Evolutionary Biology
(Unit-9)
Sem 6 Hons (CC-6-14-TH)

Scientific Classification –

Why do biologists classify organisms? The major reason is to make sense of the incredible diversity of life on Earth. Scientists have identified millions of different species of organisms. Among animals, the most diverse group of organisms is the insects. More than one million different species of insects have already been described. An estimated nine million insect species have yet to be identified. As diverse as insects are, there may be even more species of bacteria, another major group of organisms. Clearly, there is a need to organize the tremendous diversity of life. Classification allows scientists to organize and better understand the basic similarities and differences among organisms. This knowledge is necessary to understand the present diversity and the past evolutionary history of life on Earth.

Phylogeny –

Phylogeny, the history of the evolution of a species or group, especially in reference to lines of descent and relationships among broad groups of organisms. Fundamental to phylogeny is the proposition, universally accepted in the scientific community, that plants or animals of different species descended from common ancestors. The evidence for such relationships, however, is nearly always incomplete, for the vast majority of species that have ever lived are extinct, and relatively few of their remains have been preserved in the fossil record. Most phylogenies therefore are hypotheses and are based on indirect evidence. Different phylogenies often emerge using the same evidence. Nevertheless, there is universal agreement that the tree of life is the result of organic descent from earlier ancestors and that true phylogenies are discoverable, at least in principle.

Phenetics versus Cladistics

The methodology of phylogenetic work rests on two approaches at present: numerical taxonomy (phenetics) and phylogenetic systematics (cladistics). The most-direct difference between the two methods is that phenetics classifies species by using as many characteristics as possible and arranges them by similarity regardless of any evolutionary relationships.

The phenetics approach, which arose in the 1950s, based classification strictly on similarities between organisms and emphasized numerical analyses of a set of phenotypic characteristics (that is, biological characters that are observable). In the name of objectivity, one simply counted common characters without respect to ancestry, and divisions were made on the basis of totals: the more characters in common, the closer the classification. However, in phenetics, the shared history between one organism and another, such as the archosaur ancestry of both crocodiles and birds, was simply irrelevant. Other problems, such as the precise definition of a “character” (that is, an observable feature, or trait, of an organism), required subjective decisions, thereby reducing the credibility of phenetics as an objective approach to phylogeny. Although the tabulation of common characters remains very important in developing a species’s phylogeny, taxonomists have moved away from phenetics as a viable approach.

Cladistics, on the other hand, does not base species classification on an assemblage of all shared characters between one species and another. It bases the classification of a group of species solely on their most-recent common ancestor. Taken from work by German zoologist Willi Hennig in the 1950s, cladistics uses only shared derived characters—that is, selected characteristics that infer monophyly (descent from a single species) or those that are expressed in all descendants of a common ancestor. Such uniquely shared historical (or derived) characteristics are called synapomorphies.

For example, suppose that there is an original species marked by character *A*, and from that three species eventually evolve. The original species first breaks into two successor groups, in one of which *A* evolves into the character *a*; that successor group then breaks into two daughter groups, both of which have *a*. The other original successor group retains *A* throughout, with no further division. In that case, *a* is a synapomorphy, since the two species with *a* evolved from an ancestral species that had *a* uniquely. Therefore, the possessors of *a* must be classified more closely to each other than to the third species. Consequently, by means of cladistics, crocodiles and birds are classified together, before they can be jointly linked to lizards. (For additional information on the philosophical underpinnings of phenetics and cladistics, *see* biology, philosophy of: taxonomy).

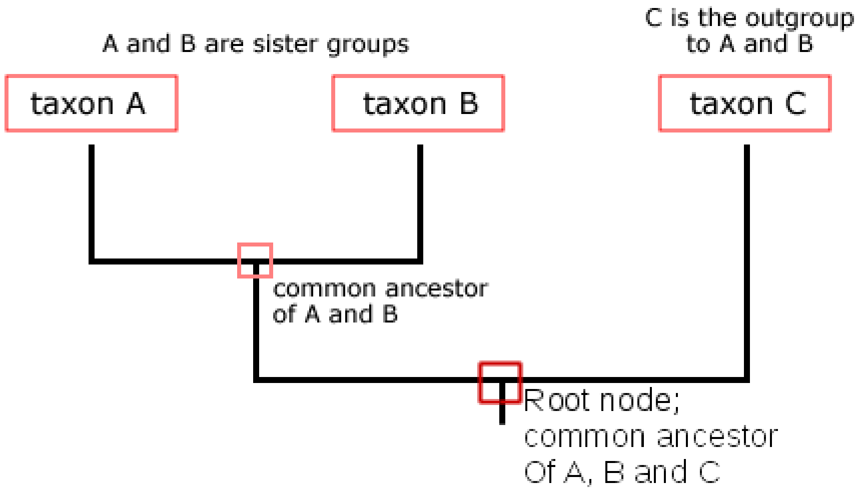
Phylogenetic tree –

All organisms that ever existed on this planet are related to other organisms in a branching evolutionary pattern called the tree of life. To decipher this relatedness between the diversity of organisms, both living and extinct, "tree thinking" is invaluable. Tree thinking, or phylogenetic thinking, helps us unravel the branching evolutionary relationships between extant species, while thinking about the passage of time and the ancestors of each of those living species. **Phylogenetic tree**, also called **Dendrogram**, is a diagram showing the evolutionary interrelations of a group of organisms derived from a common ancestral form. The ancestor is in the tree "trunk"; organisms that have arisen from it are placed at the ends of tree "branches." The distance of one group from the other groups indicates the degree of relationship; *i.e.*, closely related groups are located on branches close to one another. Phylogenetic trees, although speculative, provide a convenient method for studying phylogenetic relationships. A phylogenetic tree is a visual representation of the relationship between different organisms, showing the path through evolutionary time from a common ancestor to different descendants. Trees can represent relationships ranging from the entire history of life on earth, down to individuals in a population. Trees that show species help us understand how new species form from common ancestral species. The process of new species formation, called **speciation**, is the starting point for a discussion of biological diversity. The natural endpoint will be extinction.

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A **phylogenetic tree** is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, a "tree of life" can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms. Unlike a taxonomic classification diagram, a phylogenetic tree can be read like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees 'rooted,' which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains (Bacteria, Archaea, and Eukarya) diverge from a single point and branch off. The small branch that plants and animals (including humans) occupy in this diagram shows how recent and miniscule these groups are compared with other organisms. Unrooted trees don't show a common ancestor but do show relationships among species.

Each group of organisms went through its own evolutionary journey, called its phylogeny. Each organism shares relatedness with others, and based on morphologic and genetic evidence, scientists attempt to map the evolutionary pathways of all life on Earth. Many scientists build phylogenetic trees to illustrate evolutionary relationships.

