals. Asexual organisms can be assigned to species only by the grouping of clones that have the same structural and biochemical characteristics.

There are many other species concepts with more restricted usage. One example is the phylogenetic species concept which emphasizes common evolutionary history. It is defined as a irreducible basal cluster of organisms diagnosably different from other such clusters, and within which there is a parental pattern of ancestry and descent. Any

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character that distinguishes a population would define it as a species, regardless of whether it interbreeds with others or not. This species concept will lead to a classification of organisms that can sometimes be different from BSC. It also applies to asexual organisms.

Patterns/Forms of Speciation

Evolutionary theory must explain macroevolution, the origin of new taxonomic groups (e.g., new species, new genera, new families). Speciation, or the origin of new species, is a central process of macroevolution because any genus, family, or higher taxon originates with a new species novel enough to be the first member of the higher taxon.

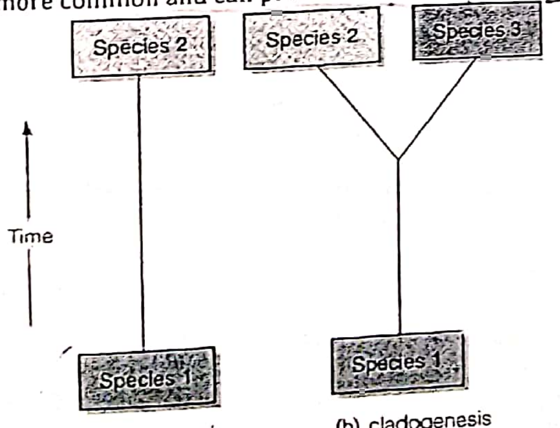
The term **evolution** describes a change in genotypic frequencies, which usually results in a population of individuals better adapted to the environment than their ancestors were. **Speciation** comes in two different forms. (1) It may be the evolution of a population over time until the current population cannot be classified as belonging to the same species as the original population. This process is known as **anagenesis, or phyletic evolution** (*an* is Latin for without, *genesis* is Latin for birth or creation). (2) Speciation may also be the divergence of a population into two distinct forms (species) that exist simultaneously. This branching process is known as **cladogenesis** (*clado* is Greek for branch)

1. Anagenesis (phyletic evolution):

The transformation of an unbranched lineage of organisms, sometimes to a state different enough from the ancestral population to justify renaming it as a new species.

2. Cladogenesis (branching evolution):

The budding of one or more new species from a parent species that continues to exist; is more important than anagenesis in life's history, because it is more common and can promote biological diversity.



(a) anagenesis (b) cladogenesis

Reproductive isolation barriers

Any barrier or factor that impedes two species from producing viable, fertile hybrids contributes to reproductive isolation. No single barrier may be completely impenetrable to genetic exchange, but many species are genetically isolated by more than one type of barriers. Here, we are considering only biological barriers to reproduction, which are intrinsic to the organisms. Of course, if two species are geographically segregated, they cannot possibly interbreed, but a geographical barrier is not considered equivalent to reproductive isolation because it is not intrinsic to the organism themselves. Intrinsic reproductive barriers prevent population belonging to different species from interbreeding, even if their ranges overlap. Intrinsic reproductive barriers are actually "evolved characters" that prevents interbreeding between different species. For instance, Courtship, is an example of reproductive barrier. If two species do not interbreed because their courtship differs, then the courtship behaviour of at least one of those species must have undergone evolutionary change and it became a new evolved character which leads to reproductive isolation.

The various types of reproductive barrier that isolate the gene pools of species can be categorized as prezygotic or postzygotic, depending on whether they function before or after the formation of zygotes , or fertilized eggs.

Prezygotic Barriers

Prezygotic barriers prevents mating between species or impede formation of hybrid zygotes.