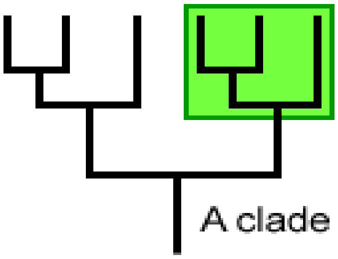
The diagram below shows a tree of 3 **taxa** (singular **taxon,** a taxonomic unit).

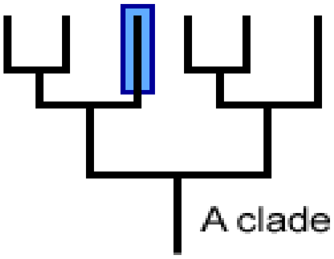


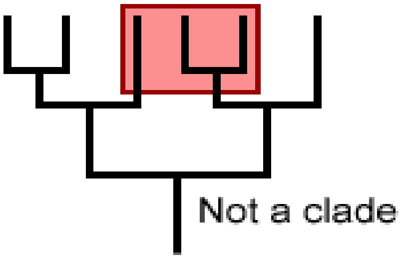
Terminology of phylogenetic trees

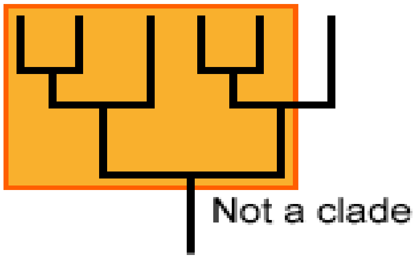
Notice that the tree above tree branches from a single trunk into two branches, the vertical lines, and then the left side branches again. In this tree, the vertical **branches** represent a **lineage**, which is a taxon, shown at the **tip**, and all its ancestors. The **nodes** are where lineages diverge, representing a speciation event from a common ancestor. The trunk at the base of the tree is actually called the **root**, and the root node represents the **most recent common ancestor** of all of the taxa represented on the tree. Time in this particular style of tree is represented vertically, proceeding from the oldest pictured here at the bottom to the most recent at the top.

What this particular tree tells us is that taxon A and taxon B are more closely related to each other than either taxon is to taxon C. The reason is that taxon A and taxon B share a more recent common ancestor than A and B do with taxon C. The least related taxon in a tree is called the **outgroup** of that phylogeny, and it often included because it has contrasting characteristics relative to the other included taxa. A group of taxa that includes a common ancestor and *all* of its descendants is called a **monophyletic group**, or a **clade**. Groups that *exclude one or more descendants* or that *exclude the common ancestor* are not monophyletic groups (clades); these groups are called paraphyletic and polyphyletic, respectively.









The “tree of life”

Ancestral relationships among species are commonly represented as phylogenetic trees (also called cladograms or dendrograms). A cladogram is a physical diagrammatic representation of a hypothesis of inferred relationship between species. The evolutionary relatedness between species is reflected by branching pattern of the tree and the relative distance between species on the tree. Any two species will have a common ancestor at the point where their respective branches are traced back to intersect. The more recent a common ancestor to humans, the more closely related it is to humans. For example, the common ancestor of modern humans and Neanderthals would be traced back to approximately 500,000 years ago. Similarly, the common ancestor of humans/Neanderthals and chimpanzees existed approximately 6.5 million years ago. Thus, since humans and Neanderthals share a common ancestor not shared by chimpanzees, we have reason to believe that humans are more closely related to Neanderthals than to chimpanzees. Similar retracing can be done farther and farther back on the branches of the tree of life to connect the common ancestry humans have with unicellular species some billions of years ago.

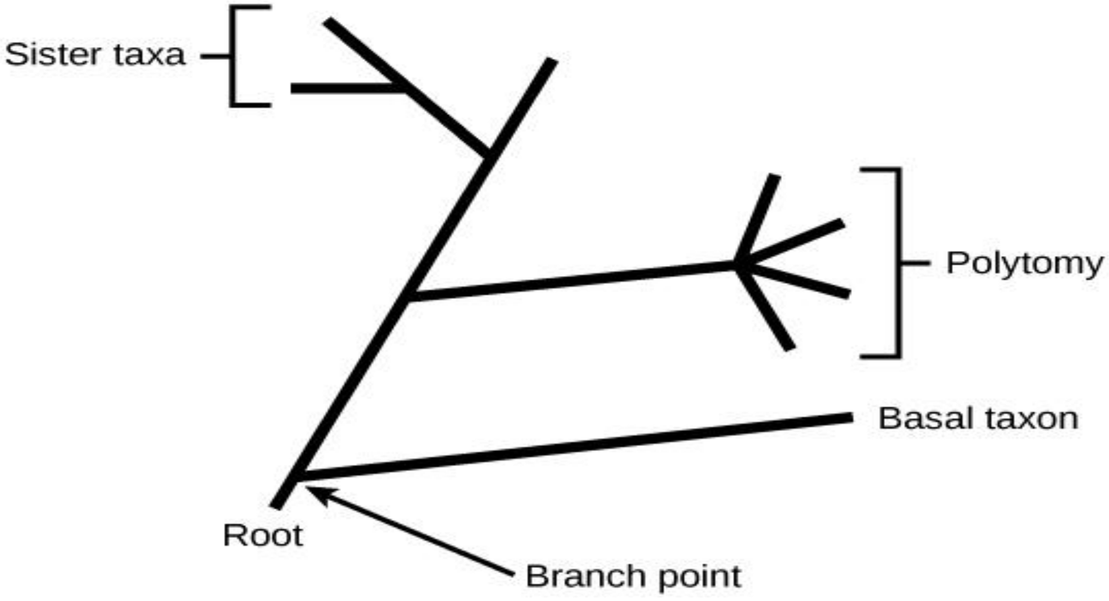
Estimating relatedness

Cladograms can be constructed with the aid of technologies that estimate molecular divergences in key sequences of DNA or protein amino acids. Similar to the progress seen in estimating the age of organic substances with the use of radioactive decay technologies and carbon dating, the advent of molecular biological technologies in the later half of the 20th century have increasingly allowed scientists to more accurately estimate the degree of evolutionary relatedness at the genetic level. Taking two homologous DNA sequences in different species, one can estimate evolutionary distance by measuring the number of nucleotide substitutions that have occurred over time. Alternatively, using protein products of DNA expression, one can measure the number of amino acid substitutions that have occurred between homologous protein sequences.

Structure of Phylogenetic Trees

A phylogenetic tree can be read like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees rooted, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains—Bacteria, Archaea, and Eukarya—diverge from a single point and branch off. The small branch that plants and animals (including humans) occupy in this diagram shows how recent and miniscule these groups are compared with other organisms. Unrooted trees don’t show a common ancestor but do show relationships among species.

In a rooted tree, the branching indicates evolutionary relationships as shown in the figure below. The point where a split occurs, called a **branch point**, represents where a single lineage evolved into a distinct new one. A lineage that evolved early from the root and remains unbranched is called **basal taxon**. When two lineages stem from the same branch point, they are called **sister taxa**. A branch with more than two lineages is called a **polytomy** and serves to illustrate where scientists have not definitively determined all of the relationships. It is important to note that although sister taxa and polytomy do share an ancestor, it does not mean that the groups of organisms split or evolved from each other. Organisms in two taxa may have split apart at a specific branch point, but neither taxa gave rise to the other.



The diagrams above can serve as a pathway to understanding evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing back towards the “trunk” of the tree, one can discover that species’ ancestors, as well as where lineages share a common ancestry. In addition, the tree can be used to study entire groups of organisms. Rooted phylogenetic trees can serve as a pathway to understanding evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary

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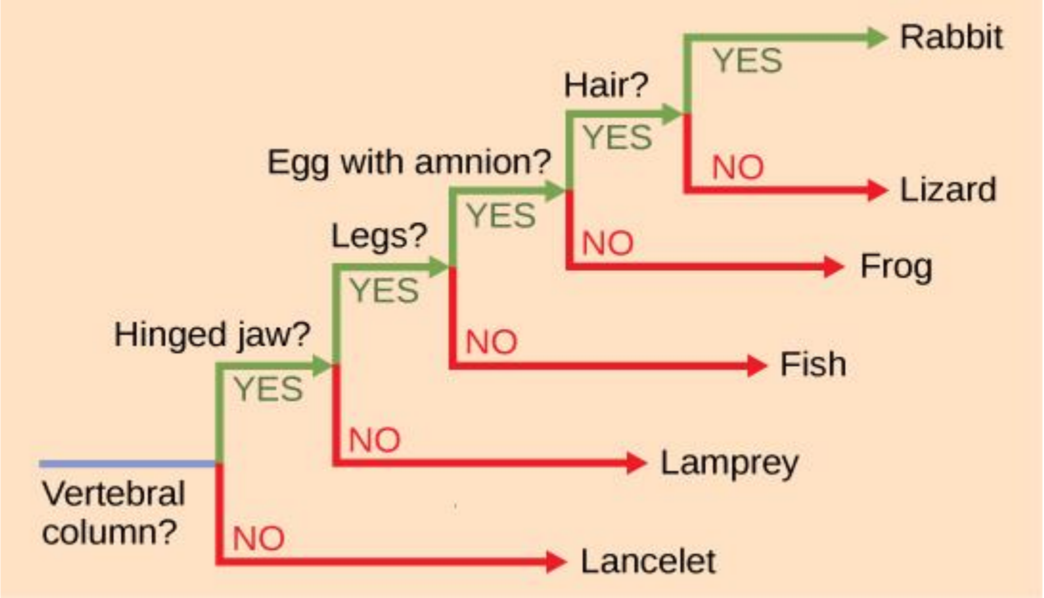
Another point to mention on phylogenetic tree structure is that rotation at branch points does not change the information. For example, if a branch point was rotated and the taxon order changed, this would not alter the information because the evolution of each taxon from the branch point was independent of the other.

Many disciplines within the study of biology contribute to understanding how past and present life evolved over time; these disciplines together contribute to building, updating, and maintaining the “tree of life.” Information is used to organize and classify organisms based on evolutionary relationships in a scientific field called systematics. Data may be collected from fossils, from studying the structure of body parts or molecules used by an organism, and by DNA analysis. By combining data from many sources, scientists can put together the phylogeny of an organism; since phylogenetic trees are hypotheses, they will continue to change as new types of life are discovered and new information is learned.

Limitations of Phylogenetic Trees

It may be easy to assume that more closely related organisms look more alike, and while this is often the case, it is not always true. If two closely related lineages evolved under significantly varied surroundings or after the evolution of a major new adaptation, it is possible for the two groups to appear more different than other groups that are not as closely related. For example, the phylogenetic tree in Figure 4 shows that lizards and rabbits both have amniotic eggs, whereas frogs do not; yet lizards and frogs appear more similar than lizards and rabbits.



Another aspect of phylogenetic trees is that, unless otherwise indicated, the branches do not account for length of time, only the evolutionary order. In other words, the length of a branch does not typically mean more time passed, nor does a short branch mean less time passed—unless specified on the diagram. For example, in Figure 4, the tree does not indicate how much time passed between the evolution of amniotic eggs and hair. What the tree does show is the order in which things took place. Again using Figure 4, the tree shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember that any phylogenetic tree is a part of the greater whole, and like a real tree, it does not grow in only one direction after a new branch develops.

So, for the organisms in the figure above, just because a vertebral column evolved does not mean that invertebrate evolution ceased, it only means that a new branch formed. Also, groups that are not closely related, but evolve under similar conditions, may appear more phenotypically similar to each other than to a close relative.

Constructing phylogenetic trees –

Phylogenetic trees are a hypothesis about how taxa are related to each other. That hypothesis is derived from existing evidence: data collected through observation of morphological or genetic **traits**, also called **character states**. Morphological data include structural features, types of organs, and specific skeletal arrangements. Genetic data include mitochondrial DNA sequences, ribosomal RNA gene sequences, and any genomic genes of interest.

These types of data are used to identify **homology**, which means similarity due to common ancestry. In that same way that individuals inherit traits from their parents, homology indicates a shared, derived ancestry for a trait. For example,

- all humans have large brains and opposable thumbs because our ancestors did.
- all mammals produce milk from mammary glands because their ancestors did.

Trees are evolutionary hypotheses constructed on the principle of **parsimony**, which is the idea that the most likely branching pattern is the pattern that requires the fewest changes. For example, it is much more likely, or parsimonious, that all mammals produce milk because they all inherited mammary glands from a common ancestor that produced milk from mammary glands, versus the alternate hypothesis that mammary glands evolved independently in multiple lineages.

As with any hypothesis, a tree can be revised if biologists gain additional data that contradicts the current thinking. Therefore, we will likely see substantial uncertainty in some of the trees we work with in this module. Instead of feeling frustrated by this, consider that you are observing the scientific process in real time. We don’t always have answers, but we can always make a new hypothesis of how lineages arose and diversified.