1. *Habitat/Ecological isolation:* Two species that live in different habitats within the same area may encounter each other rarely, if at all, even though they are not technically geographically isolated. For example, two species of garter snakes in the genus *Thamnophis* occur in the same areas, but one lives mainly in water and the other is primarily terrestrial. Habitat isolation also affects parasites, which are generally confined to certain plant or animal host species. Two species of parasites living on different hosts will not have a chance to mate.

2. *Behavioural/Ethological isolation:* It is also commonly known as ethological isolation, it represents special signals that attract mates, as well as elaborate behaviour unique to a species. It is probably the most important reproductive barrier among closely related animals. Recognition species concept is based on this type of reproductive barrier. Male fireflies of various species signal to females of their kind by blinking their lights in particular patterns. The females respond only to signals characteristic of their own species, flashing back and attracting the males.

The occurrence of different shape, colouration, habitat and the range of overlapping regions may be some of the deciding factors in behavioural isolation. The courtship rituals are specific to a species and these courtship rituals are another form of behavioural isolation. The distinctive songs of many birds, the special mating calls of certain frogs, and the sexual displays of most animals are generally attractive only to mates of the same species. Many plants have floral displays that attract only certain insect pollinators

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Even where the morphological differences between two species are minimal, behavioural differences may prevent cross-fertilization. Thus *Drosophila melanogaster* and *Drosophila simulans*, designated as sibling species because of their morphological similarity, normally do not mate with each other even when kept together in a single population cage. According to Coyne and co-workers (1994), male courtship in this group depends on their attraction to specific hydrocarbons in the female cuticle, and this behavioural isolation can be caused by only few genetic differences.

3. ***Temporal isolation***: The time period of mating of different species are never always same; two species that breed during different times of the day, different seasons, or different years cannot mix their gametes. This differential time period of mating which prevents interbreeding between two different species is known as temporal isolation. Three species of the orchid genus *Dendrobium* living in the same rain forest does not hybridize because they flower on different days. Pollination of each species is limited to a single day because the flowers open in the morning and wither that evening.

4. ***Mechanical isolation:*** Closely related species may attempt to mate, but cannot achieve the act or fail to achieve fertilization because their genetilia are anatomically not compatible or incompatible. This type of incompatibility, long thought to be a primary isolating mechanism in animals, even such kind of barriers contribute to reproductive isolation of flowering plants that are pollinated by insects or other animals. Floral anatomy is often adapted to certain pollinators that transfer pollen only among plants of the same species.

5. ***Gametic isolation:*** Even if the gametes of different species meet, they rarely fuse to form a zygote. For animals whose eggs are fertilized within the female reproductive tract (internal fertilization), the sperm of one species may not be able to survive in the environment of the female reproductive tract of another species. Many aquatic animals release their gametes into the surrounding water, where the eggs are fertilized (external fertilization). Even when two closely related species release their gametes at the same time in the same place, cross specific fertilization is uncommon. Gametes recognition may be based on the presence of specific molecules on the coats around the egg, which adhere only to complementary molecules on sperm cells of the same species. In some *Drosophila* crosses, Patterson and Stone and others have shown that an insemination reaction in the vagina of the female causes swelling and prevents successful fertilization of the egg. A similar mechanism of the molecular recognition enables prevents growth of pollen tube in the styles of foreign species.

Postzygotic Barriers

If the prezygotic barriers do not impede the successful fertilization of the gametes belonging to different species, then postzygotic barriers prevent the hybrid zygote from developing into a viable, fertile adult.

1. ***Reduced Hybrid Viability or Hybrid Inviability:*** When prezygotic barriers are crossed and hybrid zygotes are formed, genetic incompatibility between the two species may abort development of the hybrid at some embryonic stage. Of the numerous species of frog belonging to the genus *Rana*, some live in the same regions and habitats, where they may occasionally hybridize. But the hybrids generally do not complete their development.