Principle of Parsimony in Biology –

Biologists often depict relationships between species in the form of a branching tree, where each node in the tree indicates a point in time when a new species emerged through the process of evolution. Figuring out how species are related to each other and who evolved from whom can be a complex task. One of the most important principles biologists use when drawing these so-called phylogenetic trees is the principle of parsimony.

Definition

The principle of parsimony argues that the simplest of competing explanations is the most likely to be correct. Developed by the 14th-century logician William of Ockam, the theory is also known as Occam's Razor.

Biologists use the principle of parsimony when drawing phylogenetic trees. To draw a phylogenetic tree you must first determine which species in a group are most closely related to each other. Biologists generally compare the DNA or physical characteristics of species in the group and look for differences. The principle of parsimony as applied to biology says the phylogenetic tree that requires the fewest evolutionary changes is the one you should assume is correct.

Examples

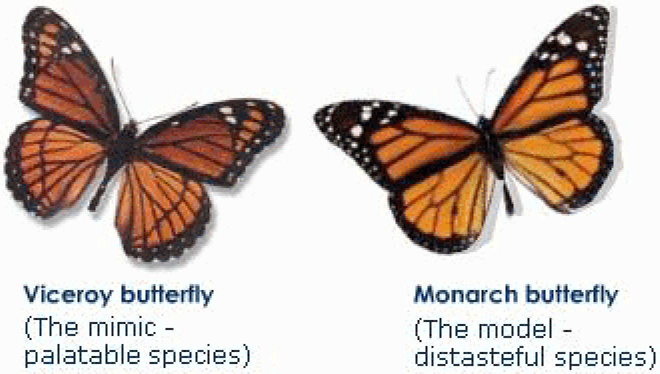
The simplest example involves a physical characteristic like feathers. Let's say you're comparing three species called A, B and C; A and B have feathers and C does not. Based on the principle of parsimony, you would conclude the two species with feathers are more closely related (i.e., share a more recent common ancestor), since in that case the feather trait would only need to have evolved once. The alternative would imply that a common ancestor gave rise to A and another species that now became the common ancestor of C and B. In that case, the feather trait would need to have evolved twice; the principle of parsimony would argue this is not the correct history.

Assumptions

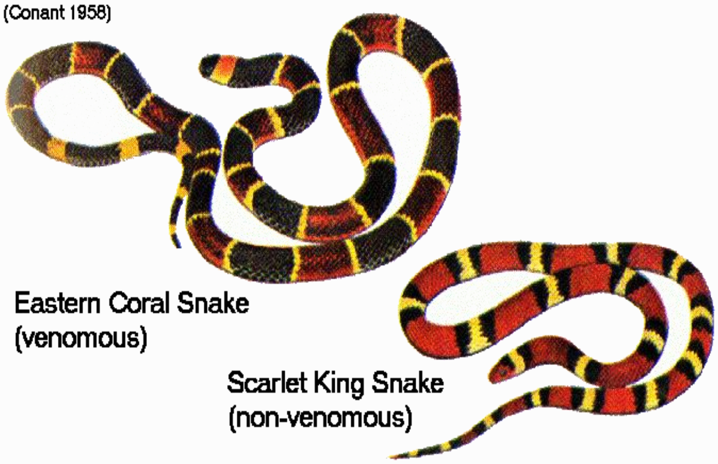
The principle of parsimony is an assumption that is probably true for most situations but need not always be true. It's possible that the actual evolutionary history of a group of species is not the one that involved the fewest changes -- because evolution is not always parsimonious. Another approach to determining relationships is so-called maximum likelihood analysis, which uses statistical analysis to determine which evolutionary tree is most likely or most probable. Both parsimony and maximum likelihood have their own advocates and critics.

Convergent Evolution –

Convergent evolution is the process by which unrelated or distantly related organisms evolve similar body forms, coloration, organs, and adaptations. Natural selection can result in evolutionary convergence under several different circumstances. Species can converge in sympatry, as in mimicry complexes among insects, especially butterflies (coral snakes and their mimics constitute another well-known example). Mimicry evolves after one species, the 'model' has become aposematic (warningly colored) because it is toxic or poisonous and therefore protected (Wickler 1968). Two distinct kinds of mimicry are recognized, Batesian and Müllerian. In Batesian mimicry, the mimic is palatable or unprotected, but gains from being mistaken for the model, which is unpalatable or protected. Two protected model species can also converge because of the advantage of being mistaken for each other (Müllerian mimicry).



Mimicry is an interesting consequence of warning coloration that nicely demonstrates the power of natural selection. An organism that commonly occurs in a community along with a poisonous or distasteful species can benefit from a resemblance to the warningly colored species, even though the 'mimic' itself is nonpoisonous and/or quite palatable. Because predators that have experienced contacts with the model species, and have learned to avoid it, mistake the mimic species for the model and avoid it as well. Such false warning coloration is termed Batesian mimicry after its discoverer.



Many species of harmless snakes mimic poisonous snakes (Greene and McDiarmid 1981); in Central America, some harmless snakes are so similar to poisonous coral snakes that only an expert can distinguish the mimic from the 'model.' A few experts have even died as a result of a superficial misidentifications. Similarly, certain harmless flies and clearwing moths mimic bees and wasps, and palatable species of butterflies mimic distasteful species. Batesian mimicry is disadvantageous to the model species because some predators will encounter palatable or harmless mimics and thereby take longer to learn to avoid the model. The greater the proportion of mimics to models, the longer is the time required for predator learning and the greater the number of model casualties. In fact, if mimics became more abundant than models, predators might not learn to avoid the prey item at all but might actively search out model and mimic alike. For this reason Batesian mimics are usually much less abundant than their models; also, mimics of this sort are frequently polymorphic (often only females are mimics) and mimic several different model species.

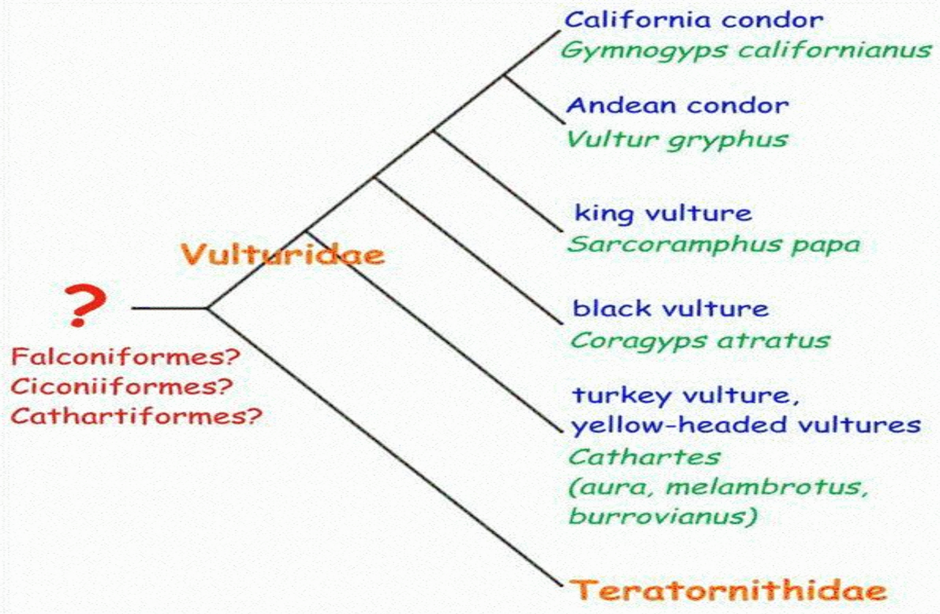
Müllerian mimicry is different, and occurs when two species, both distasteful or dangerous, mimic one another. Both bees and wasps, for example, are usually banded with yellows and blacks. Because potential predators encounter several species of Müllerian mimics more frequently than just a single species, they learn to avoid them faster, and the relationship is actually beneficial to both prey species. The resemblance need not be as precise as it must be under Batesian mimicry because neither species actually deceives the predator; rather, each only reminds the predator of its dangerous or distasteful properties. Müllerian mimicry is beneficial to all parties including the predator; mimics can be equally common and are rarely polymorphic.

Molecules can evolve convergently, especially when parasites mimic molecular messages that signal 'self' to immune responses of hosts, which allows the parasite to elude its host's defenses. Molecular convergence could also take place when a particular metabolic function requires similar or identical molecular structure (Doolittle 1994). Some gene circuits and gene networks appear to have undergone convergent evolution by single-gene duplications in higher eukaryotes (Amoutzias et al. 2004, Conant and Wagner 2003). Convergence in DNA nucleotide sequences would lead to erroneous phylogenetic conclusions, which would be problematical for molecular systematic studies.

Evolutionary convergence involving unrelated organisms living in similar environments but in different places (allopatry) can also occur in another way. This usually takes place in relatively simple communities in which biotic interactions are highly predictable and the resulting number of different ways of exploiting the environment are limited. Similar environments pose similar challenges to survival and reproduction, and those traits that enhance Darwinian fitness are selected for in each environment. Such organisms that fill similar ecological roles in different, independently-evolved, biotas are termed "ecological equivalents" (Grinnell 1924, Hubbell 2006). Examples are legion.

Wings and wing-like structures have evolved independently several times, in insects, reptiles (pterosaurs and birds) and in mammals (bats). Flight first evolved in insects about 330 million years ago (mya), second in pterosaurs (about 225 mya), later in birds (about 150 mya), and still later in bats (50-60 mya). Some frogs, lizards, and mammals have also evolved the ability to glide, presumably a precursor to flight.

In order to land safely, such hang gliders must time their stall precisely at the right moment and place.



For many years, avian systematists classified Old World and New World vultures as close relatives, both thought to be allied to raptors (hawks and owls). However, DNA hybridization suggested that, although Old World vultures are indeed related to raptors, New World vultures are not, but are descendents of common ancestors to storks and cranes (more recent studies are equivocal but still support independent evolution of the two clades). Morphological convergence was strong enough to actually mislead students of bird classification. Interestingly, a behavioral trait was conserved in the evolution of new world vultures: when heat stressed, storks defecate/urinate on their own legs to dissipate excess heat. New World vultures do this, whereas Old World vultures do not.

New World Cactus

African Euphorb

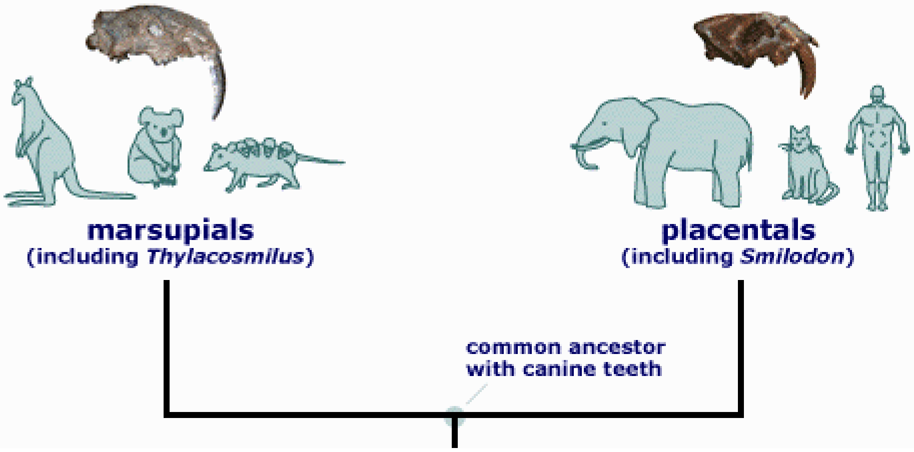
Arid regions of South Africa support a wide variety of euphorbeaceous plants, some of which are strikingly close to American cacti phenotypically. They are leafless stem succulents, protected by sharp spines, presumably adaptations to reduce water loss and predation in arid environments. Similarly, evergreen sclerophyll woody shrubs have evolved convergently under Mediterranean climates in several different regions (Mooney and Dunn 1970).

African *Macronix*

American Medolark

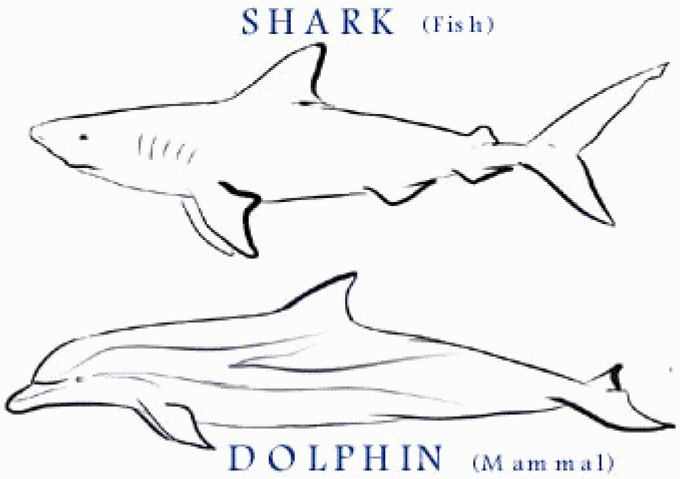
A brown bird of some African prairies and grasslands, the African yellow-throated longclaw (*Macronix croceus*), a motacillid, has a yellow breast with a black chevron "V". This motacillid looks and acts so much like an American meadowlark (*Sturnella magna*), an icterid, that a competent bird watcher might mistake them for the same species, yet they belong to different avian families. Another example is the North

American Little Auk and the Magellan Diving Petrel, two superficially very similar aquatic birds, which belong to different avian orders.