2. ***Reduced Hybrid Fertility or Hybrid Sterility:*** Even if two species mate and produce the hybrid offspring that are vigorous, reproductive isolation is intact if the hybrids are completely or largely sterile. Since the infertile hybrids cannot backbreed with either parental species, genes cannot flow freely between the species. One cause of this barrier is a failure of the meiosis to produce normal gametes in the hybrid if chromosomes of the two parent species differ in number or structure. A familiar case of a sterile hybrid is the mule, a robust cross between horse and a donkey; horses and donkeys remain distinct species because, except very rarely, mules cannot backbreed with either species.

3. ***Hybrid breakdown:*** In some cases when species crossmate, the first-generation hybrids are viable and fertile, but when these hybrids mate with one another or with either parent species, offsprings of the next generation are feeble or sterile. For example, different cotton species can produce fertile hybrids (F_1 generation), but breakdown occurs in the next generation (F_2 generation) when offspring of the hybrids die as seeds or grow into weak and defective plants

Modes of Speciation

The crucial event for the origin of a new species is reproductive isolation. The members of a species usually differ genetically, ecologically, and in their behaviour and morphology from other species, as well as in who they will interbreed with. Some biologists prefer to define species not by reproductive isolation but by other properties, such as genetic or ecological differences. Probably no single property can provide a universal species definition, applicable to all animals, plants, and microorganisms. However, many species do differ by being reproductively isolated, and even if the evolution of if the evolution of reproductive isolation is not always the crucial event in speciation, it is certainly the key event in research on speciation.

In 1889 A. R. Wallace proposed that natural selection might favour the establishment of mating barriers among population if the hybrids were adaptively inferior. That is, genotypes that did not mate to produce inferior hybrids would be selected over genotypes that did. According to this hypothesis, which Dobzhansky and others supported, selection for reproductive isolation arises because most races and species are strongly adapted to specific environments.

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Hybrids between two such highly adapted populations therefore represent a genetic dilution of their parental gene complexes that can be of great dis- advantage in the original environments. Thus genotypes that have incorporated prezygotic isolating mechanisms would have the advantage of not wasting their gametes in producing deleterious offspring.

There are four general modes of speciation based on different geographic conditions and how the gene flow is interrupted in the speciating populations. If a new species evolves in geographic isolation from its ancestors, the process is called *allopatric speciation*. If the new species evolves in a geographically contiguous population, it is called *parapatric speciation*. If the new species evolves within the geographic range of its ancestor, it is called as *sympatric speciation*. If small founder populations colonize an area outside the main population range and forms new species it is termed as *peripatric speciation*.

Reproductive isolating mechanisms are barriers to **gene flow**, the spread of genes between populations. These isolating mechanisms can evolve in three different ways, each of which defines a different mechanism of speciation. Usually, the mode of speciation is dictated by both the properties of the genetic systems of the organisms and stochastic (random) or accidental events. For example, vertebrates tend to have different speciation modes than phytophagous (plant-feeding) insects.

1. Allopatric and Parapatric Speciation

The appearance of a geographic barrier, such as a river or mountain, through the range of a species physically isolates populations of the species. Physical isolation can also occur if migrants cross a particular barrier and begin a new population (founder effect). The physically isolated populations can then evolve independently. If reproductive isolating mechanisms evolve, then two distinct species are formed, and if they come together in the future, they remain distinct species. Speciation that occurs because reproductive isolating mechanisms evolve during physical separation of the populations is called **allopatric speciation**. As evolutionary biologist Guy Bush pointed out, "Although examples in nature are difficult to substantiate . . . it [allopatric speciation] has been convincingly demonstrated in frogs . . .and lizards." Reproductive isolating mechanisms usually originate incidentally to the speciation process. That is, they arise incidentally during the process of evolution in isolated populations rather than being selected for. When isolated populations come together again, incomplete isolating mechanisms may allow hybrids to form. If the hybrids are normal and viable and can freely interbreed with individuals of each parent population, then no speciation has taken place. However, if the hybrids are at a disadvantage, natural selection may favor stronger isolating mechanisms.

In this case, organisms that mate with individuals from the other population leave fewer offspring. The result is a more effective barrier to hybridization. Regions in which previously isolated populations come into contact and produce hybrids are called hybrid zones. Until recently, evolutionary biologists believed that allopatric speciation was the general rule. Many now believe that two other modes of speciation may occur frequently in certain groups of organisms.

Parapatric speciation occurs when a population of a species that occupies a large range enters a new niche or habitat. Although no physical barrier arises, the new niche acts as a barrier to gene flow between the population in the new niche and the rest of the species. Here again, reproductive isolating mechanisms evolve to produce two species where there was only one before. Parapatric speciation is believed to have occurred often in relatively non vagile animals such as snails, flightless grasshoppers, and annual plants.

Sympatric speciation occurs when a polymorphism, which is the occurrence of alternative phenotypes in the same population, arises within an interbreeding population before a shift to a new niche. This mode of speciation may be common in parasites and phytophagous insects. For example, if a polymorphism arises within a parasitic species that allows an individual with a certain genotype to adapt to a new host, this genotype may be the forerunner of a new species. If the parasite not only feeds on the new host but also mates on the new host, a barrier to gene flow arises, although the parasite may be surrounded by other members of its species with the original genotype. Sympatric speciation can thus occur in the middle of a species range rather than at the edges.

An example of incipient sympatric speciation has been seen recently in host races of the apple maggot fly (*Rhagoletis pomonella*) in North America. This fly was found originally only on hawthorn plants. However, in the nineteenth century, it spread as a pest to newly introduced apple trees. In fact, races are now known on pear and cherry trees and on rose bushes. These races have developed genetic, behavioral, and ecological differences from the original hawthorn-dwelling parent. Evolutionary biologists view this as an opportunity to observe sympatric speciation as it occurs.

Another form of sympatric speciation occurs when cytogenetic changes take place that result in "instantaneous speciation." These cytogenetic changes include polyploidy and translocations. For example, if polyploidy offspring cannot produce fertile hybrids with individuals from a parent population, then the polyploid is reproductively isolated. This mechanism is much more common in plants because they can exist vegetatively despite odd ploidy and they usually do not have chromosomal sex-determining mechanisms, which are especially vulnerable to ploidy problems. The end result of cladogenesis is the divergence of a homogeneous population into two or more species.

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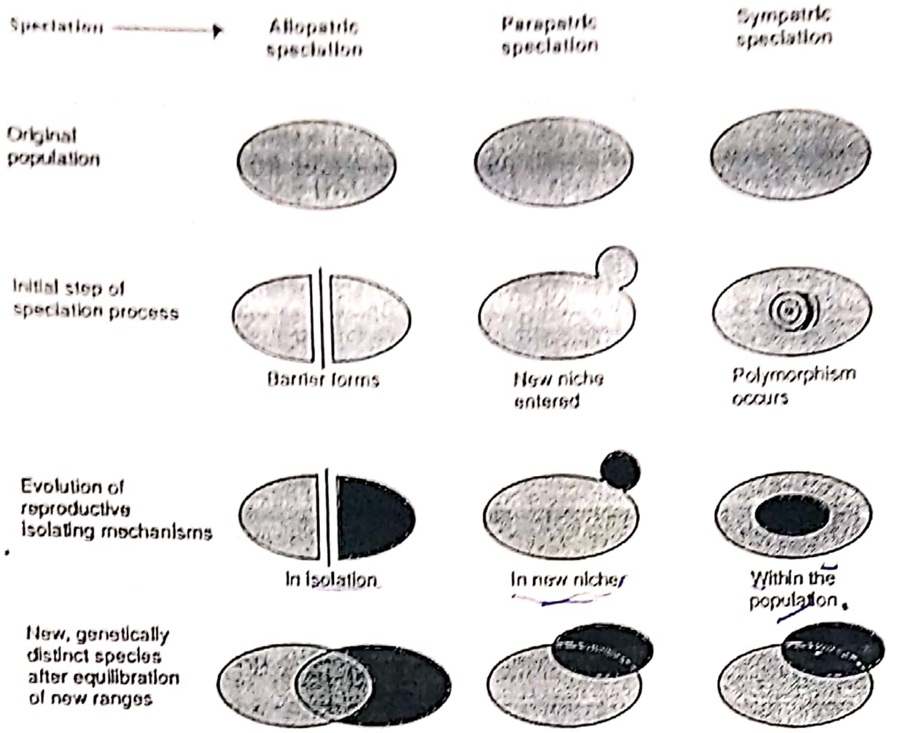