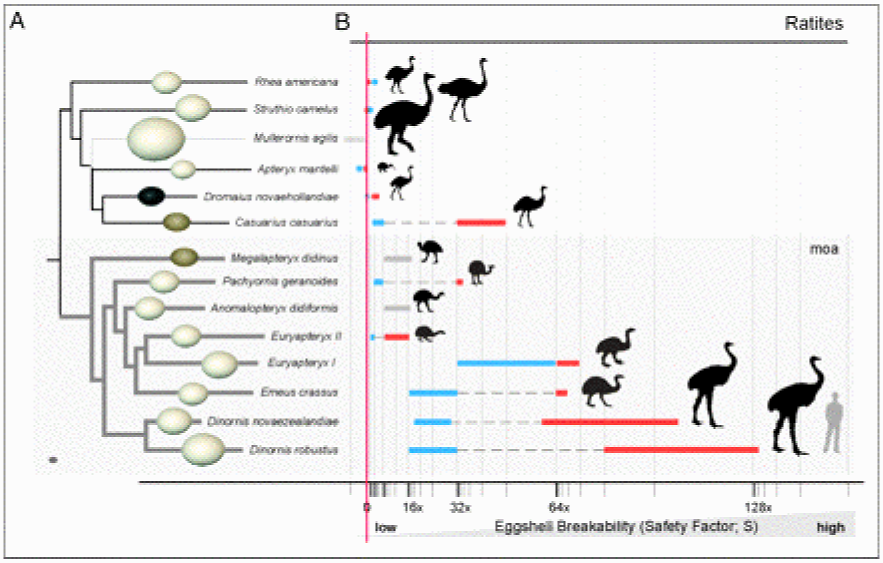


South American *Thylacosmilus* North American *Smilodon*

Convergence sometimes occurs under unusual conditions where selective forces for the achievement of a particular mode of existence are particularly strong. Presumably in response to thick-skinned prey, two fossil saber-tooth carnivores, the South American marsupial 'cat,' *Thylacosmilus*, and the North American placental saber-toothed tiger, *Smilodon*, evolved long knife-like canine teeth independently (but these were not contemporary). Many other marsupial mammals have undergone convergent evolution with placentals, including moles, mice, wombats (woodchucks), numbats (anteaters), quolls (cats), and thylacines (wolves).

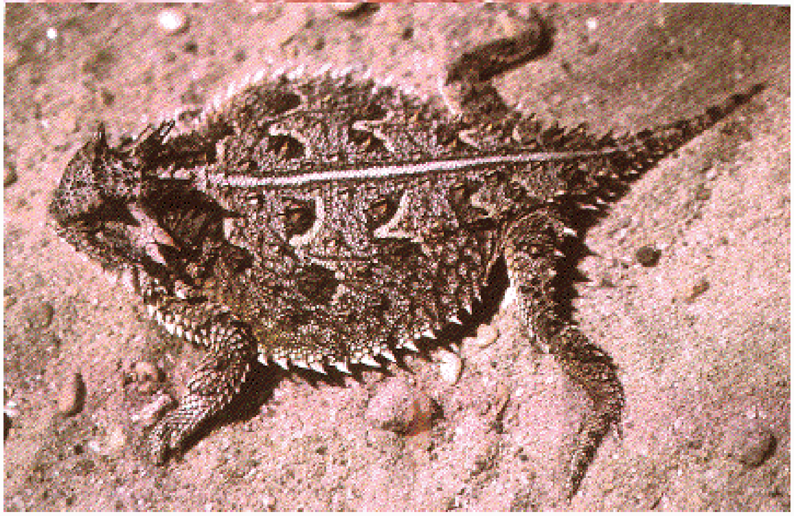


Still another example of convergent evolution is seen in the similar shape and coloration of fish and cetaceans, both of which have adapted to the marine environment by developing a fusiform body and neutral buoyancy (an extinct group of marine reptiles known as ichthyosaurs evolved the same body plan). Sharks and dolphins are also countershaded, with a light underbelly and a darker upper surface, which makes them less visible from both below and above. However, countershading is actually the rule among both arthropods and vertebrates, so it is presumably an ancestral state that has been retained throughout the evolution of both groups.



Flightless birds such as the emu, ostrich, and rhea fill very similar ecological niches on different continents. If ratites evolved from a Gondwanan common ancestor, they would not represent evolutionary convergence but instead would constitute an example of a shared (and conserved) ancestral flightless state. Now thought to be convergent, DNA evidence suggests that these "ratites" do not share a common ancestry but have evolved independently.

Live bearing, or viviparity, has evolved over 100 times among squamate reptiles (lizards and snakes) (Blackburn 1992), usually in response to cold climates. The probable mechanism behind the evolution of viviparity is that, by holding her eggs, a gravid female can both protect them from predators and, by basking, warm them, which would increase rate of development. Eventually, such selective forces favoring egg retention could lead to eggs hatching within a mother and live birth (Huey 1977). This has happened even in geckos, all of which lay eggs except for one genus in New Caledonia and several related cold temperate New Zealand forms, which bear their young alive. In some skinks and xantusiid lizards, embryos attach to their mother's oviducts and grow, gaining nutrients during development via placental arrangements reminiscent of those in mammals.



Thorny Devil *Moloch horridus* Horned Lizard *Phrynosoma cornutum*

Convergent evolutionary responses of lizards to arid environments are evident between continents. For example, Australian and North American deserts both support a cryptically-colored and thornily-armored ant specialized species: the thorny devil, *Moloch horridus*, an agamid, exploits this ecological role in Australia, while its counterpart the desert horned lizard (*Phrynosoma*), an iguanid, occupies it in North America. No Kalahari lizard has adopted such a life style. Interestingly, morphometric analysis demonstrates that the thorny devil and desert horned lizard are actually anatomically closer to one another than either species is to another member of its own lizard fauna, which are much more closely related (Pianka 1993).

Emerald Tree Boa *Corallus caninus*   Green tree python *Chondropython viridis*

Emerald Tree Boas from South American Amazonian rainforests are strikingly convergent with Green Tree Pythons found halfway around the world in similar rainforests in Australia, a spectacular example of ecological equivalents. Both of these snakes live high up in the canopy and eat birds. Adults are green, cryptically colored, matching the colors of leaves. Juveniles of both species are bright yellow or orange.

Juvenile Emerald Tree Boa Juvenile Green Tree Python Blue-tailed anguid from Mexico (*Celestes*) A skink (*Morethia butleri*) from Australia

Colorful, blue, red and yellow tails have evolved repeatedly among distantly related lizards in many families (agamids, anguids, gymnopthlamids, lacerids, skinks, and teiids), presumably a ploy to attract a predator's attention away from the head to the tail, which can be broken off and regenerated should a predator attack it.

The New World iguanid *Basiliscus*, sometimes called 'Jesus lizards,' because they can run across the surface of water, have undergone convergent evolution with the Old World agamid *Hydrosaurus*.
Both *Basiliscus* and *Hydrosaurus* have enlarged rectangular, plate-like, fringed scales on their toes, which allow these big lizards to run across water using surface tension for support.

Open sandy deserts pose severe problems for their inhabitants: (1) windblown sands are always loose and provide little traction; (2) surface temperatures at midday rise to lethal levels; and (3) open sandy areas offer little food or shade or shelter for evading predators. Even so, natural selection over eons of time has enabled lizards to cope fairly well with such sandy desert conditions. Subterranean lizards simply bypass most problems by staying underground, and actually benefit from the loose sand since underground locomotion is facilitated. Burrowing is also made easier by evolution of a pointed, shovel-shaped head and a countersunk lower jaw, as well as by small appendages and muscular bodies and short tails. Such a reduced-limb adaptive suite associated with fossorial habits has evolved repeatedly among squamate reptiles in both lizards and snakes (Weins and Slingluff 2002).

During the hours shortly after sunrise, but before sand temperatures climb too high, diurnal lizards scurry about above ground in sandy desert habitats. Sand specialized lizards provide one of the most striking examples of convergent evolution and ecological equivalence. Representatives of many different families of lizards scattered throughout the world's deserts have found a similar solution for getting better traction on loose sand: enlarged scales on their toes, or lamellae, have evolved independently in six different families of lizards: skinks, lacertids, iguanids, agamids, gerrhosaurids, and geckos (Luke 1986). A skink, *Scincus*, appropriately dubbed the 'sand fish,' literally swims through sandy seas in search of insect food in the Sahara and other eastern deserts. These sandy desert regions also support lacertid lizards (*Acanthodactylus*) with fringed toes and shovel noses. Far away in the southern hemisphere, on the windblown dunes of the Namib desert of southwestern Africa, an independent lineage of lacertids, *Meroles* (formerly *Aporosaura) anchietae*, has evolved a similar life form. In North America, this body form has been adopted by members of the iguanid genus *Uma*, which usually forage by waiting in the open and eat a fairly diverse diet of various insects, such as sand roaches, beetle larvae and other burrowing arthropods. They also listen intently for insects moving buried in the sand, and dig them up.

Sometimes they dash, dig, and paw through a patch of sand and then watch the disturbed area for movements.

Meroles (Aporosaura) anchiete

Toes of *Uma scoparia*

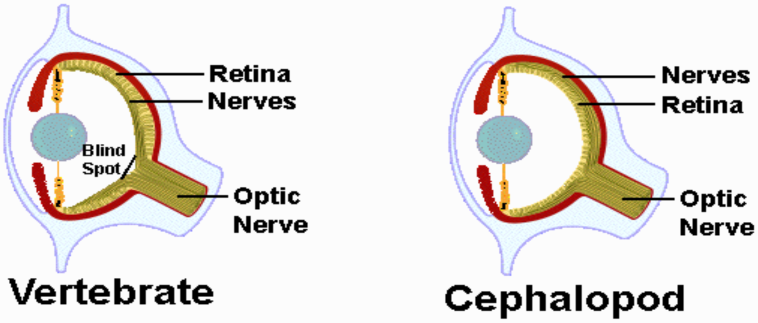
All of these lizards have flattened, duckbill-like, shovel-nosed snouts, which enable them to make remarkable 'dives' into the sand even while running at full speed. The lizards then wriggle along under the surface, sometimes for over a meter. One must see such a sand diving act to appreciate fully its effectiveness as a disappearing act. Some Namib desert lizards have discovered another solution to gain traction on powdery sands: frog-like webbing between the toes as seen in the geckos *Kaokogecko* and *Palmatogecko* (now *Pachydactylus*).

Pachydactylus (formerly*Palmatogecko) rangeri*

Other lizards that have undergone convergent evolution include rock mimics such as the North American horned lizard *Phrynosoma modestum*, an iguanid, and the Australian agamid *Tympanocryptis cephalus*. New World teiids (*Tupinambis*) have converged on Old World varanids (*Varanus*): members of both genera are large predatory lizards with forked tongues which they use as edge detectors to find scent trails and track down their prey (other vertebrates).

Rock Mimic *Tympanocryptis cephalus*

Sometimes, roughly similar ecological systems support relatively few conspicuous ecological equivalents but instead are composed largely of distinctly different plant and animal types. For instance, although bird species diversities of temperate forests in eastern North America and eastern Australia are similar (Recher 1969), many avian niches appear to be fundamentally different on the two continents. Honeyeaters and parrots are conspicuous in Australia whereas hummingbirds and woodpeckers are entirely absent. Apparently different combinations of the various avian ecological activities are possible; thus, an Australian honeyeater might combine aspects of the food and place niches exploited in North America by both warblers and hummingbirds. An analogy can be made by comparing the 'total avian niche space' to a deck of cards. This niche space can be exploited in a limited number of ways, and each bird population or species has its own ways of doing things, or its own “hand of cards,” determined in part by what other species in the community are doing.



A very striking example of evolutionary convergence involves the eyes of vertebrates and cephalopod mollusks. Both have independently evolved complex camera-like eyes complete with an aperture, lens, and retina. Prominent anti-Darwinian Charles Hodges once suggested that the vertebrate eye was too complex to have evolved by natural selection and therefore must have been “designed.” However, vertebrate eyes are poorly designed as compared to cephalopod eyes. In vertebrates, nerve fibers pass in front of the retina creating a blind spot, whereas nerves lie behind the retina in the superior cephalopod eye which does not have a blind spot.

Divergent Evolution –

Divergent evolution is the process whereby groups from the same common ancestor evolve and accumulate differences, resulting in the formation of new *species*.

Divergent evolution may occur as a response to changes in *abiotic factors*, such as a change in environmental conditions, or when a new *niche* becomes available. Alternatively, divergent evolution may take place in response to changes in *biotic factors*, such as increased or decreased pressure from *competition* or *predation*.

As selective pressures are placed upon organisms, they must develop adaptive traits in order to survive and maintain their *reproductive fitness*. Differences may be minor, such as the change in shape, size or function of only one structure, or they may be more pronounced and numerous, resulting in a completely different body structure or *phenotype*.