2. Allopatric Speciation

Speciation that occurs when the initial block to gene flow is a geographical barrier that physically isolates the population. Such occurrences include emergence of mountain ranges, movement of glaciers, formation of land bridges, subsidence of large lakes. Geographical populations often differ genetically, which includes genetic markers associated with reproductive isolation.

One of the classic examples of cladogenesis appears in the ground finches of the Galápagos Islands. These birds are very well studied not only because they present a striking case of speciation, but also because Darwin studied them and was strongly influenced by them in his views. An original flock of finches somehow reached the Galápagos Archipelago from South America, 700 miles away, and with time spread to the various islands of the Galápagos Archipelago. Given the limited ability of the birds to get from island to island, **allopatric speciation** took place. On each island, the finch population evolved reproductive isolating mechanisms while evolving to fill certain niches not already filled on the islands. For example, in South America, no finches have evolved to be like woodpeckers because many woodpecker species already live there. But the Galápagos Islands, being isolated from South America, have what is called a **depauperate fauna**, a fauna lacking many species found on the mainland. The islands lacked woodpeckers, and a very useful food resource for birds—insects beneath the bark of trees—was going unused. Finches that could make use of this resource would be at an advantage and would thus be favored by natural selection. On one island, a finch did evolve to use this food resource. The woodpecker finch acts like a woodpecker by inserting cactus needles into holes in dead trees to extract insects.

Darwin wrote: "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."

Phyletic Gradualism V/S Punctuated Equilibrium

Darwin visualized cladogenesis as a gradual process, which we refer to as **phyletic gradualism.** But paleontologists rarely find gradual transitions of fossil forms but often observe species appearing as new forms suddenly in the rock layers. These species persist virtually unchanged and then disappear as suddenly as they appeared. Even Darwin, who believed species from a common ancestral stock evolve differences gradually, was perplexed by the lack of transitional forms in the fossil record. Advocates of punctuated equilibrium have redrawn the evolutionary tree to represent fossil evidence for evolution occurring in spurts of relatively rapid change instead of gradual divergence.

An alternative view arose in 1972, when N. Eldredge and S. J. Gould suggested that speciation itself, and the morphological changes accompanying speciation, occur rapidly, separated by long periods of time when little change occurs (*stasis*). They called their model **punctuated equilibrium** (periods of stasis punctuated by rapid evolutionary change). It depicts species undergoing most of their morphological modification as they first separate from the parent species then showing little change as they produce additional species. In this theory gradual change is replaced with long periods of stasis punctuated with episodes of speciation.

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The origin of new polyploid plants through genome changes is one mechanism of sudden speciation. For a population facing new environmental conditions, genetic drift and natural selection can cause significant change in only a few hundred or thousand generations. A few thousand generations is considered rapid in reference to the geologic time scale.

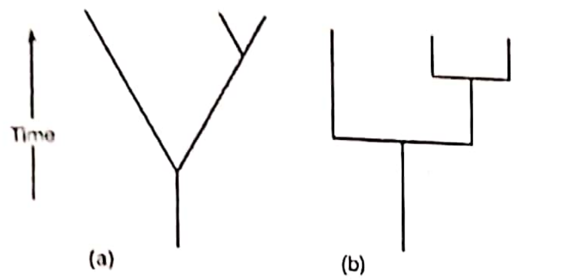

Figure Diagrammatic interpretation of cladogenesis.
(a) Phyletic gradualism is depicted as a gradual divergence over time. (b) Punctuated equilibrium is depicted as a rapid divergence of two groups after long periods of no change. The horizontal axis is some arbitrary measure of species differences.

Although figure presents what appear to be two clear alternatives, in practice the models are very hard to tell apart. They both start with the same ancestral species and predict the same number of modern species. Allopatric, parapatric, and sympatric speciation mechanisms apply to both punctuated equilibrium and phyletic gradualism. The only major difference between the models is the rate of change, and this can only be discovered from an almost complete fossil record.

The fossil record indicates that successful species survive for a few million years on average. If a species survives for five million years and most of its morphological changes occur in the first 50,000 years; then the speciation episode occurred in just 1% of the species' lifetime. With this time scale, a species will appear suddenly in rocks of a certain age, linger relatively unchanged for millions of years, then become extinct.

An evolutionary spurt preceding a longer period of morphological stasis would explain why paleontologists find so few transitions in the fossils record of a species. Because "sudden" can refer to thousands of years on the geological time scale, differing opinions of punctuationalists and gradualists about the rate of speciation may be more a function of time perspective than conceptual difference.

There is clear disagreement, however, over how much a species changes after its origin. Hybrid sterility has a continuous range, from none to complete, and may be caused by two main factors generation of aneuploid gametes due to structural chromosomal differences between the genes of the parents, which may interact "disharmoniously", as opposed to the "co-adapted" gene complexes within the species.

Arguments against this hypothesis are morphology can change within lineages, stable lineages in the fossil record do fluctuate, the low resolution of the fossil record (<100000yr). If its resolution was higher, the argument goes, one would observe that the apparently sudden transitions are actually gradual transitions.

Punctuated gradualism: Character evolution is episodic, but not necessarily associated with speciation. The most contentious issue here is between hypothesis one and two. To distinguish between the two, one has to assess whether morphological change is usually associated with speciation.

Missing links: They are frequent in the fossil record (e.g., body plan types), and there are two alternative possibilities for why they occur. First, if most major phenotypic changes were brought about by macromutations (saltatory evolution then no links would exist. Goldschmidts macro-mutations were proposed as a complete "repatterning" of the chromosomal material, not single gene mutations. There is no evidence for such large scale repatterning leading to viable organisms. Single gene "macromutations" occur (e.g., homeotic mutations), but they usually are highly deleterious. If most phenotypic evolution occurs according to the punctuated equilibrium hypothesis via founder effect speciation, the frequent absence of missing links would be explicable by the small transitional population sizes involved. Thus, the phenotypic changes may be continuous, but poorly preserved.

The punctuated equilibrium model has brought much excitement to modern evolutionary biology. We await a time in the near future when we can decide which model has predominated in evolutionary history.

CONVERGENT EVOLUTION

Convergent evolution is the process by which unrelated or distantly related organisms evolve similar adaptations. Organisms displaying these similarities usually live in similar environments, and the force driving convergence is natural selection. Similar environments pose similar challenges to survival, and traits that aid in survival are selected for in each environment. Convergent evolution is seen in the fusiform (tapering toward the end) shapes and similar countershading coloration of sharks and dolphins, both of which are adapted to marine environments. Their shape facilitates rapid and efficient movement through water, and their light underbelly and a gray upper surface make them less visible from both below and above.

Convergent Evolution in Desert Lizards

Some of the most striking examples of convergent evolution are found in desert lizards throughout the world. Australian and North American deserts each support a cryptically colored lizard species that is specialized to eat ants and is protected by sharp spines. The Australian species, the thorny devil (*Moloch horridus*, Agamid family) is only distantly related to the

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