Divergent evolution leads to *speciation*, and works on the basis that there is variation within the *gene pool* of a *population*. If a reproductive barrier separates two groups within a population, different genes controlling for various aspects of an organism's ability to survive and reproduce increase or decrease in frequency as *gene flow* is restricted. *Allopatric speciation* and *peripatric speciation* occur when the reproductive barrier is caused by a physical or geographical barrier, such as a river or mountain range. Alternatively, *sympatric speciation* and *parapatric speciation* take place within the same geographical area.

Through divergent evolution, organisms may develop *homologous* structures. These are anatomically similar structures, which are present in the common ancestor and persist within the diverged organisms, although have evolved dissimilar functions.

Examples of Divergent Evolution

Darwin’s Finches

One of the most famous examples of divergent evolution was observed by Charles Darwin, and documented in his book *On the Origin of Species*.

Upon visiting the Galapagos Islands, Darwin noted that each of the islands had a resident population of finches belonging to the same taxonomic family. However, the bird populations on each island differed from those on nearby islands in the shape and size of their beaks.

Darwin suggested that each of the bird species had originally belonged to a single common ancestor species, which had undergone modifications of its features based on the type of food source available on each island. For example, the birds that fed on seeds and nuts evolved large crushing beaks, while cactus eaters developed longer beaks, and finer beaks evolved in birds that fed by picking insects out of trees.

When the ancestral form of finches initially colonized each island, each group contained individuals who were able to better adapt to the conditions and the available food source. These individuals survived and reproduced in their new habitat. In doing so, the genes that controlled for certain favorable aspects (e.g., longer beaks suitable for accessing nectar deep inside flowers) were spread throughout the gene pool, while the individuals without favored features died out. This is the process of *natural selection*.

The case of ‘Darwin’s Finches’ (the birds actually belong to the *tanager* family and are not true finches) is an example of *adaptive radiation*, which is a form of divergent evolution.

Adaptive radiation is a common feature in archipelagos such as the Galapagos Islands and Hawaii, as well as on metaphorical ‘island habitats’ such as mountain ranges. This is because gene flow between islands is limited when migration is not constant; however, the scale of the effect depends on the dispersal ability of the organism.

The Evolution of Primates

All of the primates on Earth evolved from a single common ancestor, most likely a primate-like, insectivore mammal, which lived around 65 million years ago in the *Mesozoic Era*. At that time, the world’s continents were mostly connected. Fossil evidence suggests that these primitive animals lived an arboreal life, with good eyesight and hands and feet adapted to climbing through trees.

Around 55 million years ago, the first true primates evolved, diverging into the *prosimians* and *simians*.

Ancestral prosimians mostly resembled modern prosimians, which include the lemurs (endemic to Madagascar), lorises, tarsiers and bush babies. These are small-brained and relatively small-bodied, with a wet nose similar to that of a dog. They are often nocturnal, with body features that are considered ‘primitive’, compared to other primates.

The next big divergence occurred around 35 million years ago in the other *phylogenetic branch* of primates, the *simians*. This event resulted in the divergence of the common ancestor of all New World monkeys and Old World monkeys.

It is speculated that the two groups underwent divergent evolution as a consequence of allopatric speciation. As the continents of America and Eurasia had by this point separated, the split could have been caused by a chance migration across the Atlantic Ocean.

The New World monkeys or *Platyrrhines*, are native to Central and South America, as well as Mexico. They evolved flat noses and prehensile tails, which act as a fifth limb and have the ability to grasp on to trees and branches. These include familiar families such as capuchins and spider monkeys (family: *Cebidae*), marmosets (*Callitrichidae*), and howler monkeys (*Atelidae*).

The common ancestor of the Old World monkeys and apes split around 25 million years ago. Old World monkeys, or *Catarrhini*, are native to Africa and Asia, displaying a range of different adaptions to many types of habitat, from rainforests to savannah, mountains and shrubs. There are both terrestrial and arboreal Catarrhini, many of which are familiar, such as macaques genus: *Macaca*), baboons (*Papio*) and langurs (*Semnopithecus*).

The apes, or *Hominoidea*, further diverged into two groups: the lesser apes, such as gibbons (family: *Hylobatidae*), which are all native to Asia, and the great apes (*Hominidae*), which are native to Europe, Africa and Asia, and include orangutans (genus: *Pongo*), gorillas (*Gorilla*), chimpanzees (*Pan*) and humans (*Homo*).

It is important to remember that the modern primates we see today are not evolved from each other despite their similarities (for example, great apes are not evolved from lesser apes), but that they are descended from a single common ancestor that formed two different species through divergent evolution.

The Kit Fox and the Arctic Fox

Two species that are very closely related and have undergone divergent evolution are the kit fox (*Vulpes macrotis*) and the Arctic fox (*Vulpes lagopus*).

The kit fox is native to Western North America, and is adapted to desert environments; it has sandy coloration, and large ears, which help it to remove excess body heat.

The Arctic fox is native to Arctic regions and lives in the Arctic tundra biome of the Northern Hemisphere. Best adapted to cold climates, it has thick fur, which is white in the winter and brown in the summer, and a small, round body shape that minimizes heat loss.

Having diverged from a recent common ancestor, both these species have had to adapt to their extremely different habitats. They have evolved into two species that are clearly very distinct in terms of their ears and coats, although they still retain the majority of their ancestral features.

Convergent vs. divergent evolution

The classical examples of evolution, such as Darwin's finches, demonstrate the opposite process: divergent evolution. Popularized in the late 1800s by American missionary and naturalist J. T. Gulick, the term describes one single species becoming many to fit different roles in a given setting. Among the Galápagos finches, for instance, beak shape changed (or diverged) to better match the different types of food available on various islands.

By contrast, convergent evolution happens when species start out distinct and then grow more similar. For instance, imagine you were to dump an assortment of parrots and toucans onto the same island. Individuals with beaks that were inefficient for snagging bugs might go hungry and die without passing their bad-beak genes on to offspring. But the parrots and toucans lucky enough to have beaks that were more successful at grabbing bugs, would survive and pass on the genes for those bug-nabbing beaks. Generations later, the descendents of both species could converge on the same beak shape, as it's the most successful design for surviving in that habitat.

The concepts underlying convergent evolution can be traced back to Richard Owen, a British biologist who, despite doubting Darwin's theory of evolution, in the mid 1800s pointed out the difference between animals with body parts that are built similarly (homologues) and body parts that just have similar purposes (analogues). A dolphin's fin and a human hand, for instance, are homologous because they have the same bone structure, despite their functions diverging since our last common ancestor. On the other hand, the dolphin's fin is an analogue of the shark's fin — they have the same purpose but different shapes because they evolved independently (and convergently).